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Cover illustration: *Ancyrodella* element (Conodont), Cashaqua Shale, Upper Devonian, New York State, ×70.

THE EYES OF *ASAPHUS RANICEPS* DALMAN (TRILOBITA)

by E. N. K. CLARKSON

ABSTRACT. The holochroal eyes of the Lower Ordovician trilobite *Asaphus raniceps* Dalman have been studied using light and electron microscopy.

In these eyes the refractive elements are elongated calcite prisms underlying a cornea which is continuous with, although structurally dissimilar to, the 'outer cuticular layer' described by Dalingwater. The prisms are orientated with their *c*-axes normal to the surface. Some of the material studied (from Öland) showed the effects of at least two phases of diagenesis, which in one case had resulted in the production of secondary prisms growing syntaxially on the primary prisms, and confusingly similar to primary structures.

The visual surface approximates a segment of an almost perfect spheroid whose radii of curvature in vertical and horizontal planes all converge to a single point, in a manner very similar to that of some superposition eyes in modern arthropods, with which analogies are drawn.

Problems in the use of calcite as a primary refractive medium are discussed, and it is concluded that the effects of birefringence could have been minimized by suitable pigment screens, like those of insects and crustaceans, underlying the prismatic layer.

The 'sensory fossettes' on the eye-socket are craters, each with a central perforation communicating with the internal surface.

TRILOBITES of the family Asaphidae have distinctive compound eyes whose range in form is quite well known from palaeontological literature. These eyes, often well preserved, are usually rather large and prominent, and often rise above the glabella; one remarkable species, *Asaphus kovalevskii* Lavrov, has eyes situated upon very elongated bases resembling long stalks. Asaphid eyes were referred to by various authors working in the nineteenth and early twentieth centuries; Schmidt's (1904) monograph, for instance, contains good illustrations. More recent authors have also described and figured asaphids with intact eyes, and Whittington's studies (1963, 1965) included many details of external eye morphology. Hupé (1953) has provided an excellent figure of the eye of *Asaphus cornutus* (Pander), reproduced in the 'Treatise' by Harrington (1959), and Rose (1967) has shown that in *Nileus* and *Isotelus* growth of the visual surface is accomplished by the addition of new lenses round the lower margin of the eye.

Although we possess a reasonably good understanding of the range in form and external morphology of asaphid eyes, there have been only two serious attempts to investigate their internal morphology; the first being that of Lindström (1901), who described sections and fracture surfaces of the eyes of several Scandinavian asaphids. He showed that the refractive elements were elongated prisms (rather than lenses) underlying the cornea, and gave a good account of their anatomy. Balashova (1948) confirmed that the eye had a prismatic structure, and further indicated that the eye-socket (Lindström's reticulate or spongy zone) was permeated with very fine pore-canals and that there were 'fossae' on the socket opening downwards into fine calcite-filled tubes, to which she imputed a sensory (tactile) function. The advent of the scanning electron microscope stimulated further study of the eyes of asaphids, and, as expected, revealed many details invisible to Lindström.

In 1967 Dr. John Dalingwater kindly sent me a number of finely preserved specimens of *Asaphus* which he had collected from Böhlin's (1949) locality where the glauconitic '*raniceps*' limestone is exposed at the cliff of Haget, northern Öland. Tjernvik (1972, p. 305) gives the age of this limestone as lower Llanvirnian (*bifidus* zone). Specific identification of these was somewhat difficult as most of the specimens were fragmentary, but Dr. Dalingwater and I agree that they most closely approximate *A. raniceps* Dalman, *sensu* Angelin (1878, p. 53).

During the investigation of these eyes, using light and electron microscopy, it became evident that different specimens had been variously affected by diagenesis. This made the interpretation of the original structure difficult, for it was not immediately apparent in all cases which structures were primary and which were the results of secondary recrystallization. In one specimen, for instance, there were radially arranged microstructures extending quite deep inside the eye, these were so regularly formed that they could have been mistaken for primary structures, but they proved, in fact, to be secondary, growing syntaxially upon primary elements of the 'refractive' zone.

Part of this study has been therefore orientated towards an understanding of the nature of primary structures and how they were affected by diagenesis; the rest is more closely concerned with the organization of the eye as a functional visual organ.

The specimens were prepared for examination as follows. The prefix 'Gr I' refers to the collections of the Grant Institute of Geology, University of Edinburgh.

External surface only. Gr I 5501.

Internal structure using thin sections, polished surfaces, and cellulose peels. Gr I 5502, 5503, 5510, 5511, 5512.

External and internal features (fracture surfaces and etched sections) using the Stereoscan. Gr I 5504, 5505, 5506, 5507, 5508, 5513.

THE CUTICLE OF *ASAPHUS*

Dalingwater (in press) in a study of the structure of trilobite cuticles has shown that *Asaphus raniceps* (from the same locality as my material) has a cuticle of two distinct layers. The outer layer, less than one-tenth of the total thickness, is composed of fairly regular perpendicular crystallites which have a fibrous appearance. The thick inner area is less distinctly structured, and no individual crystallites could be seen. Neither layer extinguished uniformly in polarized light implying that the calcite of which the bulk of the cuticle is composed does not occur in regularly arranged crystallites. There was also some organic matter remaining, which could be isolated by decalcifying the cuticle with EDTA.

These two cuticular layers have their direct counterparts in the eye. The thin outer layer passes laterally into the cornea, losing its fibrous appearance at the periphery of the eye-socket, and becoming thinner. The thick inner cuticular area is directly equivalent to that part of the eye underlying the cornea, consisting of large hexagonal prisms of calcite, which acted as refractive units, directing light to the photoreceptive organs below. These large prisms unlike the inner cuticular area are regularly structured and have their *c*-axes orientated near normal to the outer surface of the eye.

VISIBLE STRUCTURES IN THE EYE OF *ASAPHUS RANICEPS*

External surface. The external form of the eye (text-fig. 1a-c) closely approximates that of *Asaphus cornutus* Pander, from the Ordovician of Estonia, figured by Hupé (1953, p. 77, fig. 31) and reproduced by Harrington (1959, p. O.88, fig. 64i). It is large and strongly curved in plan, projecting well above the glabella. The visual surface, which has a much higher profile curvature anteriorly, is situated upon a vertical 'eye-socle' rising abruptly from the librigena (*sensu* Shaw and Ormiston 1964), upon which are shallow funnel- or basin-shaped cavities, irregularly distributed and decreasing in size towards the base of the eye-socle. These were described by Hupé as sensory fossettes. The facial suture is semicircular, separating the visual surface from the palpebral lobe, which slopes sharply down to the glabella, and carries terrace-line ornamentation.

There is a thin pellucid cornea covering the surface, merging laterally into the outermost layer of the cuticle (text-fig. 4c; Pl. 50, fig. 9). Through this cornea the many quadrate or hexagonal lenses can be seen by translucence, especially if the specimen is immersed in a medium of high refractive index. Hupé's specimen showed patches of larger irregularly distributed lenses, which he thought had resulted from damage during ecdysis.

Even with the Stereoscan the external surface of the best-preserved specimens appears to be smooth and structureless; a microgranular effect is not evident until magnifications of over $\times 500$ is reached. Relative granularity, however, varies according to the quality of preservation of the material.

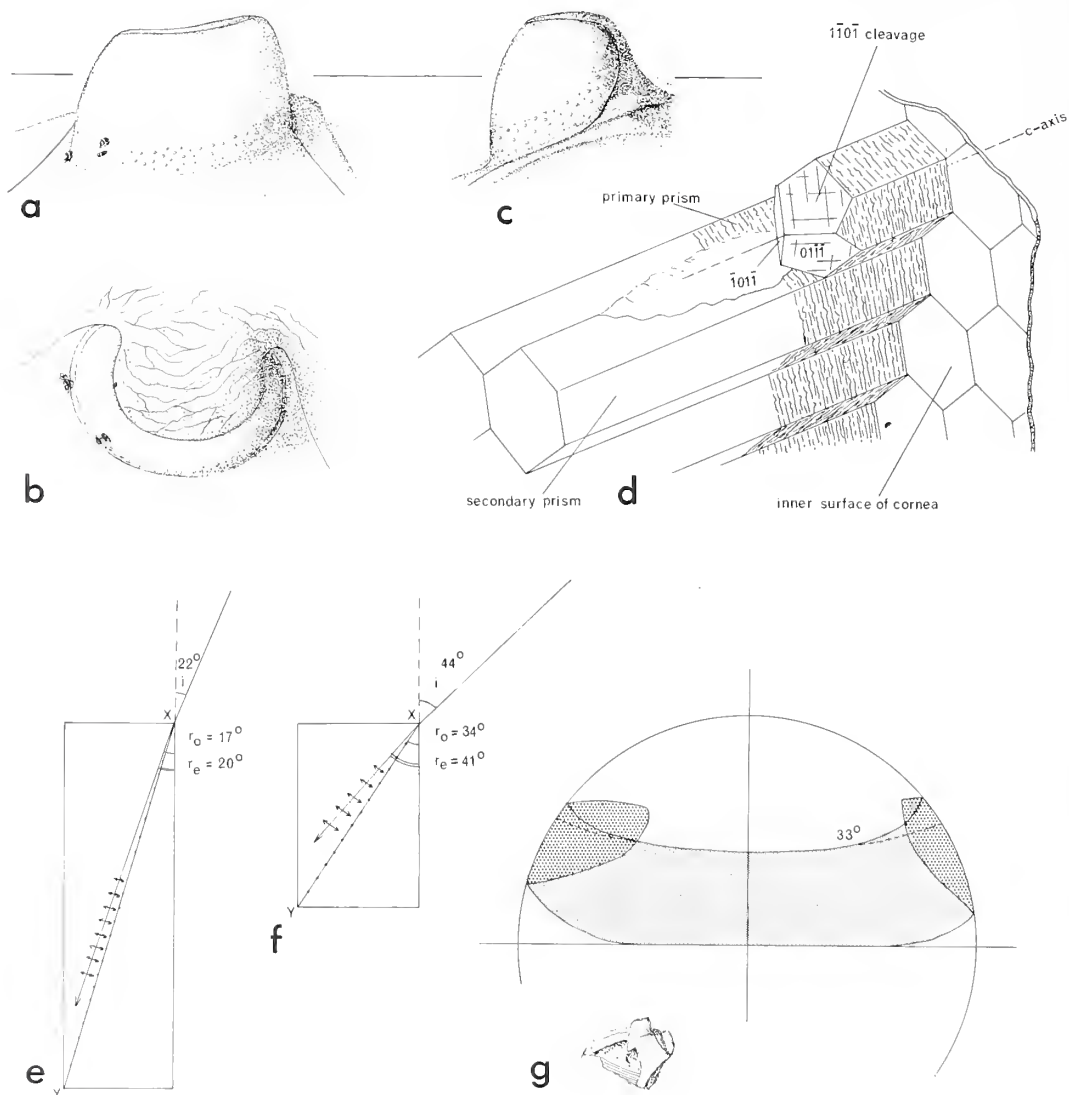
Internal structure. Lindström (1901, pp. 28, 37-43, pl. 1, figs. 8-30) gave a good account of the eye structure in asaphids as known to him, and noted the following main points. Welded to the inner surface of the cornea are the refractive organs, appropriately termed prisms, which are closely packed hexagonal pillars, arranged radially. (This zone is here termed the primary prismatic region.) If the eye is fractured the prisms separate cleanly from one another, and can be seen under low magnification like columns of basalt lying on their sides. Vertical sections show that the prisms generally become longer and thinner near the margins of the eye, and especially towards the lower rim of the visual surface.

Above and below the visual surface the prisms pass into a rather structureless 'marginal zone', twice as thick (in section) as the primary prismatic region. Lindström referred to this also as the 'spongy' or 'reticulate' zone, in view of its spongy appearance in slightly decomposed specimens. He noted the fossettes on the eye-socle also but did not impute a sensory function to them.

The use of the Stereoscan has given more information upon the nature of most of these regions, and most particularly of the primary prismatic layer.

In the best-preserved specimens, each prism is a single crystal of calcite with its optic axis normal to the surface (text-fig. 1d). The optic axes of neighbouring prisms diverge slightly. Thin sections made horizontally through a complete eye and examined using crossed nicols show that the prisms undergo extinction in the NS. and EW. positions; this pattern remains constant on rotation. Tests with a sensitive tint plate show that the *c*-axes of the calcite crystals are normal to the surface. It is difficult to imagine how such a system as this, with regularly diverging optic axes,

can be other than primary, for although further impregnation with calcite during diagenesis might take place in optical continuity with the existing crystal lattices, more extensive recrystallization would very likely destroy the regularity of the pattern, as has actually happened to some extent in some of the less well-preserved specimens. The eyes in living specimens of *Asaphus raniceps* must therefore have had a high



TEXT-FIG. 1. *a-c*. Left eye of *A. raniceps* Dalman. $\times 6.5$. Gr I 5501, in lateral, dorsal, and posterior views. The black specks are adherent glauconite grains. *d*. Diagrammatic construction showing crystallography of the primary and secondary (diagenetic) prisms underlying the cornea. *e-f*. Polarization of light rays passing through a peripheral (*e*) and a central (*f*) primary prism. The o-ray (XX) is shown passing along the long diagonal (XY). For full explanation see text, p. 438. *g*. Minimal visual field of *A. raniceps*, from Gr I 5501, orientated as in the small diagram (the latter $\times 2/3$).

proportion of calcite, each prism being a single calcite crystal, presumably associated with protein and other organic material.

It is not surprising to find calcite used as a structural component in the eyes of trilobites, for many modern arthropods which have cuticles reinforced with calcite are found to have calcite in the eye as well. It is not, however, used in the same way, for although the prisms of *A. raniceps* have an extremely regular arrangement, there is no regularity of structure in the rest of the cuticular inner area. The arrangement of calcite crystals in the eyes and cuticle of many modern arthropods is singularly irregular. According to Richards (1951, pp. 103-105), crystallization of calcite in very many modern arthropods begins independently at various loci and each crystal simply continues growth until it contacts another crystal. This is true for the calcite crystals within the eye as well, as Düdich (1931) clearly showed; for randomly orientated calcite crystals cut across the ommatidia at all angles without any relationship at all to organic boundaries. In *A. raniceps* on the other hand each visual unit, or at least the upper part, was individually calcified, and, as argued later, calcite was probably the primary refractile material.

In thin sections the cleavages in the prisms often appear distinct, each prism having its own set of cleavages, orientated slightly differently to its neighbours. Not infrequently, however, two or three neighbouring lenses in some sections can be seen to have the same cleavages running through all of them, and the small block or 'domain' of lenses goes into extinction as a unit with sharply marked edges. Rotation of the stage thus produces a stepwise rather than a regular extinction. It is likely that such domains were secreted together and retained their optical continuity throughout life. It has been suggested to me by C. Eccles that this may have resulted from a crystallographic constraint, and that neighbouring prisms had to grow in the same optical orientation as the angle of divergence of individual prisms was too small to permit crystallographic separation. Only when there was a critical angle of divergence could another domain grow at a different crystallographic orientation. It is not clear whether new prisms were always secreted in domains but it is not unlikely, for the individual prisms often seen in section with separate orientation could belong to a small domain of three or four lenses of which only one was cut in the plane of the section.

The tendency for small groups of neighbouring lenses to have the same crystallographic orientation is shown also in Stereoscan photographs, such as Pl. 49, fig. 3 where two adjacent prisms lying below the cornea have cleavages running through both of them without a break.

The sides of intact prisms as shown in Stereoscan photographs are remarkably rough, with corrugated granular surfaces (Pl. 48, figs. 1-3; Pl. 49, fig. 5). These corrugations are always parallel with the cornea, and are related to the underlying cleavage directions (text-fig. 1*d*). Usually, though not always, the prisms become long and thin towards the top and particularly the bottom of the visual surface (Pl. 48, fig. 2). Here they may be up to twice the length in other parts of the eyes. In some specimens, however, this tendency is far less evident. It is possible that the former condition occurs only in immature specimens. It is clear that the new visual units must, as in *Phacopina* (Beckmann 1951; Clarkson 1966*a*) have been produced in a generative zone at the periphery of the eye and the work of Rose (1967) confirms

that they were added only at the base of the visual surface. In *Asaphus* the generative zone seems to have lain at the lower junction of the visual surface and the marginal zone. New prisms were first of all the same width (in section) as the marginal zone and very thin; they shortened and grew thicker as they became functional.

Some of Lindström's specimens showed concentric layering within the lenses. Such concentric structure was not visible in any of my material, and neither did etching with dilute acid (Pl. 48, fig. 5) reveal any structures other than the cleavages which were picked out by the acid. The apparent absence of layering may have been because Lindström's material was less fresh than mine, and that mild weathering might have revealed primary structures in his specimens which were not clear or evident in mine though they may have been present.

The sensorial fossettes. Hupé (1953) noted a series of irregularly distributed, shallow excavations on the eye-socle, which he described as sensorial fossettes. Lindström (1901) had previously noted the presence of these little pits, but imagined them to be the excavations of some boring organism. Some thin sections and polished surfaces made in the present study showed that each fossette is set at the summit of a narrow canal (now calcite filled) which can be traced to the inner surface of the eye-socle though little structure can be seen, even in the posterior part of the socle where the best and largest examples are normally located (text-figs. 4a, b, c; Pl. 50, fig. 9). Stereoscan photographs of the external surface simply show the fossettes as shallow rimless craters and contribute nothing further to our knowledge (Pl. 48, fig. 6).

Hupé's interpretation of the fossettes as sensory structures seems appropriate; similar structures in the neighbourhood of some insect eyes are the sites of vibro-sensory organs whose nerves are connected with the third optic lobe (Burt and Catton 1966a). Very many trilobite eye lobes are provided with pit-like structures, narrow vertical grooves, small tubercles (often only properly visible with the Stereoscan), or other such organs, usually located on the eye-socle; these may all be the sites of sensory organs of some kind, hence the fossettes of *Asaphus*, though exceptionally large, are not unusual amongst the trilobites.

EFFECTS OF DIAGENESIS

Recrystallization of the primary prisms. The course of diagenesis was followed in thin sections of the eyes of different specimens following Friedman (1964). Some sections, or parts of sections, showed the original form of the calcite prisms, either as single crystals or as small domains. In these, the cleavages are always distinct

EXPLANATION OF PLATE 48

Asaphus raniceps Dalman (Stereoscan photographs all of fracture surfaces except figs. 5 and 6).

Fig. 1. Prisms near lower margin of the visual surface. $\times 110$. Gr I 5505.

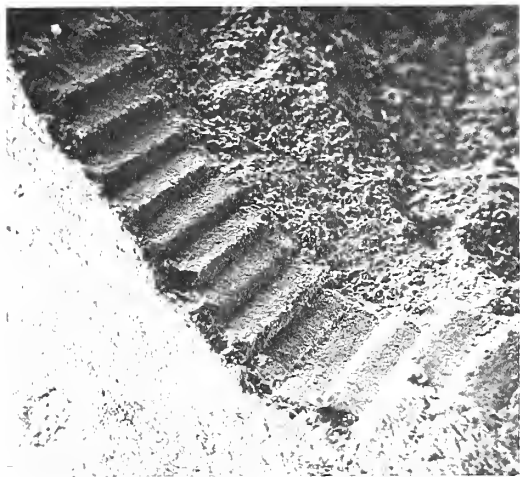
Fig. 2. Elongated prisms near the lower margin of the visual surface. $\times 440$. Gr I 5504.

Fig. 3. Corrugated surfaces of prisms in the central part of the eye. $\times 2300$. Gr I 5507.

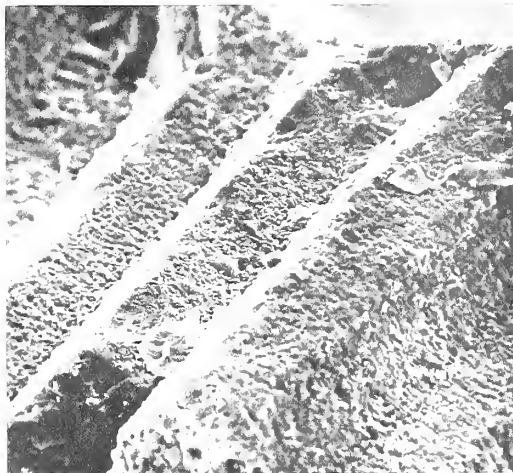
Fig. 4. Similar prisms showing cleavages parallel with the corrugations. $\times 1100$. Gr I 5507.

Fig. 5. Horizontal ground surface, cutting through prisms and etched with dilute HCl. $\times 525$. Gr I 5510.

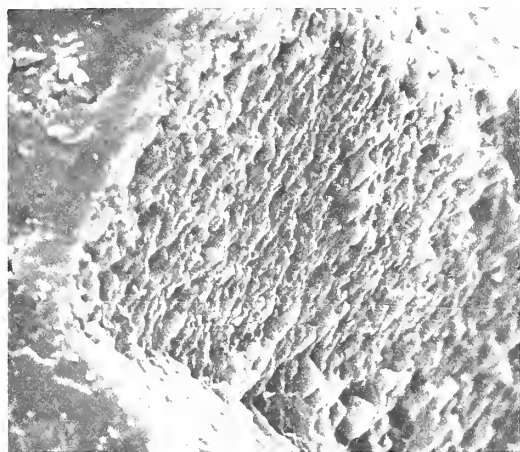
Fig. 6. Surface of the eye-socle in the posterior region, showing sensory fossettes. $\times 110$. Gr I 5507.



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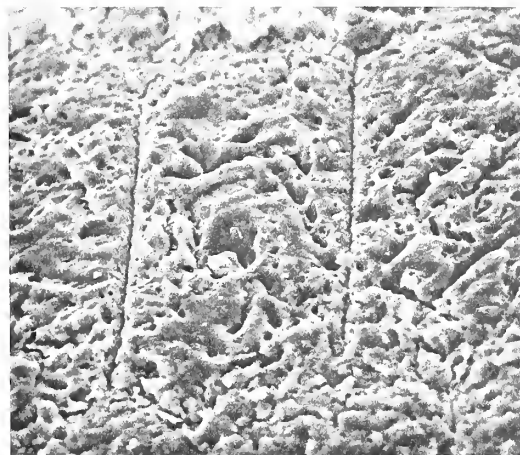
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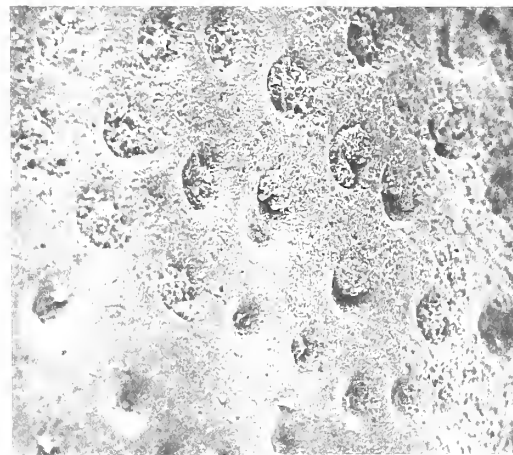
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6

CLARKSON, *Asaphus* eyes

(Pl. 50, fig. 1), and extinction follows a stepwise pattern. The lower ends of the prisms may be rounded or somewhat ragged in appearance, but never show crystal faces.

Two stages of diagenesis have been differentiated. The first stage involved some degree of recrystallization of calcite *in situ*, into a microcrystalline form, resulting in the crystal boundaries and cleavages becoming indistinct, and blurring the extinction pattern (Pl. 50, fig. 6). This was seen in its early stages in certain parts of otherwise unaltered eyes. The recrystallized areas (yellow-brown under crossed nicols) are often darker in colour than the primary crystals.

In some sections diagenesis has been carried a stage further, with a second development of microcrystalline calcite invading the already altered primary prismatic region (Pl. 50, figs. 7, 8). This second stage microcrystalline calcite is variable in colour, but is usually a very light yellow, contrasting with the darker yellow-brown of the first-stage diagenetic material. Sometimes it appears as randomly orientated flecks or patches within the prisms. Often it is seen as a 'front' which has advanced into the prismatic region from either surface. On occasion it has picked out the boundaries of the altered prisms, which then appear as thin yellow lines, and it may have invaded the interior of each prism from all its edges at once. In such cases all that is left of the original prismatic layer is a series of elongated kernels (already altered during the first stage in diagenesis) surrounded by lighter coloured microcrystalline calcite of the second stage. These kernels may be regular in appearance, but are sometimes truncated by a 'front' of second-stage microcrystalline material, where the latter has grown more rapidly in one direction than in others (Pl. 50, fig. 8).

Recrystallization of primary structures is less easy to recognize in fracture surfaces or in etched sections using the Stereoscan. It has been observed, however, that whereas certain calcite prisms have sharp, well-defined corrugations on the surface, parallel with the cleavages, other calcite crystals in the same eye may have much less regular corrugations, and only a rough granularity to the surface. As unaltered primary crystals have well-defined cleavages, it would seem likely that the crystals with roughly granular surfaces have undergone some measure of diagenesis.

Secondary growths below the primary prisms. In one specimen (Gr I 5508), both fracture surfaces and thin sections revealed inward extensions of the primary prisms.

EXPLANATION OF PLATE 49

Asaphus raniceps Dalman (Stereoscan photographs, all of fracture surfaces).

Fig. 1. Slightly oblique view of primary prisms (corrugated), with smooth secondary (diagenetic) prisms growing syntaxially upon them. $\times 180$. Gr I 5508 (cf. text-fig. 2).

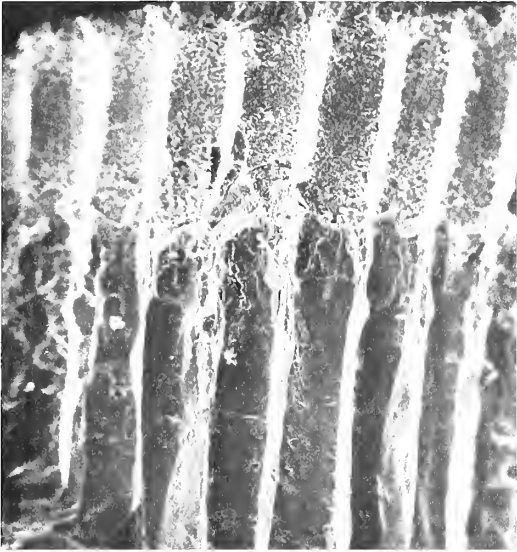
Fig. 2. Lower terminations of the same secondary prisms and subjacent area of recrystallized calcite. $\times 130$. Gr I 5508 (cf. text-fig. 2).

Fig. 3. Several prisms underlying the cornea, visible as an upstanding wall near the top of the photograph. Two adjacent prisms are fractured showing a common cleavage direction running through both. $\times 325$. Gr I 5506.

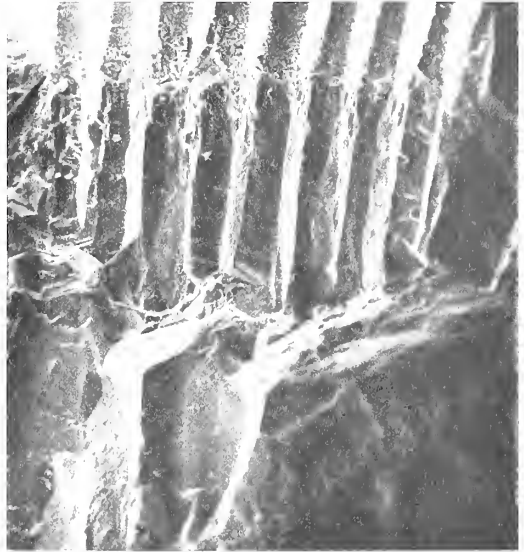
Fig. 4. Junction between primary and secondary prisms (cf. Pl. 49, fig. 1). $\times 485$. Gr I 5508.

Fig. 5. Enlarged surface of corrugations on the outer surface of a prism (cf. Pl. 48, fig. 2). $\times 2400$. Gr I 5504.

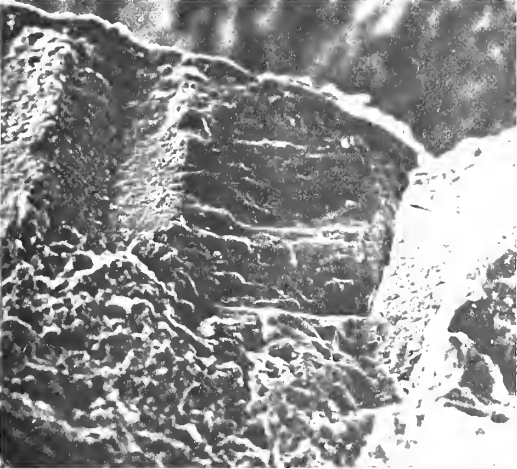
Fig. 6. Prisms near the lower margin of the visual surface. $\times 65$. Gr I 5505.



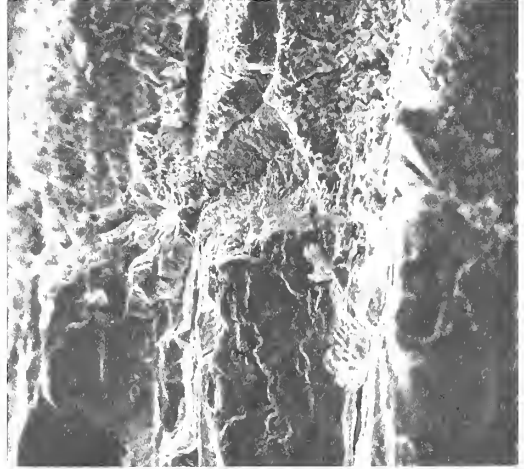
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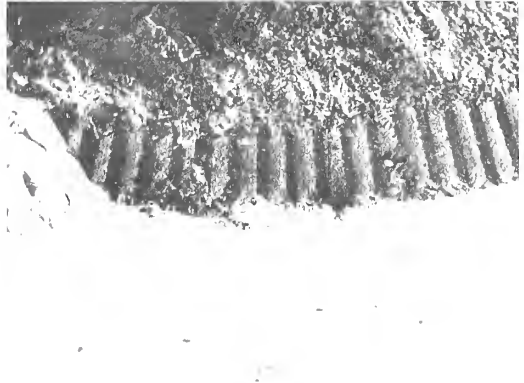
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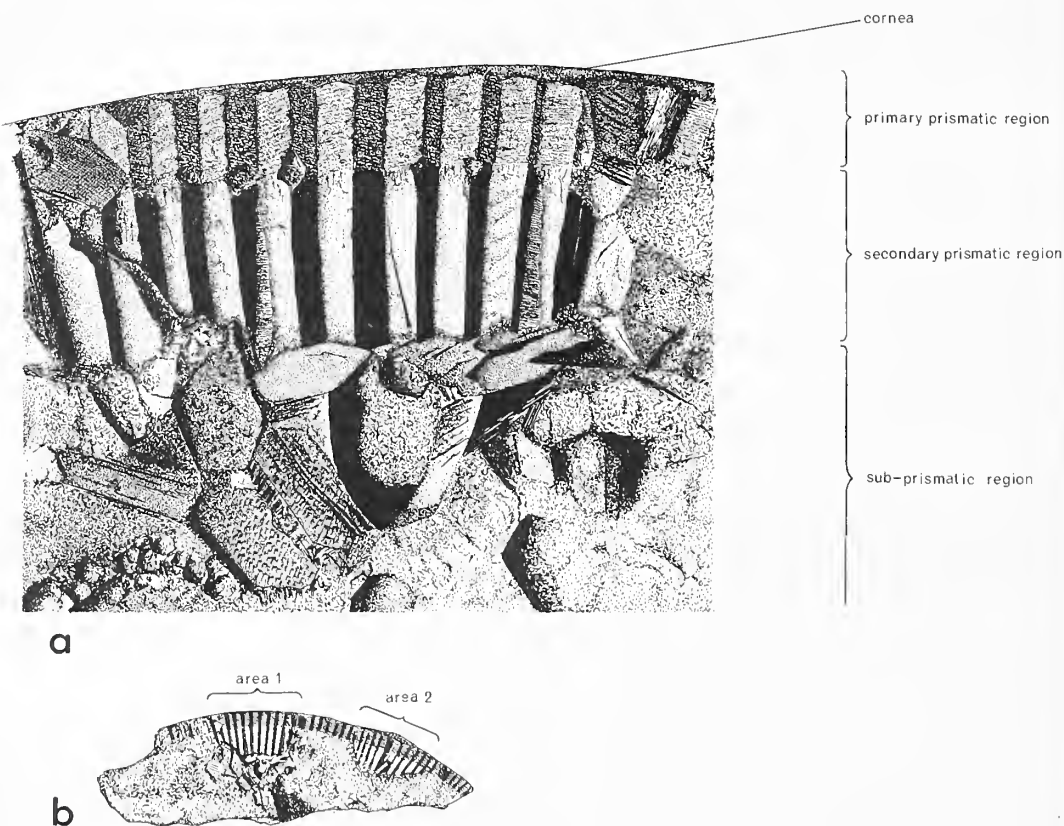
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CLARKSON, *Asaphus* eyes

Stereoscan photographs showed these to be of extremely regular form, being syntaxial, pillar-like extensions of the outer prisms (Pl. 49, figs. 1, 2; text-fig. 2*a*, *b*). They are found only in certain parts of the eye, and in all the Stereoscan preparations extend to about the same level. Between and around these areas lie micrite and finely recrystallized sparite, in patches. These extensions, referred to as 'inner' or 'secondary prisms', have very smooth outer surfaces, and the transition from the corrugated outer zone is sharp, being marked usually by a line of somewhat irregular fractures (Pl. 49, fig. 4). One example showed the edges of a primary prism being met by the sides of an inner prism, but normally the edges of a primary prism are continuous with those of a secondary one.

Below the inner prisms (sub-prismatic region in text-fig. 2) are large, equant calcite crystals with patches of micrite and sparite. Some of these are syntaxial with the inner prisms. Several orientated crystals of dog-tooth spar cemented together by a calcitic jacket were noted in one area; these had near-perfect crystal faces.

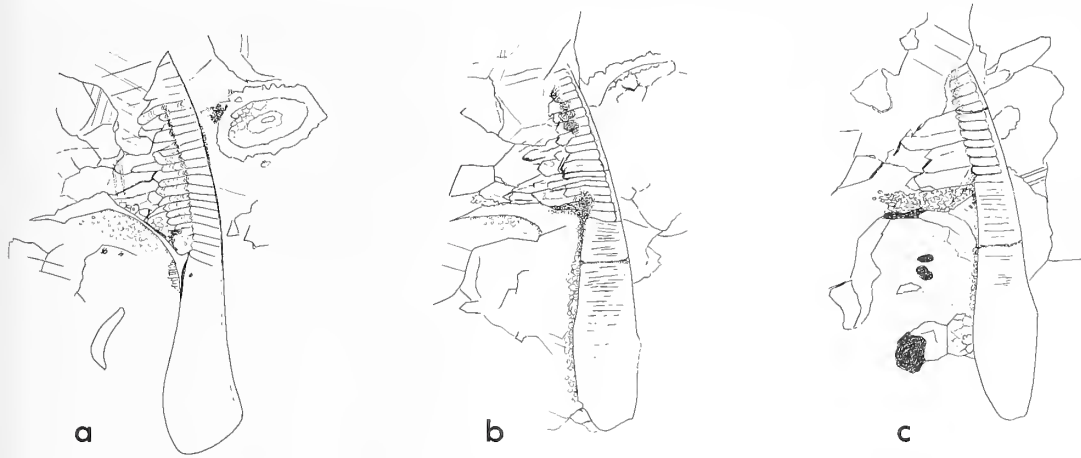
Though there would be little doubt that all the structures in this sub-prismatic



TEXT-FIG. 2. Drawings made from fracture surface of Gr I 5508 showing areas of primary and secondary (diagenetic) calcite. *a*. Enlargement of area 1 $\times 120$. *b*. Fragment of eye showing the two areas of secondary prisms, one of which is enlarged in *a*. $\times 18$.

region are secondary, the regular appearance of the inner prisms in the Stereoscan photographs might suggest that at least these could be of primary origin, though other Stereoscan evidence is equivocal. Thin sections, however, indicate that the inner prisms are very probably secondary. The series illustrated in text-fig. 3*a-c* are vertical sections made obliquely through the posterior region of the eye of Gr I 5508.

Text-fig. 3*a* (Pl. 50, fig. 3) shows a cellulose acetate peel stained with methylene blue (Dickson 1966). The primary layer has been differentially affected by first-stage diagenesis, though crystal boundaries are clear in places. There is a pronounced



TEXT-FIG. 3. Effects of diagenesis shown in thin sections and cellulose peels of Gr I 5502. *a*. Oblique vertical section near posterior margin stained with methylene blue, showing primary and secondary prisms. *b*. Similar section, stained with alizarine red-S and acid fuchsine, with very irregular secondary prisms. *c*. Thin section through the same area, showing complete recrystallization of the secondary and partial alteration of the primary prisms. All $\times 20$.

line of demarcation between the primary and the inner prisms. The latter, though regular in places, are elsewhere of differing lengths, and sometimes overgrow one another. They show clear evidence of secondary growth on the bases of the primary prisms in that a record is left of the past position of the euhedral crystal faces. The structure becomes very irregular at depth, but even here some crystals are still more or less syntaxial with the primary prisms. Similar, though much smaller, secondary growths were visible in other calcitic shells in the same section.

Cellulose peels stained with alizarine red-S and acid fuchsine (Pl. 50, fig. 2; text-fig. 3*b*), through the same general region but more posteriorly, showed much the same kind of structural elements but picked out slightly different details. The section illustrated was more strongly affected by second-stage diagenesis, and the boundary between primary and secondary structures was indistinct. In general, there was far less regularity, which emphasizes the secondary nature of the inner prisms. This section also showed a fringe of small secondary calcite crystals, elongated and with axes normal to the surface of the cuticle, growing on the inside of the eye-socket. These are clearly analogous to the inner prisms.

In an optical thin-section (Pl. 50, fig. 8; text-fig. 3*c*), there are very large elongated euhedral crystals, growing below the primary layer, each encompassing the bases

of several (altered) primary prisms. They are in optical continuity with the latter, though these are altered by first-stage diagenesis, but they are not in optical continuity with the light yellow material of the second diagenetic stage. Probably these large euhedral crystals resulted from the coalescence of several smaller crystals which originated in contact with the primary prisms.

It is clear from the foregoing observations that all the calcitic elements below the primary prismatic layer are of secondary origin. The great regularity of their structure in some parts of the eye (which is not always maintained in other regions) is merely a reflection of the regular arrangement of the large prisms above, which provided suitable foci for continued growth of calcite, provided that there was a void below. It may have been that there were partially calcitized elements below the primary prisms which could have controlled the direction of subsequent calcitization, but there is no direct evidence of this.

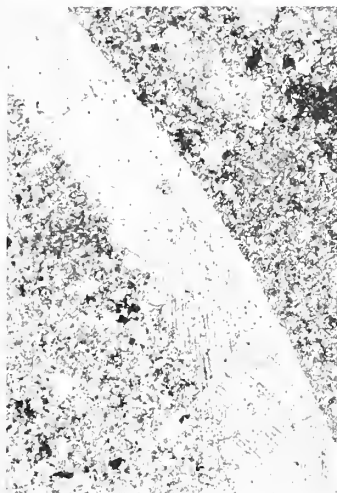
VISION IN *ASAPHUS RANICEPS*

Visual field. A provisional determination of the visual field has been made, using similar apparatus and techniques to those described formerly (Clarkson 1966a, b). Since the prisms are normal to the surface it was possible to use a graticule and protractor to measure the inclination of the upper and lower margins of the visual surface, every 10° of longitude from front to rear, in a manner comparable with the measurement of the axial bearings of individual phacopid lenses. Plotting these inclinations on a Lambert net gave an angular range of vision quite similar to that of many phacopids (text-fig. 1g), overlapping at front and rear to give some degree of binocular vision. The relatively narrow latitudinal extent of vision may be contrasted with that of many holochroal eyes, where latitudinal ranges of up to 120°

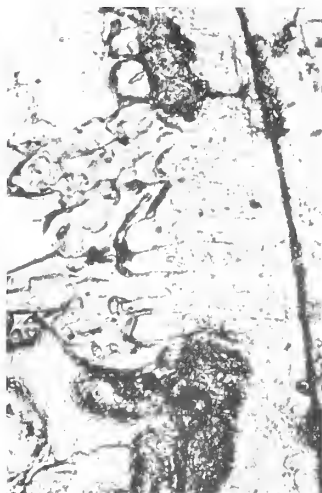
EXPLANATION OF PLATE 50

Asaphus raniceps Dalman (Photomicrographs of thin sections, except Figs. 2 and 3 which are acetate peels).

- Fig. 1. Horizontal section through eye showing the cleavages running through the prisms and the rounded terminations of the latter. Plane polarized light. $\times 80$. Gr I 5512.
- Fig. 2. Oblique vertical section (acetate peel) stained with alizarine red-S and acid fuchsine, with very irregular secondary prisms. $\times 65$. Gr I 5502 (cf. text-fig. 3b).
- Fig. 3. Similar section (acetate peel) stained with methylene blue, showing primary and secondary prisms. The latter are rather irregular and exhibit growth lines. $\times 65$. Gr I 5502 (cf. text-fig. 3a).
- Fig. 4. Oblique vertical section showing primary prisms only. $\times 18$. Gr I 5511.
- Fig. 5. The same under crossed nicols. $\times 18$. Gr I 5511.
- Fig. 6. Part of vertical section through an eye somewhat altered by first-stage diagenesis, showing primary prismatic layer, with indistinct prisms, and the thin cornea (lower part of this section in fig. 9). $\times 40$. Gr I 5503 (cf. text-fig. 4c).
- Fig. 7. Part of a vertical section, showing advanced diagenesis, passing through the uppermost part of the visual surface (upper marginal zone of Lindström). $\times 80$. Gr I 5503.
- Fig. 8. Oblique vertical thin section showing complete recrystallization of the secondary prisms and partial alteration of the primary prisms. $\times 37$. Gr I 5502 (cf. text-fig. 3c).
- Fig. 9. Downward continuation of section in Pl. 50, fig. 6, showing inward extension of a sensory fossette and the upward passage of the vertically laminated outer cuticular layer of Dalingwater into the cornea at the base of the eye-socket. $\times 40$. Gr I 5503 (cf. text-fig. 4c).



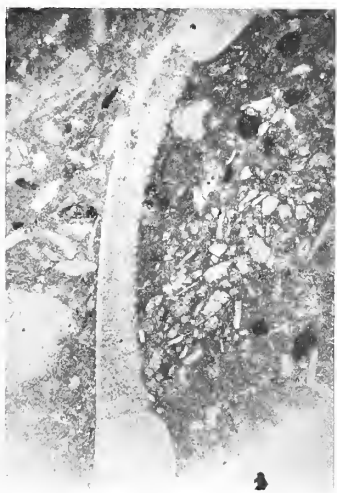
1



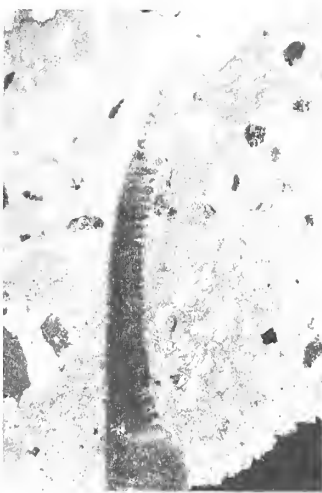
2



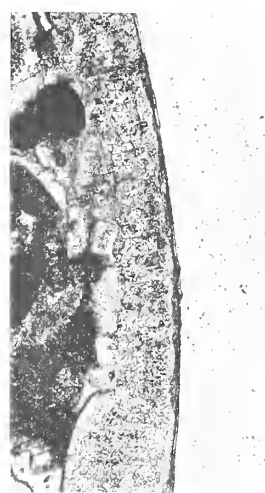
3



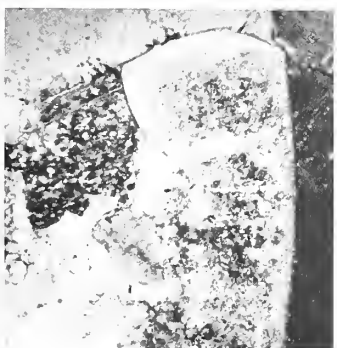
4



5



6



7



8



9

CLARKSON, *Asaphus* eyes

for each eye, with marked overlap above, are not uncommon. This plot represents the minimum possible range of vision, assuming that the peripheral prisms receive only light coming parallel with the c -axis. The eye may have actually been capable of receiving light from outside this zone and transmitting it to the photoreceptors; this would depend upon whether or not screening pigment was present, isolating the ommatidia as in modern compound eyes.

Optics of the calcite prisms. Calcite was used as a primary structural component in trilobite cuticle. It was also present in the eye, where it was of particular value, being rigid, easily secreted in the same way as the rest of the cuticle, and above all refractive and transparent. But calcite is an anisotropic mineral with the property of double refraction, and its use in an optical system raises problems. Some modern arthropods have an irregular mosaic of calcite crystals within the eye as mentioned earlier.

In the following discussion on calcite optics each prism is considered as an individual calcite crystal, though it is recognized that each was probably penetrated throughout by organic matter. How far this would have altered the refractive index, if at all, cannot be assessed but the birefringent properties of calcite would not have been eliminated by such interpenetration. The calcite cornea may also have had an organic association.

Each prism is a single hexagonal crystal with its optic axis (c -axis) normal to the surface of the eye. Any light rays entering the crystal normal to the visual surface (i.e. parallel with the optic axis) would be transmitted, unpolarized, straight through the crystal without any change of direction. A light ray entering obliquely, however, will be resolved into two linearly polarized rays vibrating perpendicular to each other. The ordinary ray has constant velocity whatever the direction of incidence, but the extraordinary ray increases in velocity as the angle of incidence increases from the normal. Oblique incident rays not only polarize, but produce double images at different depths. Herein lies the disadvantage of calcite; some interference with the visual process would be expected, unless there were some system within the eye for ensuring that only normal or near normal rays were actually let through to the photoreceptive organs below.

Let us consider the angular light receptivity of each crystal. Median sections of two crystals, of the dimensions actually found in different parts of the eye, are illustrated in text-fig. 1*e, f*. Text-fig. 1*f* is the typical form, occurring in all but the peripheral regions of the eye, whereas text-fig. 1*e* is a crystal from the generative zone near the lower margin. If each prism is considered as an isolated unit, the most oblique incident ray which it could transmit would be refracted along the line XY which is the path and wave-normal of the ordinary ray.

Light entering at a higher angle of incidence would be refracted against the wall of the prism. The angle of incidence for such a refracted ray travelling along the line XY can be calculated using Snell's Law and the following refractive indices ($n_{\text{water}} = 1.33$, $n_{\text{o-ray}} = 1.66$). The highest angles of incidence are then 44° and 22° respectively for the two prisms. If $n_{\text{e-ray}} = 1.48$, then using the optical indicatrix for calcite, the path of the extraordinary ray incident at O may be constructed as in the diagram; as it travels faster it is less highly refracted. Thus each prism, considered by itself, has quite a high range of angular receptivity.

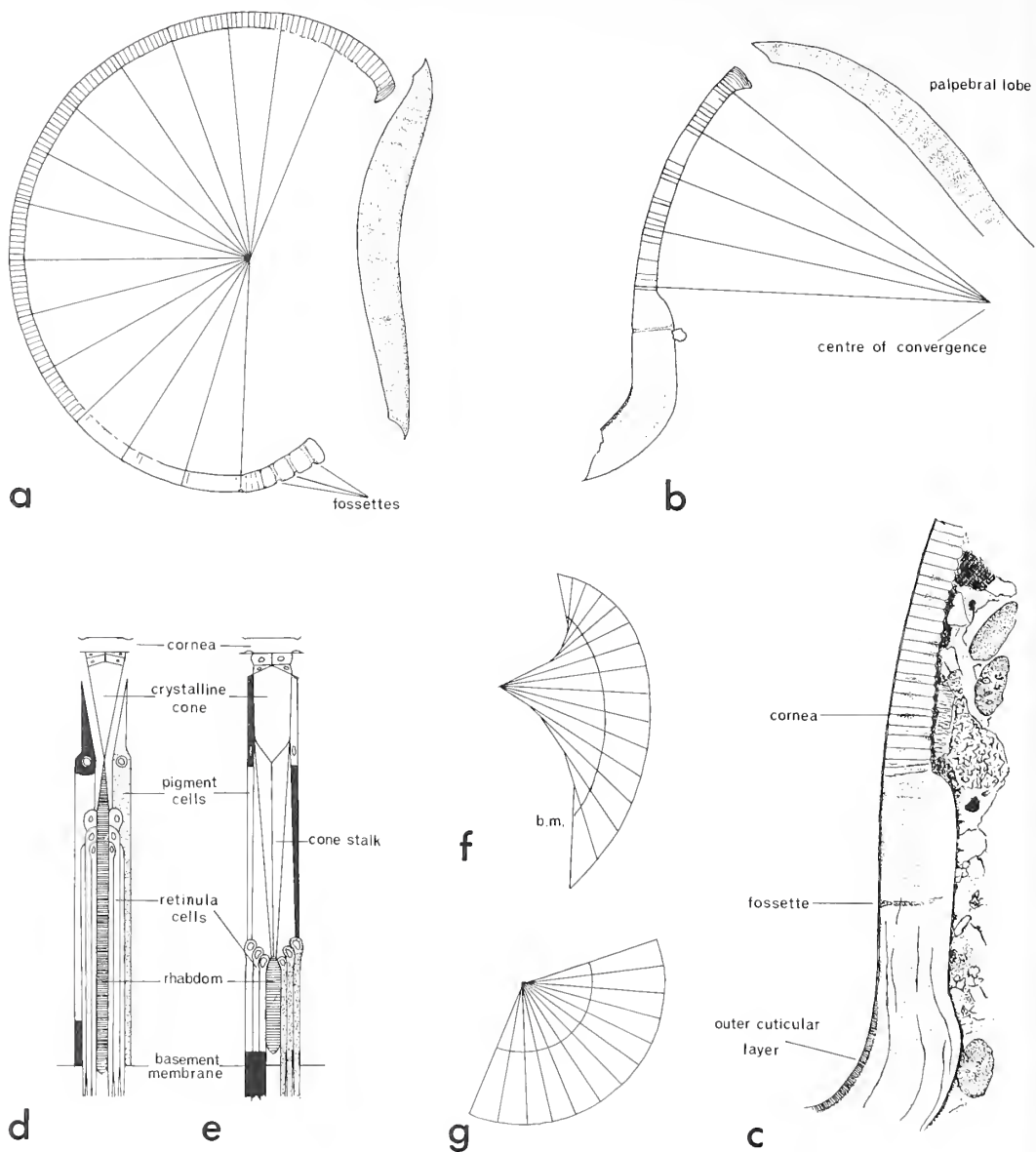
The prisms in the eye do not, however, exist in isolation, but are contiguous one with another. It is not known, of course, whether in life they were optically separated by organic layers along their walls. There is no evidence of such layers, and their former presence is rendered unlikely both by the close contiguity of the prisms and the fact that there are small domains of optically associated prisms where the cleavages pass through from one crystal to another. The lenses of modern insect and crustacean eyes, where contiguous like those of *Asaphus*, are sometimes optically isolated one from another by such highly refractive layers but not always, and indeed the superposition system of vision, as mentioned later, depends upon their close optical contiguity.

If, therefore, as we assume, the prisms of *Asaphus* were originally in optical contiguity, then the dioptric system as a whole would actually be receptive to a much higher range of light incidence, for the light could pass through neighbouring crystals. In such a case the divergence between the path of the extraordinary and the ordinary ray would increase, resulting in more extreme double refraction and hence double images at different depths.

Such double images, however, could have been virtually eliminated and not transmitted to the photoreceptors if the *Asaphus* eye were provided with a layer of absorbing pigment, just below the prismatic region, exactly as with the 'distal retinal pigment' of many known crustaceans (text-fig. 4*d, e*), which occurs in both apposition and superposition eyes. In the latter, there is a cylindrical sleeve of black or brown pigment surrounding the upper parts of each ommatidium below the lens, embracing the crystalline cone and the area below it, which absorbs unwanted light rays. A similar pigment sleeve in *Asaphus* located just below the prisms, would fulfil an identical function, and if the central bore were narrow, would effectively restrict most of the oblique rays, and screen them from the other ommatidia. If this were the case a mosaic-type image could then be formed by the eye, using only rays parallel with the axis or only slightly oblique and thus cutting out most of the adverse effects of double refraction. Such a system would allow a degree of mosaic vision not greatly inferior to that of modern arthropods. The extreme sphericity of the visual surface would give a more or less undistorted image of the mosaic kind, and it might also relate to a kind of superposition vision, as discussed in the next section.

Arrangement of deeper-lying structures. The visual surface of *Asaphus raniceps* has an almost constant horizontal curvature, the radius of which is slightly less than that in the vertical plane, though the latter is less regular, and decreases towards the top of the eye. Thus the visual surface approximates a segment of a prolate spheroid in which the vertical axis is slightly greater than the horizontal ones.

The eye has a slightly higher profile curvature anteriorly than posteriorly, and the visual field is expanded latitudinally towards the front (text-fig. 1*g*). Apart from this slight difference the curvature of the eye is otherwise regular, and follows the almost perfectly radial arrangement of the primary prisms. In horizontal and vertical sections of well-preserved specimens the edges of the prisms are clearly visible, and may be used as a basis for some reconstruction of the internal parts. If lines are drawn along the edges of adjacent prisms and extended inwards, they are found to meet at a common centre.



TEXT-FIG. 4. *a*. Horizontal section through *A. raniceps* eye, with radii of curvature passing through every tenth prism marked. From a thin section. $\times 12.5$. Gr I 5512. *b*. Vertical section. $\times 12.5$. Gr I 5503. *c*. Thin section through lower part of visual surface and eye-socket. The outer cuticular layer of Dalingwater passes upwards into the cornea at the base of the eye-socket. $\times 30$. Gr I 5503. *d*. A single ommatidium of the apposition eye of a shore crab. *e*. Ommatidium of the superposition eye of a lobster.

In *d* and *e*, the left-hand side is shown as dark-adapted, the right as light-adapted. Both after Kampa (1965).

f, *g*. Diagrams illustrating surface convexity and centres of ommatidial convergence in the eyes of the insect *Apis mellifica* (apposition eye), and *Samia cecropia* (superposition eye). Both redrawn from Portillo (1936).

The radii of curvature in the two directions are illustrated in text-fig. 4*a, b*. It is very probable that those parts of the eye, now destroyed, lying below the primary prisms, were elongated ommatidia, following the radii of curvature more or less exactly, just as in the eyes of many insects and crustaceans, though how deep they were cannot be assessed. In modern arthropods the first optic ganglion of synaptic region occupies the central part of the underlying space and the same was probably true of the trilobites. Almost certainly the ommatidia must have terminated some distance short of the centre of curvature.

The regularity of surface curvature, ommatidial separation, and radial arrangement of the ommatidia, evident in *Asaphus raniceps*, is also characteristic of the structure of many superposition eyes in modern arthropods. In this respect the eye of *A. raniceps* is unlike both modern apposition eyes, and those of phacopid trilobites.

Anatomical differences between apposition and superposition eyes are very well known, and have been synthesized in various reviews (Waterman 1961; Goldsmith 1964; Wigglesworth 1965). Apposition eyes (text-fig. 4*d*) have the rhabdom in contact with the crystalline cone, whereas in superposition eyes (text-fig. 4*e*), the cone and rhabdom are separated by a long cone-stalk, believed to be a light conductor. The rhabdom here is very much shorter than in apposition eyes.

These anatomical differences have been greatly discussed since the time of Exner (1891), but their physiological significance is still controversial (Goldsmith 1964; Miller *et al.* 1968).

Superposition eyes, which are typical of nocturnal crepuscular or deep-water arthropods, have an elaborate system of adaptation to dark conditions. In light-adapted superposition eyes, when screening pigment surrounds each ommatidium, the visual system probably forms a mosaic image rather like an apposition eye. (Actually the 'mosaic theory' of image formation, first propounded by Müller in 1826, is now held to be too simple, and Burt and Catton (1962, 1966*a, b*) have shown the important role of diffraction processes in arthropod vision, so as to modify greatly and extend the mosaic theory.)

In dark-adapted superposition eyes, the pigment migrates away from the cone-stalk region so that the isolation of the ommatidia is lost. In this way light coming through many lenses can pass freely to any rhabdom, and is not confined to any specific ommatidium. Sensitivity seems to be increased thereby, though resolution is lost.

It is interesting that the only modern arthropod eyes of spherical, geometrically perfect form with the radii meeting at the centre are of superposition type (Portillo 1936), though not all superposition eyes do, in fact, have such perfect form. Portillo believed that such a structure was highly desirable for superposition vision, both optically and physiologically.

The parallels between the regular structure of the eye of *Asaphus raniceps*, and typical modern superposition eyes are illustrated in text-fig. 4*a, b, f, g*; it is possible that the number of points in common may imply some degree of functional similarity.

Some recent work by Stuermer (1970) appears at first sight to militate against the above suggestions. Stuermer subjected the schizochroal eyes of some Devonian phacopid trilobite to X-ray examination and found within the eyes very long, closely

packed bundles of fibres extending from the lentiferous region right into the axial part of the body of the trilobite. He interpreted these as light guides (presumably equivalent to very long cone-stalks in modern arthropods), which conducted light from the lenses to the photoreceptors.

I have assumed that in *Asaphus raniceps*, as in virtually all recent arthropods, the photoreceptive organs were of ommatidial kind, arranged radially, following the radii of curvature more or less exactly and that optic ganglion was present centrally. Though Stuermer's material is tectonically distorted, it is clear that the structures he described do not follow this pattern; they are numerous and quite thick and because of their extreme length a radial pattern is not evident. As far as can be seen they terminate outside the optic region altogether so that if they were really light guides the optic ganglion would be displaced towards the central part of the body.

Thus the eye as interpreted by Stuermer bears very little resemblance to any other kind of arthropod eye. Even in certain mysids and euphausiids where the cone-stalks are of exceptional length (thus accommodating multiple diffraction images at different depths), the optic ganglion remains centrally located, and the external part of the eye becomes expanded outwards during ontogeny to accommodate the extra length. It is difficult to see what purpose could be served in the large-lensed phacopids by such an improbable distance between lens and photoreceptor, and it is likely that the fibre-bundles are not part of the optical system at all. They could be part of a circulatory system like the alimentary prosopon of many Cambrian trilobites (Öpik 1961) only located below the surface, or, as Dr. J. Bergström (pers. comm.) has suggested, filaments of the 'gill' or exite branch of the appendages. Various factors seem to support this suggestion, and in particular the random and oblique orientation of the fibre-bundles, and their indistinct preservation directly below the palpebral furrow, which would have acted as a ridge crushing against the filaments. Such filaments may have been preserved only where trapped in the void below the eye and the glabella, and that is why they extend only to the visual surface and not beyond, thus giving the impression of being part of the optical system.

Until further evidence is forthcoming, therefore, Stuermer's structures cannot be unequivocally accepted as being light guides. And though the internal organization of the schizochroal system may well have differed from that of holochroal eyes the external morphology of the latter approximates that of insects and crustaceans in so many ways that it seems more appropriate to infer some internal resemblance, at least in so far as having radially arranged photoreceptors and a centrally placed ganglion.

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REMOPLÉURIDES AND OTHER UPPER ORDOVICIAN TRILOBITES FROM NEW SOUTH WALES

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ABSTRACT. Thirteen trilobite species are described and illustrated from Upper Ordovician successions of central New South Wales. They include the new species, *Remopleurides saenuros*, *R. exallos*, *R. acer*, *Pseudobasilicus? fortis*, and *Illaeus (Parillaenus)? incertus*, and records of *Shumardia*, *Geragnostus?*, and a harpid. A discussion of possible dimorphism in *Remopleurides* is presented.

IN previous contributions on the Upper Ordovician trilobite fauna of central New South Wales, several new genera and species were proposed. Webby, Moors, and McLean (1970) introduced the new genera *Malongullia* and *Encrinuraspis*, and Campbell and Durham (1970), *Parkesolithus*. In the following year Webby (1971) added two new species of *Pliomarina*. The present work completes descriptions of the Upper Ordovician agnostids, shumardiids, remopleuridids, asaphids, illaenids, and harpids from central New South Wales based on collections housed in the Department of Geology and Geophysics, University of Sydney.

The faunas have been collected through a considerable stratigraphic thickness of beds, and from widely scattered localities on the Molong Rise and Parkes Platform of the Lachlan Geosyncline (Packham 1969). *Remopleurides acer* sp. nov. and *Pseudobasilicus? fortis* sp. nov. occur with *Pliomarina prina* Webby and a scutellid (not *Eobronteus*) in the lower part of the Cliefden Caves Limestone. *R. saenuros* sp. nov., *R. sp. A*, *Pseudobasilicus? sp. A*, and a harpid are represented, together with *Pliomarina austrina* Webby, *Amphilichas*, *Sphaerocoryphe*, and an encrinurid, in the Ordovician limestone at Billabong Creek, considered to be approximately equivalent in age to the upper part of the Cliefden Caves Limestone. Another, stratigraphically younger fauna, with *Illaeus (Parillaenus)? incertus* sp. nov. as the dominant form, is found in calcarenites at the top of the Ballingool Formation (upper part of the Bowan Park Group of Semeniuk 1970). Other elements of the fauna are too fragmentary to determine to species level, but include *Remopleurides*, an asaphid, a proetid, a trinucleid, and encrinurid. The three stratigraphically distinct trilobite faunas from the limestones correlate quite well with the three stromatoporoid/coral faunas I, II, and III outlined previously (Webby 1969).

In the shales of the Malongulli Formation, directly overlying the Cliefden Caves Limestone, at Trilobite Hill and Copper Mine Creek, *R. exallos* sp. nov., *Malongullia oepiki* Webby, Moors, and McLean, *Encrinuraspis optimus* Webby, Moors, and McLean, *Parkesolithus*, and a scutellid (not *Eobronteus*) are found. These beds, from their associated graptolites (Moors 1970), are taken to have an Upper Eastonian age (*Dicranograptus hians* Zone). A similar fauna has been collected from near Mirrabooka homestead, north of Cheeseman's Creek, with additions of *R. sp. B*, *Illaeus (Parillaenus)? sp. A*, and *Toernquistia*. Another distinct species of *Remopleurides*, *R. sp. C*, occurs in a near-by locality, just north of the Cheeseman's Creek

Post Office, and possibly comes from a higher stratigraphic horizon. The scutelluids from the lower part of the Cliefden Caves Limestone and the Malongulli Formation, previously assigned to *Eobronteus* (Webby 1971, p. 612; Whittington and Hughes 1972, p. 273), more correctly belong to a new genus having closest affinities to the Silurian genera *Kosovopeltis* Šnadjr and *Planiscutellum* R. and E. Richter.

The beds of the Oakdale Formation in the Mumbil area, with their *Geragnostus*? and *Shumardia*, have previously been assigned an Upper Eastonian age on the basis of occurrences of associated species of *Climacograptus*, *Dicellograptus*, and *Orthograptus* (Strusz 1960, 1961). They could be comparable in age to the beds of the Malongulli Formation, but are probably slightly older, perhaps Gisbornian or Lower Eastonian (above the base of the *Nemagraptus gracilis* Zone). It seems that the Oakdale Formation includes two separate successions, an older belt to the west containing the 'upper Eastonian' graptolites, and *Geragnostus*? and *Shumardia*, and a much younger sequence in the core of the Oakdale anticline to the east, with a rich coral fauna at the top, suggesting either an Upper Bolindian or, more probably, a late Llandoveryan age (see further discussion in Webby 1972).

Pittman (1900, p. 10) has recorded a probable agnostid from Ordovician graptolitic shales at Junction Reefs, near Mandurama. Alluding to this same trilobite, Chapman (1914, p. 227) related it to *Shumardia*. Stevens (1957, p. 48) considered the beds containing the trilobite to be associated with occurrences of *Glyptograptus teretiusculus*, and Smith (1966) grouped these beds in the Malongulli Formation. The region is east of the type area of the Malongulli Formation (Upper Eastonian age) near Cliefden Caves, and the beds contain definite Darriwilian (Llanvirn-Llandeilo) graptolite assemblages (Packham 1969, p. 80). According to Packham, the upper limit of age of these beds is probably near the base of the Eastonian. Smith's 'Malongulli Formation' is therefore a distinct, older, Darriwilian-Gisbornian unit. Pittman's original trilobite is confirmed as a species of *Shumardia* closely similar to the Oakdale form. It is possible that it is conspecific with the Oakdale species. Perhaps both come from similar, Gisbornian, horizons.

In the silicified residues from the Ordovician limestone at Billabong Creek (Packham 1967), there is abundant material belonging to the small species of *Remopleurides*, *R. saenuros*, allowing virtually complete description, and fragmentary specimens of the thorax and pygidium of a much larger and broader form, *Remopleurides* sp. A (Pl. 52). The cephalon and anterior thoracic segments of this latter form remain unknown, but it can be estimated to have been about four times larger than *R. saenuros*. It is relatively much broader, especially across the axis, and appears to lack a median axial spine on the third thoracic segment in front of the pygidium. It has a large, rather undifferentiated, sub-trapezoidal, posteriorly rounded pygidium, totally different from the pygidium of *R. saenuros*, which has a weakly differentiated triangular axis, two pairs of short pleural spines, and a deeply incised median longitudinal furrow. Another very large, incomplete and rather similar specimen, referred to *Remopleurides* sp. B, occurs in the shales of the Malongulli Formation associated with *R. exallos* (Pl. 51, figs. 3-13). These associations suggest the possibility of the New South Wales *Remopleurides* exhibiting a most distinctive type of dimorphism, though the cephalon of the large form must be found to demonstrate the relationship convincingly. Whittington (1963) has mentioned the possibility of dimorphism be-

tween his two species of *Remopleurides*, *R. eximius* and *R. simulus*, from the Lower Edinburg Formation of eastern North America, but these are separated by comparatively minor morphological characteristics compared with the features distinguishing the large and small New South Wales forms. *R. eximius* has a tiny spine at the genal angle, long, curving pleural spines on the seventh thoracic segment, and deep furrows on the pygidial axis. *R. simulus*, in contrast, has a slender spine originating in front of the genal angle, the pointed ends of the pleurae are equally extended, the axis of the pygidium is less inflated, the furrows shallower, and it is only about two-thirds the size of *R. eximius*.

A micrometer ocular and, for larger dimensions, a pair of dividers have been used for taking measurements. Unfortunately, however, there are considerable errors in taking linear measurements across curved surfaces of exoskeletons, especially in more highly convex forms. Therefore, only measurements taken across less convex surfaces are cited.

SYSTEMATIC DESCRIPTIONS

Family AGNOSTIDAE McCoy 1849

Genus GERAGNOSTUS Howell 1935

Type species. Agnostus sidenbladhi Linnarsson 1869

Geragnostus? sp.

Plate 51, fig. 1

Material. One internal mould of a fairly complete specimen (SUP 26900) from locality G (Strusz 1961, p. 334, text-fig. 1) of the Oakdale Formation, 1½ miles NNE. of Newrea, south of Wellington.

Description. Although margins of cephalon not exposed, general appearance suggests subquadrate outline; slightly wider than long. Glabella expanded anteriorly, bounded by deep, broad axial and preglabellar furrows, and divided into anterior and posterior lobes by pronounced transglabellar furrow situated about glabellar mid-length, slightly convex forwards. From nature of freshly broken surface immediately behind transglabellar furrow, it seems likely that small median glabellar node may have been present originally. Anterior lobe gently convex, widest just behind mid-length (sag.), wider than long, with convexo-concave outline. Posterior lobe narrower (tr.), moderately strongly convex, parallel-sided with posterior part sloping steeply backward and having sharply V-shaped posterior outline. V-shaped occipital furrow separates posterior lobe from pair of triangular, lateral occipital lobes (Whittington 1963, p. 28).

Cheeks and preglabellar area convex, with narrow, steeply sloping inward edge to axial and preglabellar furrows, and wider more gently sloping outward margin. Border unknown.

Thorax of two segments, subequal in size. Axis of anterior segment broad, divided into median trapezoidal lobe and pair of ovate lateral lobes elongated inward and forward at about 45°; each pleura divided almost equally by pleural furrow. Posterior segment similar, differing in having more obviously quadrate median lobe, suboval lateral lobes elongated transversely, and each pleura curving forward with prominent pleural furrow situated on anterior part.

Pygidium slightly wider than long; axis convex, rounded posteriorly, and widest about mid-length, limited by deep, broad axial furrows. Transverse furrow well defined, gently concave anteriorly and situated about one-third of total length of axis from anterior margin. Anterolateral corners of axis exhibit pair of elongated, triangular-shaped lobes. Weakly developed rounded median node forms highest point on pygidium, just in front of transverse furrow. Posterior lobe of axis has concavo-convex outline. Inner edge of pleural lobes inclined steeply in towards axial furrow; outwardly more or less of equal width and convexity, bounded by border furrow. Border poorly preserved; no spines seen. Ornamentation not observed.

Remarks. The New South Wales species seems to be nearest to *Geragnostus mccoyii* (Salter) from the Llandeilo and basal Caradoc of Wales and the Welsh Borderland (Whittard 1955; Hughes 1969), a form with a deeply impressed transglabellar furrow. However, it has a much more expanded anterior glabellar lobe, more sharply V-shaped posterior margin to the posterior lobe of the glabella, and more or less equal thoracic segments. Since the borders are incompletely preserved and the anterior glabellar lobe is rather enlarged, the species is only tentatively assigned to the genus.

Species of *Geragnostus*, as Whittington (1963, 1966) has pointed out, range from Upper Cambrian to Middle Ordovician, with a doubtful record in the Ashgill of Poland (Kielan 1960), and have a wide geographical distribution. There seems to be no known occurrence of a species of *Geragnostus* with strongly developed transglabellar furrow in beds younger than basal Caradoc.

EXPLANATION OF PLATE 51

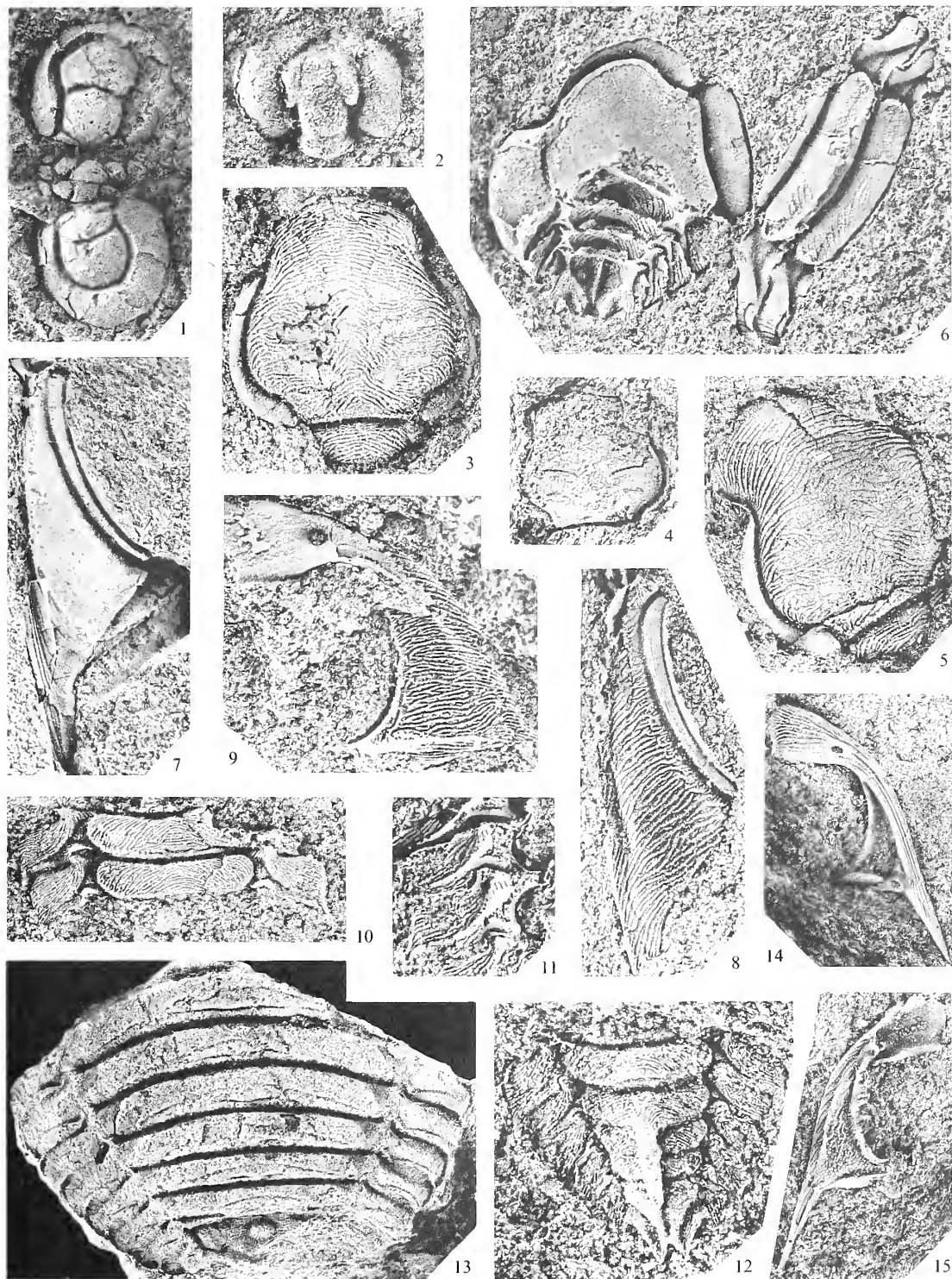
Fig. 1. *Geragnostus*? sp. Dorsal view of internal mould of incomplete exoskeleton from Oakdale Formation near Newrea; SUP 26900, $\times 6$.

Fig. 2. *Shumardia* sp. Latex impression of cephalon from Oakdale Formation, near Newrea; SUP 26901, $\times 8$.

Figs. 3–12. *Remopleurides exallos* sp. nov., from the Malongulli Formation. 3–4, 6, 9–10, and 12 from Copper Mine Creek, 11 from Trilobite Hill, and 5, 7–8 from near Mirrabooka homestead, Cheeseman's Creek area. 3, Dorsal view of latex impression of external mould of cranidium; holotype SUP 28913, $\times 4$. 4, Dorsal view of internal mould of cranidium; paratype SUP 19937, $\times 5$. 5, Oblique view of latex cast of external mould of cranidium; paratype SUP 27905b, $\times 6$. 6, Partly disarticulated specimen showing internal mould of dorsal side of part of cranidium and two thoracic segments, and ventral side of last three thoracic segments and pygidium; paratype SUP 28911a, $\times 6$. 7–8, Oblique views of internal and external moulds of left free cheek; paratype SUP 28905, $\times 6$. 9, Ventral view of compressed specimen showing internal mould of anterior part of doublure and large pit, and external mould of free cheek with distinctive anastomosing lines; paratype SUP 28914, $\times 6$. 10, Dorsal view of latex impression of external mould of two thoracic segments; paratype SUP 26942b, $\times 4$. 11, Ventral side of thoracic pleurae; paratype SUP 19917, $\times 8$. 12, Dorsal view of latex cast of external mould of articulated posterior part of exoskeleton with four thoracic segments and pygidium. Note median axial spine on third thoracic segment in front of pygidium; paratype SUP 28910, $\times 6$.

Fig. 13. *Remopleurides* sp. B from the Malongulli Formation near Mirrabooka homestead, Cheeseman's Creek area; SUP 28904, $\times 2$. Internal mould of six thoracic segments and damaged pygidium.

Figs. 14–15. *Remopleurides* sp. C. Ventral and dorsal views of latex impressions of left free cheek from shales just north of Cheeseman's Creek P.O.; SUP 28908, $\times 4$.



WEBBY, *Geragnostus*?, *Shumardia*, *Remopleurides*

Family SHUMARDIIDAE Lake 1907

Genus SHUMARDIA Billings 1862

Type species. *S. granulosa* Billings 1862

Shumardia sp.

Plate 51, fig. 2

Material. An incomplete external and internal mould of a cephalon (SUP 26901) and a fragment of the thorax (SUP 26902) from locality G (Strusz 1961, p. 334, text-fig. 1) of the Oakdale Formation, 1½ miles NNE. of Newrea, south of Wellington.

Description. Cephalon convex, approximately subsemicircular; glabella occupying almost one-half cephalic width. Anterior part of glabella expanded with pair of elongate, ovoid antero-lateral lobes, isolated by lateral glabellar furrow *2p* running forward and slightly inward from deeply indented axial furrow; posterior part of glabella semicylindrical; lateral glabellar furrow *1p* not seen, and apparently no basal lobes. Antero-lateral lobes narrower than intervening frontomedian lobe of glabella. Axial furrow deeply impressed in posterior part of glabella but shallows as it curves forward around antero-lateral lobe, being confluent with preglabellar furrow, and coming together with a V-shaped outline, viewed from the front, with an angle of about 90° between either side. Occipital furrow separates convex occipital ring from rest of glabella; slightly wider than posterior part of glabella.

Cheek convex, sloping steeply distally, especially postero-laterally, narrowing into preglabellar area anteriorly; also sloping steeply into posterior part of axial furrow. Facial suture not observed. Posterior border furrow not shown. Surface of cephalon appears to be unornamented.

Remarks. A specimen (MMF. 3414) in collections of the Geological and Mining Museum, Geological Survey of N.S.W., from Ordovician graptolitic shales near Junction Reefs, Mandurama (Pittman 1900), proves to exhibit a species of *Shumardia* which may be conspecific with the Oakdale form. The slab shows two separate cephalons and a pygidium. The form and size of the cephalons are similar to that of the Oakdale species. The relatively slightly shorter, less slender glabella is probably not a significantly diagnostic feature for differentiation of a separate species. These specimens exhibit a little more of the posterior part of the cheek than in the Oakdale cephalon. The posterior border is very deep, and undercuts the cheek on its inner course, but shallows and curves slightly forward distally, dying out inside the lateral margin, and not apparently continuous into a lateral border furrow. The posterior border has a prominent wedge-shaped, distally widening outline. The pygidium is subtriangular, with raised, almost smooth axis, tapering backward to bluntly rounded point. Anteriorly, the articulating furrow and articulating half-ring are well developed. Seven very weakly differentiated axial rings are seen. The pleural regions exhibit a prominent first pair of pleural furrows, curving backward and outward to the posterior edge of the articulating facet, and the next three, progressively shorter and much weaker. Posteriorly the pleural regions are smooth. Broad (sag.), shallowly curved posterior border furrow separates an elongated, flattened, tongue-like posterior border from the steeply declined, convex pleural region behind the axis.

An internal mould of the pygidium shows the inner edge of the doublure extending from immediately behind axis in smooth, gentle curve antero-laterally toward posterior edge of articulating facet, with the result that the doublure has a much expanded, crescent-shaped outline. Pygidia of Koroleva's (1964) species of *Shumardia*, *S. lacrima* and *S. analoga*, from the Middle Ordovician of northern Kazakhstan, seem to show a similar tongue-like projection of the posterior border, but both exhibit more conspicuous differentiation of axial rings and pleural ribs.

The Oakdale species appears to bear close resemblances to *S. minutula* Harrington from the Upper Tremadoc and Arenig of Argentina (Harrington and Leanza 1957). However, the glabella differs in being better differentiated with longer and more slender antero-lateral lobes. *S. sagittula* Whittington (1965) from the Middle Table Head Formation of Newfoundland may also be compared, but has a longer (sag. and exsag.) occipital ring, a shorter subcylindrical part of glabella in front of occipital furrow and more bulbous antero-lateral lobes. The present species bears little resemblance to known Upper Ordovician species, *S. scotica* Reed (1903) from the Whitehouse Group (late Caradoc or early Ashgill) of Girvan, Scotland, and *S. polonica* Kielan (1960) from the Middle Ashgill of Poland. The posterior part of the glabella of both these species is much broader, and they exhibit weakly differentiated basal lobes and a relatively wider occipital ring. Of Koroleva's (1964) species of *Shumardia* from the Middle Ordovician of northern Kazakhstan, *S. analoga* has most similar cephalic proportions, but differs in exhibiting slightly shorter (exsag.) antero-lateral lobes, and sub-quadrate outline of both anterior parts of the cephalon and the glabella. The outline of both the cephalon and glabella of the Oakdale species is more conspicuously V-shaped anteriorly.

Family REMOPLEURIDIDAE Hawle and Corda 1847

Genus REMOPLEURIDES Portlock 1843

Type species. *R. colbii* Portlock 1843; subsequently designated by Miller 1889.

Remopleurides saenuros sp. nov.

Plate 52, figs. 1-28

Material. Holotype (SUP 27932) and eleven paratypes (SUP 27933-27936, 27938-27941, 27948-27949, 28900) from Ordovician limestone at Billabong Creek. All fragmentary silicified specimens.

Description. Glabella convex, especially anteriorly along sagittal line, less convex transversely; glabellar tongue broad, elevated, vertical to very slightly overhanging anterior cephalic margin. Maximum width of glabella about three-fifths total distance behind anterior margin (sag.). Length of glabella (including occipital ring) slightly greater than maximum width. Width at base of glabellar tongue slightly more than width at base of median glabellar area, adjacent to occipital furrow; glabellar tongue exhibits slight widening towards antero-lateral extremities. No lateral glabellar furrows visible. Occipital ring gently convex, set below raised median glabellar area, elongate (sag. and exsag.) but tapering rapidly towards distal ends; occipital furrow transverse, with steep slope in front on to median glabellar area.

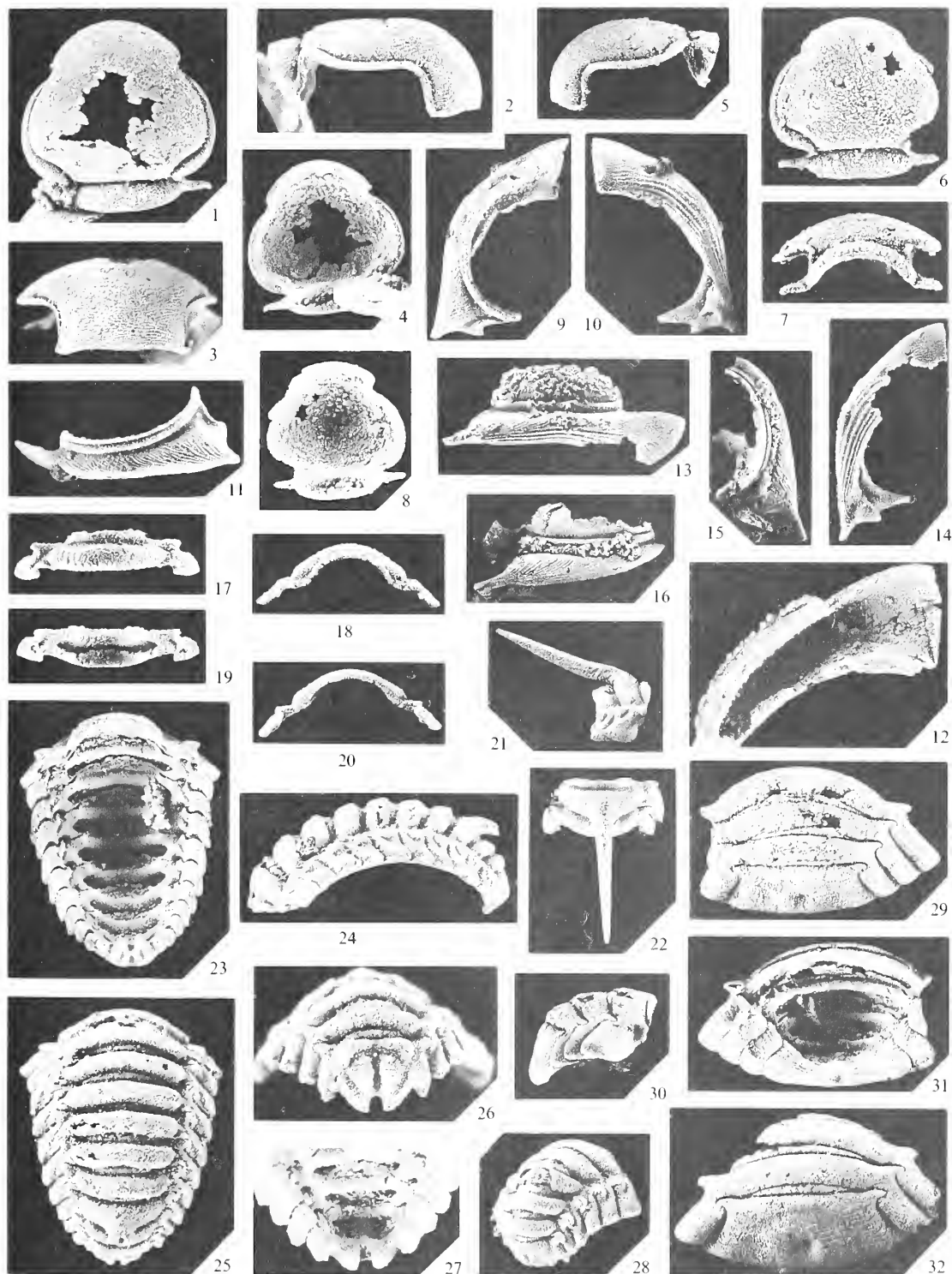
Glabellar tongue bounded laterally by axial furrow, with small anterior pit placed in furrow at antero-lateral extremity; preglabellar furrow continuous with axial furrow, becoming shallower and closer to anterior margin until it dies out a short distance in from extremities. As seen in frontal view, anterior margin flattened to very weakly concave ventrally (Pl. 52, fig. 3). Axial furrow continuous with palpebral furrow to rear. Palpebral rim flat, tilted slightly forward and outward (eye lobe has similar tilt), widens posteriorly to maximum width adjacent to postero-lateral part of median glabellar area; narrows rapidly as it descends to occipital furrow. Posterior area of fixed cheek narrow (exsag.), relatively short (tr.), though not for genus, near horizontal, tapering towards backwardly deflected tip; articulation with first thoracic segment facilitated by small axial process on axial furrow, gently transversely arched posterior flange and large fulcral sockets at distal end of posterior area (Pl. 52, figs. 1, 6-7). Doublure extends forwards slightly more than one-half sagittal length of occipital ring. Surface ornamentation on glabella and occipital ring consists of faint Bertillon pattern of lines; also row of small granules developed along posterior margin of occipital ring (Pl. 52, fig. 7).

Eye lobe long (exsag.) with visual surface curved through about 150° ; anterior part of lobe lies close to antero-lateral cephalic extremity, and posterior part virtually overhangs distal edge of occipital ring. Anterior branch of facial suture descends subparallel with axial furrow across anterior end of eye lobe, then turns sharply inwards and forwards to meet at mid-line; posterior branch of suture, after curving gently backward and inward between visual surface and palpebral rim, turns sharply downwards and outwards to pass along anterior margin of posterior area of fixed cheek, and then deflected sharply backwards to cut posterior margin between rounded projection on free cheek and fulcral socket on posterior area of fixed cheek. Rounded projection continuous into narrow, curved ridge of posterior border on free cheek; posterior border furrow similarly curved and intersecting posterior margin between rounded projection and short, slender genal spine (Pl. 52, figs. 9, 11); genal spine projects backward and slightly outward from about opposite occipital ring. Cheek outside eye lobe narrow, outward sloping, and subtriangular in

EXPLANATION OF PLATE 52

Figs. 1-28. *Remopleurides saenuros* sp. nov., from Ordovician limestone at Billabong Creek. 1-4, Dorsal, lateral, anterior, and ventral views of cranium; holotype SUP 27932; 1-3, $\times 5$; 4, $\times 4$. 5-8, Lateral, dorsal, posterior, and ventral views of cranium; paratype SUP 27933; 5-7, $\times 5$; 8, $\times 4$. 9-12, Dorsal, ventral, dorso-lateral, and oblique interior (enlarged) views of left free cheek; paratype SUP 27940; 9-11, $\times 5$; 12, $\times 8$. 13-14, Lateral and ventral views of right free cheek; paratype SUP 27935, $\times 5$. 15-16, Dorsal and lateral views of right free cheek; paratype SUP 28900, $\times 5$. 17-20, Dorsal, anterior, ventral, and posterior views of thoracic segment; paratype SUP 27949, $\times 5$. 21-22, Lateral and dorsal views of two thoracic segments; paratype SUP 27941, $\times 5$. Note median axial spine. 23-25, Ventral, lateral, and dorsal views of ten thoracic segments and pygidium; paratype SUP 27936, $\times 5$. 26-27, Magnified views of dorsal and ventral surfaces of pygidium in articulated specimen of figs. 23-25; paratype SUP 27936, $\times 8$. 28, Oblique view of five thoracic segments and pygidium; paratype SUP 27948, $\times 5$. Median axial spine damaged.

Figs. 29-32. *Remopleurides* sp. A from Ordovician limestone at Billabong Creek, $\times 4$. 29-31, Dorsal, lateral, and ventral views of pygidium and last three thoracic segments; SUP 27946. 32, Dorsal view of pygidium and two thoracic segments of SUP 27945.



WEBBY, *Remopleurides*

outline, with terrace lines running obliquely out to margins, separated from visual surface by convex external rim. Visual surface not well enough preserved to show facets.

Doublure of free cheek widest anteriorly towards mid-line; cut by median suture. Beneath eye lobe innermost part of doublure exhibits tendency to curl upward. Doublure narrows to just behind widest part of glabella, then widens posteriorly on to genal spine and into short, rounded projection of posterior margin. Crescent-shaped, convex forward, facet in doublure lies in front of, and between base of genal spine and rounded projection, allowing forward movement of first thoracic pleura during enrolment (Pl. 52, figs. 10, 14). Large pit on external surface of doublure in vertical line with anterior pit on antero-lateral corner of glabellar tongue; no cone-like structure seen to be developed. On inner part of doublure adjacent to median suture there is sharp downward deflection of inner edge of doublure forming one side of funnel-shaped opening on median suture (Pl. 52, figs. 9–10, 12). A similar feature is shown in *R. caphyroides* and *R. ligulus* (see Whittington 1959, pl. 7, figs. 4–7; 1963, pl. 4, fig. 3). Terrace lines prominent around doublure, running subparallel to lateral margins; also run out along genal spine.

Broad, convex axis of thorax tapers back to about one-half its width in length of ten thoracic segments; short, paddle-shaped pleurae inclined backward and outward beyond prominent fulcrum. Axial rings raised, with gentle slope forward (sag.), steepening on to anterior margin, and even steeper slopes around lateral and posterior margins. Relatively deep articulating furrow and moderately long (sag.) articulating half-ring. Median axial spine placed on third segment in front of pygidium; almost straight, tapering nearly to point in backward and upward direction, inclined at about 30° to crestal profile of adjacent axial rings. Spine 4.0 mm long, supported by axial ring 2.6 mm wide (Pl. 52, figs. 21–22). Articulating structures along short, transverse and horizontal anterior and posterior margins of inner part of pleurae. Anterior flange extends along anterior margin between enlarged rounded fulcral process antero-laterally, and small axial socket lying on axial furrow; on posterior side, posterior flange seems to be raised slightly between enlarged fulcral socket and small rounded axial process, protruding as ridge on to dorsal surface of inner part of pleura (Pl. 52, fig. 20). Vague suggestion of ring processes and sockets inside axial furrow, but not clearly differentiated. Outer parts of pleurae backwardly turned, with outer ends rather bluntly rounded, and more sharply pointed, posteriorly directed tips. Weak, diagonal pleural furrow runs across inner part of pleura, becoming ill defined near posterior margin on outer part of pleura.

Inner edge of doublure with gentle sigmoidal course from fulcral process backward to point just outside fulcral socket, giving over-all zigzag appearance to doublure along inner margin of thorax (Pl. 52, fig. 23). Posterior part of doublure on outer part of pleura flattened to form articulating facet for under-riding during enrolment of succeeding pleura; sharp curved (convex forward) break-in-slope between facet and gently convex anterior part of doublure. Tongue-like extension of doublure beneath axial ring, reaching forward about two-thirds total sagittal length. Ornamentation of thorax virtually restricted to faint lines in Bertillon pattern on dorsal surface of axis and pleurae; also a few granules scattered on pleurae, and along posterior margin of axial rings. Terrace lines run subparallel to lateral margins on doublure.

Pygidium subrectangular, wider than long, with lateral margins diverging slightly backwards; axis relatively long, subtriangular, tapering backward seemingly almost to deep U-shaped median notch on posterior border (Pl. 52, fig. 26). Articulating furrow sharply impressed, becoming deeper distally; articulating half-ring relatively long (sag.). First axial ring expands distally, and second axial ring divided by deep median longitudinal furrow. Owing to fusion of furrows it is rather difficult to interpret the precise nature of segmentation in posterior part of axis and relationships with pleural regions. Suggestion of pair of moderately large, oval muscle attachment areas lying over ring furrow between first and second axial rings, just inside weakly developed axial furrow. Two pairs of pleural ribs, with short, weak interpleural furrow between them; ribs extend into short, pointed pleural spines; the first pair shorter and diverging slightly outwards, the second pair tending to converge backwards. Prominent fulcral process on antero-lateral corner of pygidium. Doublure extends beneath pleural regions, and apparently beneath posterior part of axis just in front of deep median notch (Pl. 52, fig. 27). Extension of pygidial doublure in front of deep median notch perhaps implies axis is rather shorter than appears to be the case on the dorsal surface. Terrace lines continue subparallel to margin on pygidial doublure. In two specimens (Pl. 52, figs. 26, 28) pygidium has sagittal length of 1.6 and 1.5 mm, and maximum width of 2.1 and 2.2 mm, respectively.

Remarks. *R. saenuros* has a median axial spine placed on the third segment in front of the pygidium, whereas in most North American and European species of *Remopleurides* it occurs on the fourth segment in front of the pygidium, i.e. on the eighth thoracic segment where eleven thoracic segments are typical for the genus (Whittington 1950a, 1959; Shaw 1968; Ingham 1970). But in the most complete specimen of *R. saenuros* only ten thoracic segments occur (Pl. 52, figs. 23–27), and though it remains doubtful, there is nevertheless the possibility that this represents the full complement of thoracic segments for the species.

Even more distinctive is the pygidium of *R. saenuros*. Instead of the characteristic short and rapidly tapering two-segmented axis, and much broader and longer, flattened pleural regions, the axis of *R. saenuros* is relatively larger, triangular, and appears to extend back almost to the median notch, being virtually bisected by a deep and most prominent median longitudinal furrow, while the pleural regions are relatively narrow, having two pairs of short, pointed pleural spines, the outer pair divergent and the inner pair converging backward to either side of the median notch. Other small New South Wales species (*R. exallos* and *R. acer*) have a similar type of pygidium. None of the European and North American species seems to have a closely comparable pygidial construction. The pleural regions of the pygidium of *R. validus* Thorslund (1940) from the Lower Chasmops Limestone of Jemtland, Sweden, are similar, but this is the only resemblance. The pygidium as a whole is much broader, and the posterior part of the axis much shorter, with median longitudinal furrow shallower and considerably less extended.

Remopleurides exallos sp. nov.

Plate 51, figs. 3–12

Material. Holotype (SUP 28913) and seven paratypes (SUP 19937, 20902, 26942b, 28910, 28911a, 28912, 28914) from Copper Mine Creek, one paratype (SUP 19917) from Trilobite Hill, and three paratypes (SUP 27905b, 28905, 28906) from near Mirrabooka homestead, north of Cheeseman's Creek P.O. All specimens come from shales in the Malongulli Formation.

Comparative description. This species differs from *R. saenuros* chiefly in being somewhat larger, having a relatively longer (sag.) glabella and larger, more conspicuous spines. It has a much more marked, fine Bertillon pattern of terrace lines on the dorsal surface of the exoskeleton, excepting the furrows, and abundant granules on the median glabellar area adjacent to the occipital furrow and next to the posterior part of the palpebral furrows. Three pairs of lateral glabellar furrows are visible in some external and internal moulds (Pl. 51, figs. 3–4), equally spaced exsagittally, with the first curving and tapering outwards, the second, long, slender, and gently curved, and the third, short and transversely elongate.

Anastomosing terrace lines developed on the free cheeks and extend outward in a transverse direction from the region of the eye lobe, becoming deflected backwards near the lateral border. The posterior border has terrace lines arranged transversely along it. Granulation is also developed in the angle between the posterior part of the external rim of the eye lobe and the inner end of the posterior border furrow (Pl. 51, fig. 9). The external rim of the eye lobe has parallel lines along it, and scattered granules on its posterior part (Pl. 51, fig. 8). Visual surface is covered with many tiny, low facets arranged in diagonal rows. Well-developed genal spine with its base opposite occipital ring, and having prominent terrace lines running along its length. The posterior margin between the genal spine and the rounded posterior projection is straight and transverse, rather than curved as in *R. saenuros*.

Fine granulation is also developed on the posterior edge of axial rings of the thorax, particularly the anterior ones, and they occur to either side of the conspicuous diagonal furrow on the inner part of the thoracic pleurae (Pl. 51, fig. 11). Terrace lines run diagonally outward, parallel with the diagonal furrow on the outer part of the pleurae, towards the pointed spine-like pleural tips (more pointed than in *R. saenuros* but less drawn out than in *R. acer*). Terrace lines have forwardly convex course on axial rings, except for third axial ring in front of pygidium, where they are deflected backwards along straight, tapering median axial spine (Pl. 51, figs. 10, 12).

External moulds of pygidium show differentiation of raised, subtriangular axial region divided by long, deep, median longitudinal furrow almost intersecting first axial segment and continuous to just in front of median notch, and relatively narrow pleural region with two pairs of moderately elongated pleural spines (Pl. 51, fig. 12). First axial segment very narrow medially, widening rapidly distally. The ring furrow curves in arc outwards and backwards. Terrace lines represented on outer parts of segment, aligned diagonally in harmony with those on lateral parts of thoracic axial rings (Pl. 51, figs. 6, 12). Behind ring furrow are extensive raised triangular areas of the second axial segment to either side of longitudinal median furrow. Small

granules cover surface especially adjacent to the longitudinal median furrow. Laterally, close to angle between ring furrow and axial furrow, there is a smooth oval ? muscle area. Terrace lines run along length of pleural spines. A few granules also appear on the inner pleural area adjacent to the anterior margin. A narrow, arched, slightly elevated pleural area lies between posterior median notch and posterior tip of longitudinal median furrow, and exhibits terrace lines subparallel to the curve of the notch.

Remopleurides acer sp. nov.

Plate 53, figs. 1–10

Material. Holotype (SUP 28922) and fourteen paratypes (SUP 28915–28921, 28923–28926, 28928–28930) from the lower part of the Cliefden Caves Limestone, Fossil Hill.

Comparative description. *R. acer* closely resembles *R. saenuros* but may be distinguished mainly by having a more prominent, coarser Bertillon pattern of lines on the glabella, typically interrupted and deflected by the three pairs of lateral glabellar furrows (Pl. 53, figs. 1–3), by exhibiting more elongated, spine-like thoracic pleurae, even anteriorly (Pl. 53, fig. 8), and by having a pygidium with longer pleural spines and more conspicuous muscle scars on the axial region (Pl. 53, figs. 9–10). Again it is difficult to interpret precise nature of the segmentation in the pygidial axis because of fusion of the axial segments and imprint of deep, median longitudinal furrow. The first axial ring narrows medially, and ring furrow has a concave backward outline. The second axial ring is rather ill defined but bisected by deep, median longitudinal furrow, and appears to have large pair of oval- to crescent-shaped muscle scars antero-laterally, abutting ring furrow. Possibly another, slightly smaller, pair of scars is situated directly behind the first pair (Pl. 53, fig. 10). Terrace lines and granulation tend to be more prominent on the dorsal exoskeleton of *R. acer* than in equivalent parts of *R. saenuros*.

R. acer differs from *R. exallos* in being somewhat smaller, having a relatively less elongate (sag.) glabella, ornamented by a coarser Bertillon pattern of lines, and more elongated pleural spines on the thorax and pygidium. There is a less anastomosing, more obliquely, backwardly directed pattern of lines on the free cheek between the external rim of the eye lobe and the lateral border, and granulation is apparently lacking. The visual surface of the eye lobe also exhibits tiny eye facets in diagonal rows.

Remopleurides sp. A

Plate 52, figs. 29–32

Material. Three fragmentary silicified specimens (SUP 27945–27947) from Ordovician limestone at Billabong Creek.

Description. Only three thoracic segments in front of pygidium seen; no evidence of median axial spine on third thoracic segment in front of pygidium (Pl. 52, fig. 29). Very broad, smooth, gently convex axis, with deep, narrow articulating furrow and long (sag.) articulating half-ring. Pleurae divided by pronounced constriction at

fulcrum into narrow (tr.), transverse, gently convex inner part, strictly in continuity with axis because axial furrow not clearly imprinted on dorsal surface, and an outer part showing backward and outwardly inclined blunt, short, paddle-shaped form. Enlarged fulcral processes and sockets developed on pleurae, but no apparent diagonal furrow. Judging from rapid increase in width of thorax in successive segments forwards from pygidium, maximum width of thorax (and cephalon) is likely to be more than twice width of pygidium, perhaps considerably more. Doublure very wide, extending inwards to fulcrum; also extends forward beneath axial ring (Pl. 52, fig. 31).

Pygidium large, subtrapezoidal in outline, approximately two to two and one-half times wider than long. Deep transverse articulating furrow and long articulating half-ring at anterior margin. At antero-lateral extremities prominent fulcral processes, and laterally, facets to receive last pair of pleurae in enrolment. Axial and pleural areas not differentiated, but very broad, gently undulose surface of pygidium, weakly convex and sloping gently backwards; moderately large, rounded, median depression in posterior half of pygidium, and very shallow, smooth, elongate, transverse to gently curved furrow in front of median depression (Pl. 52, figs. 29, 32); appearing to represent pair of muscle attachment areas connected by narrower, gently forwardly curved band across mid-line; gentle depression extends in curve from outer ends of this structure to posterior margin between mid-line and postero-lateral extremities; dorsal surface exhibits raised lines running subparallel to gently curved

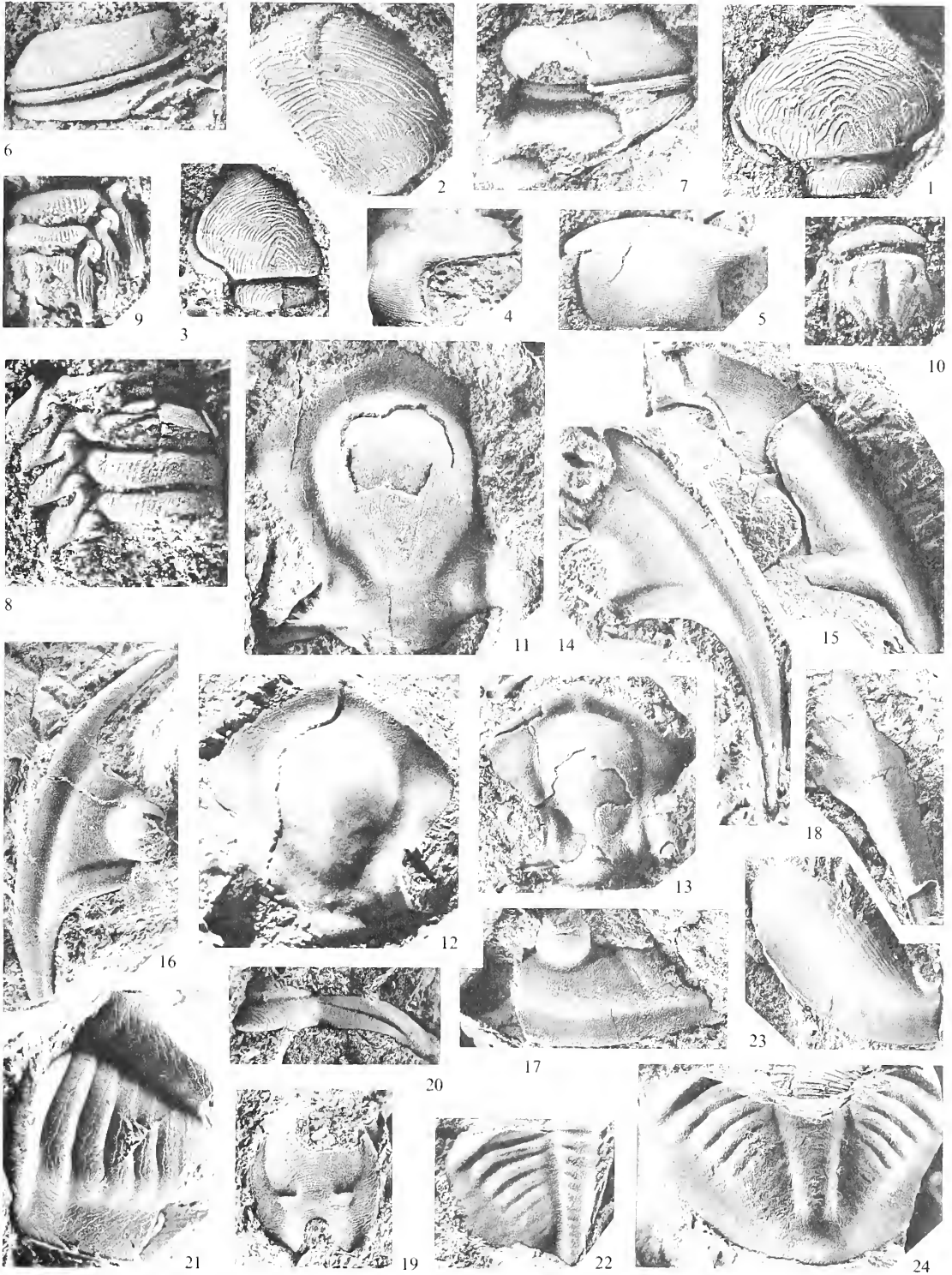
EXPLANATION OF PLATE 53

Figs. 1–10. *Remopleurides acer* sp. nov., from the lower part of the Cliefden Caves Limestone, Fossil Hill.

1, Dorsal view of latex impression of external mould of cranium; holotype SUP 28922, $\times 6$. 2, Dorsal view of latex impression of external mould of cranium; paratype SUP 28924, $\times 8$. 3, Dorsal view of latex cast of external mould of cranium; paratype SUP 28915, $\times 6$. 4–5, Lateral and anterior views of cranium; paratype SUP 28923, $\times 5$. 6, Lateral view of part of left free cheek; paratype SUP 28921, $\times 10$. 7, Lateral view of portion of right free cheek; paratype SUP 28930, $\times 10$. 8, Dorsal view of four thoracic segments; paratype SUP 28925, $\times 8$. 9, Oblique dorsal view of part of pygidium and last two thoracic segments; paratype SUP 28920, $\times 10$. 10, Dorsal view of pygidium and last thoracic segment; paratype SUP 28919, $\times 12$.

Figs. 11–24. *Pseudobasiliscus? fortis* sp. nov., from the lower part of the Cliefden Caves Limestone; 11–12, 14–17, 22–24 from 'mixed fauna' unit east of Fossil Hill; 13, 18–21 from 'lower coral' unit, Fossil Hill.

11, Dorsal view of latex impression of exfoliated cranium; holotype SUP 37900, $\times 3$. Note right, posteriorly placed palpebral lobe. 12, Dorsal view of cranium showing internal mould of lateral glabellar furrows, median tubercle, and median ridge; paratype SUP 29939, $\times 4$. 13, Dorsal view of small cranium; paratype SUP 18947, $\times 5$. Also note prominent posteriorly situated palpebral lobe. 14, Dorsal view of right free cheek and genal spine; paratype SUP 29941, $\times 2.5$. Note prominent lateral and posterior borders. 15, Dorsal view of right free cheek showing doublure anteriorly; paratype SUP 17941, $\times 2$. 16, Dorsal view of left free cheek; paratype SUP 29940, $\times 2.5$. 17, Oblique lateral view of part of left free cheek showing elevated, rounded eye; paratype SUP 18901, $\times 2.5$. 18, Ventral view of part of doublure beneath left free cheek and base of genal spine; paratype SUP 18908, $\times 2$. 19, Ventral view of relatively small hypostome; paratype SUP 29948, $\times 6$. 20, Dorsal view of part of thoracic segment; paratype SUP 17937, $\times 3$. 21, Oblique lateral view of incomplete pygidium; paratype SUP 17943, $\times 4$. Note conspicuous anastomosing lines. 22, Dorsal view of internal mould of part of pygidium; paratype SUP 37902, $\times 3$. 23, Dorsal view of doublure on left side of pygidium; paratype SUP 29947, $\times 1.5$. 24, Dorsal view of large pygidium showing prominent postero-lateral border; paratype SUP 17945, $\times 1.5$.



WEBBY, *Remopleurides*, *Pseudobasilicus*?

posterior margin, except for part of median depression and elongate furrow. Another, smaller, rounded median depression occurs at posterior margin or just beneath on posterior edge of doublure (Pl. 52, fig. 31). Doublure broad, widest antero-laterally, presumably mainly underlying undifferentiated pleural regions; narrowing slightly backwards and inwards, but medially having slight forward and upwardly directed, tongue-like extension (Pl. 52, fig. 31). Terrace lines developed along pygidial and thoracic doublure, subparallel to margin. In two specimens (Pl. 52, figs. 29, 32) pygidium has sagittal length of 2.6 and 3.5 mm, and maximum width of 5.8 and 8.0 mm, respectively.

Remarks. The association of the small *R. saenuros* and the large *R. sp. A* in the same silicified limestone fauna at Billabong Creek suggests the possibility of dimorphism (see earlier discussion, p. 446). However, until a more complete specimen is obtained, it may still be argued that this large form represents an entirely new remopleuridid.

Remopleurides sp. B

Plate 51, fig. 13

Material. A single, large internal mould (SUP 28904) from the Malongulli Formation near Mirrabooka homestead, north of Cheeseman's Creek P.O.

Comparative description. The specimen shows six thoracic segments in contact with a damaged pygidium. The thoracic segments exhibit a very wide axis with gentle forward convexity, and shorter backward and outwardly curved pleurae. Terrace lines on the thoracic doublure are more or less subparallel to the margin. On the pygidium, there is an imprint of a large rounded median elevation (depression in doublure) between anterior and posterior margins, and transversely aligned terrace lines. The specimen reaches a maximum width of 34 mm measured across the fifth thoracic segment in front of the pygidium. It closely resembles *R. sp. A*, but because of its association in the Malongulli Formation with *R. exallos*, is thought to represent a dimorph of this species, rather than of *R. saenuros*.

Possibly the Australian forms belong to a distinct species group characterized by (1) smaller 'male' dimorphs with a median spine on the third thoracic segment in front of the pygidium, and a small pygidium with relatively large, triangular axis bisected by deep, median longitudinal furrow, and narrow, marginal pleural regions, and (2) large 'female' dimorphs, lacking a median thoracic spine and with a large, wide, poorly differentiated, subtrapezoidal pygidium.

Remopleurides sp. C

Plate 51, figs. 14-15

Material. Part of a damaged cranidium (SUP 28907), free cheek (SUP 28908), and posterior part of thorax and pygidium (SUP 28909) from Ordovician shales (not *in situ*), $\frac{1}{2}$ mile north of Cheeseman's Creek P.O.

Comparative description. The character of the ornamentation on the free cheek of this species distinguishes it from other smaller New South Wales forms. Though perhaps most closely resembling *R. exallos*, the triangular area inside the lateral

border, limited by the posterior border furrow and the eye lobe, exhibits a prominent granulation (Pl. 51, fig. 15), and terrace lines are confined mainly to the genal spine, the lateral border, and the doublure. The posterior border is well developed, raised, smooth, and transversely aligned, unlike the narrow, curved ridge of the posterior border in *R. saenuros*.

Family ASAPHIDAE Burmeister 1843

Genus PSEUDOBASILICUS Reed 1931

Type species. Ptychopyge lawrowi F. Schmidt 1898.

Pseudobasilicus? fortis sp. nov.

Plate 53, figs. 11–24; Plate 54, figs. 1–4

Material. Holotype (SUP 37900) and eighteen paratypes (SUP 17940–17941, 17945–17946, 18901, 29936–29944, 29946–29947, 37902–37903) from the ‘mixed fauna’ unit east of Fossil Hill, lower part of the Cliefden Caves Limestone. Eleven paratypes (SUP 17937, 17943, 18902, 18908, 18947, 19907, 29909b, 29948, 37901, 37904–37905) from the ‘lower coral’ unit on Fossil Hill, lower part of the Cliefden Caves Limestone.

Description. Cephalon subsemicircular, wider than long (sag.), with prominent borders and strong genal spines. Glabella moderately convex, occupies between one-quarter and one-third total width of cephalon; defined by fairly well-differentiated axial furrows, continuous into preglabellar furrow anteriorly. Axial furrows not well defined posteriorly, except in small specimens and on internal moulds of larger ones, and extending more or less directly backwards on to posterior margin. One pair of prominent lateral glabellar furrows (*1p*) seen to run obliquely backwards and inwards from intersection with axial furrows near mid-length of glabella, and apparently meet at mid-line just in front of small, median glabellar tubercle, the latter situated on gentle rise of posterior part of glabella immediately in front of occipital furrow (Pl. 53, fig. 12). Internal moulds may show faintly impressed short, curved, convex forward, lateral glabellar furrows (*2p*) with weakly raised, crescent-shaped ridge just in front of each furrow; distally, *2p* furrows meet *1p* furrows, just behind their point of intersection with axial furrows. *2p* furrows subdivide convex, raised, pear-shaped anterior part of glabella into large frontal lobe and small, lateral glabellar lobes (*2p*). No observable differentiation of this pear-shaped anterior part of glabella is seen in external moulds (Pl. 53, fig. 11). Arched, subtriangular to L-shaped lateral glabellar lobes (*1p*) slope antero-medially toward *1p* furrow from raised course of axial furrow adjoining elevated palpebral lobe, and postero-laterally toward lateral development of occipital furrow. Occipital furrow becomes weakly defined and appears to be deflected slightly forwards medially. Internal moulds of glabella may show faint median ridge running forward from median tubercle across *2p* and frontal lobes (Pl. 53, fig. 12). Occipital ring gently convex, narrowing laterally owing to forward deflection of occipital furrow and slight backward curve of posterior margin medially. Frontal part of fixed cheeks expanded into flat wing-like areas, continuous into preglabellar areas. Anterior branches of facial suture dorsal-intra-marginal, but meet at margin frontally; branches of suture cut obliquely across

weak, transverse-curving antero-median ridge (representing part of antero-lateral cephalic border) on preglabellar area; median suture not developed on dorsal surface. In small specimen (Pl. 53, fig. 13) more deeply impressed preglabellar furrow separating frontal lobe from narrow, raised ridge on preglabellar area, and crossed by low, median, connecting ridge at mid-line. Palpebral lobe most elevated part of cranium, set posteriorly and adjacent to lateral glabellar lobe *1p* (Pl. 53, figs. 11 and 13). Maximum width across posterior margin of cranium similar to total width across frontal lobe of glabella and wings of fixed cheek.

Ornamentation consists of fine anastomosing lines running concentrically around frontal part of glabella, constricted posteriorly toward median tubercle (Pl. 54, fig. 1). Anastomosing lines on occipital ring also exhibit concentric, convex forward pattern. Lines directed outwards and forwards across axial furrow on to wing of fixed cheek just in front of palpebral lobe, and run more or less parallel to antero-lateral margin of cephalon on to preglabellar area. Across palpebral lobes, lines orientated longitudinally (exsag.).

Free cheek exhibits large elevated, rounded eye, situated posteriorly, only about

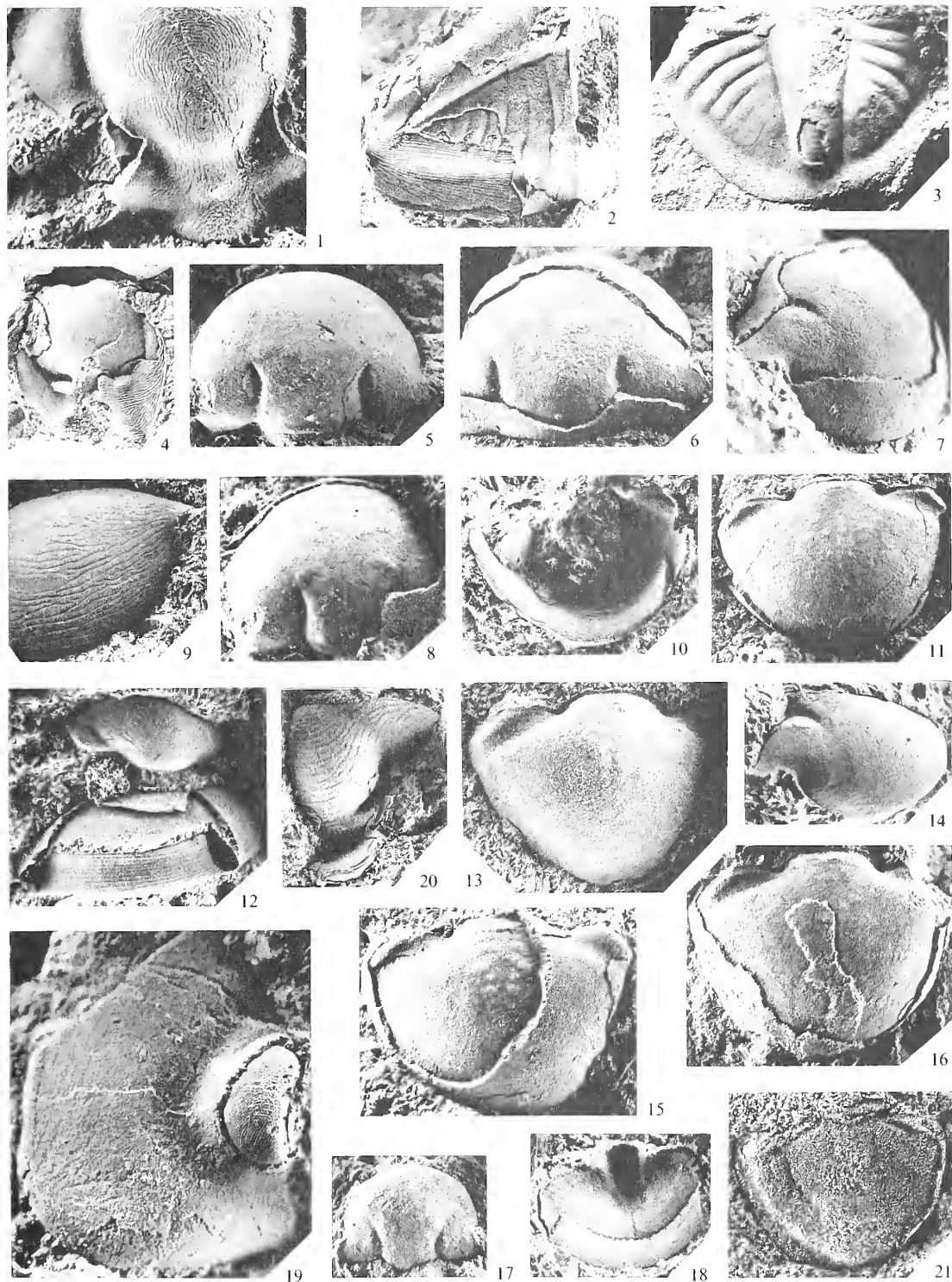
EXPLANATION OF PLATE 54

Figs. 1-4. *Pseudobasilicus? fortis* sp. nov., from the lower part of the Cliefden Caves Limestone; 1, 3, from the 'mixed fauna' unit east of Fossil Hill, and 2, 4, from the 'lower coral' unit, Fossil Hill. 1, Enlarged dorsal view of external mould of part of cranium showing pattern of concentric anastomosing lines; paratype SUP 29938, $\times 6$. 2, Oblique lateral view of exfoliated pygidium, showing part of doublure; paratype SUP 37901, $\times 2$. 3, Dorsal view of incomplete pygidium; paratype SUP 29946, $\times 3$. 4, Ventral view of incomplete hypostome; paratype SUP 29909b, $\times 4$.

Figs. 5-18. *Iliaenus (Parillaenus)? incertus* sp. nov., from the 'calcarenite' unit at the top of the Ballingool Formation, Malachi's Hill. 5, Dorsal view of internal mould of cranium, showing posteriorly situated palpebral lobe, lateral muscle impressions, and median tubercle; holotype SUP 29932a, $\times 6$. 6-7, Dorsal and oblique lateral views of exfoliated cranium; paratype SUP 18934, $\times 4.5$. 8, Dorsal view of small cranium, showing one pair of glabellar muscle scars on internal mould; paratype SUP 18931, $\times 8$. 9, Anterior view of latex impression of cranium, showing pattern of anastomosing lines; paratype SUP 19941, $\times 5$. 10, Ventral view of doublure on pygidium, showing smooth, even curve of inner edge; paratype SUP 29928, $\times 4$. 11, Dorsal view of internal mould of pygidium; paratype SUP 29931c, $\times 3.5$. 12, Antero-dorsal and oblique lateral views of paratypes SUP 18933c (upper) and SUP 18933b (lower), $\times 5$. Note smooth curve of inner edge of doublure and of terrace lines on exfoliated part of lower specimen, and fine pitting and radiating lines on dorsal surface of upper specimen. 13, Dorsal view of internal mould of pygidium; paratype SUP 29932b, $\times 4$. 14, Oblique lateral view of internal mould of cranium; paratype SUP 18933a, $\times 4$. 15, Dorsal view of partly exfoliated pygidium showing lateral muscle impression on one side and six pairs of small axial muscle scars on internal mould; paratype SUP 29928b, $\times 5$. 16, Dorsal view of exfoliated pygidium; paratype SUP 29931a, $\times 4$. 17, Dorsal view of internal mould of small cranium showing diverging axial furrows; paratype SUP 17700, $\times 6$. 18, Ventral view of small pygidium showing trace of axial furrows anteriorly, one pair of lateral muscle impressions, fine, weak median ridge (groove ventrally) posteriorly, and smooth curve of inner edge of doublure; paratype SUP 29929, $\times 8$.

Figs. 19-20. *Iliaenus (Parillaenus)? incertus* sp. nov., also from 'calcarenite' unit at top of Ballingool Formation, Malachi's Hill. 19, Dorsolateral view of left free cheek, showing moderate-sized, crescent-shaped faceted eye; SUP 29928a, $\times 8$. 20, Ventral view of internal mould of incomplete hypostome; SUP 18900, $\times 3$.

Fig. 21. *Iliaenus (Parillaenus)?* sp. A. Dorsal view of internal mould of compressed pygidium from the Malongulli Formation near Mirrabooka homestead, Cheeseman's Creek area; SUP 29935, $\times 4$.



WEBBY, *Pseudobasilicus*?, *Illaeus* (*Parillaenus*)?

one-half its exsagittal length in front of posterior margin. Almost upper three-quarters of eye surface composed of visual area, which extends in large arc of nearly 270° ; visual area merges into eye-socket without break-in-slope, but there is change in colour of exoskeleton and subhorizontal terrace lines appear on socket. Eye-socket curves smoothly down into broad, gently convex platform of free cheek inside prominent lateral border. Change-in-slope at inner edge of lateral border represents lateral border furrow, which weakens posteriorly along genal spine. Anterior part of free cheek has long, narrow extension of border, which tapers and descends approaching mid-line (Pl. 53, fig. 16). Posterior border relatively broad, gently convex, transverse on inner part but curving gently backward into genal spine laterally, flanked by shallow, depressed posterior border furrow, which appears to die out approaching lateral border. Posterior border raised slightly above convex platform area of free cheek. Genal spine has subtriangular cross section, with dorsal keel on inner edge being continuous into raised posterior border, weakly concave outward slope as continuation of lateral border, and ventro-lateral keel as extension of lateral margin of cephalon. Inner and ventral surfaces of spine flattened and at right angles to each other (Pl. 53, fig. 18). Spine estimated to extend back to near three-quarters of total length of thorax; sharply pointed and evenly curved backward in continuity with lateral border.

Doublure underlies entire free cheek except near eye lobe and apparently beneath posterior border furrow; also extends under wing of fixed cheek in front of palpebral lobe and preglabellar area. Anteriorly, crossed by median suture, and indented by prominent, broad, deep anterior notch; small, tongue-like deflection in even forward and inward curve of anterior notch close to mid-line (Pl. 53, fig. 15). Nature of inner edge of doublure postero-laterally to eye lobe not known, and Panderian structures not clearly observed. Terrace lines run subparallel to margins of cephalon, along lateral and posterior borders, genal spine, and doublure; anastomosing lines on platform area inside border curve around eye lobe, and directed backward to posterior border furrow.

Hypostome of forked asaphid type, subovate, somewhat longer than wide, and with middle body gently convex; divided by deep, transverse, slot-like, middle furrows into large anterior, and very small posterior lobe. Macula conspicuous, transversely ovate, steeply inclined forward, situated on posterior side of middle furrow. Lateral and posterior borders broad and long (exsag.) with deep posterior median notch; sides only slightly divergent; posterior notch occupies about one-quarter of total length (sag.) of hypostome. Inner edges of posterior notch, raised; laterally descending on to flattened lateral borders; just in front of hypostome mid-length, lateral borders narrow into shoulder, which dies out anteriorly. Lateral notch lies between shoulder and curving antero-lateral margin of middle body; extends upward and outward into anterior wing. No anterior border. Doublure unknown. Anastomosing terrace lines have concentric, convex forward pattern across middle body, and more or less transverse arrangement of lines on posterior and lateral borders, with forward deflection at lateral margins.

One poorly preserved specimen shows five thoracic segments and pygidium articulated together. Axial rings convex (sag. and tr.), each separated by relatively shallow articulating furrow from convex, tongue-like articulating half-ring, about three-

quarters of length (sag.) of axial ring. Inner part of pleura flat, transverse; outer part deflected slightly backwards and downwards beyond fulcrum. Character of pleural ends and doublure unknown. Deep, sharp pleural furrow commences close to front edge of inner corner of pleura and follows slightly oblique course, becoming deepest near middle of pleura about fulcrum, and dying out near rear edge of pleura some distance inside pleural termination. Large triangular facet on anterior side of pleura beyond fulcrum, allowing articulation beneath posterior edge of preceding pleura; bounded posteriorly by sharp ridge running obliquely outwards and backwards from fulcrum toward postero-lateral corner of pleural termination. Anastomosing lines on axial ring concentrically arranged convex forward, and extend in continuity across articulating furrow on to articulating half-ring. On inner part of pleura, lines directed forward and very slightly outward; articulating facet apparently smooth.

Pygidium subsemicircular, moderately convex; axis occupies about one-quarter of total width at anterior margin; articulating half-ring and articulating furrow as in thoracic segments. Axis raised, gently tapering posteriorly to rounded termination set inside broad, flattened posterior border. As seen in internal moulds, number of axial rings difficult to determine but at least twelve (seven to nine in anterior two-thirds of axis). Ring furrows more deeply impressed laterally than medially. In external moulds axial rings faintly or not at all defined. Pleural region exhibits raised first pleural rib, continuous to lateral margin, with large triangular facet on its antero-lateral surface. Broad, flattened border terminates against first pleural rib. Inside border up to seven additional pleural ribs may be differentiated in internal moulds, but only anterior four or five are clearly seen on external surfaces, separated by sharply indented pleural furrows. Faint, discontinuous interpleural furrows may be developed on a few anterior pleural ribs (Pl. 53, fig. 22). Doublure broad, extending beneath border areas and outer part of pleural field. Inner edge runs in gentle curve from fulcrum towards posterior part of axis and is deflected in smooth sharp curve around termination, giving rounded notched appearance. Broad spaced, anastomosing terrace lines on dorsal surface run in rather sharp forward curve across axis, extend outward along pleural ribs, and outward and forward across border, usually with backward deflection at margin; they also cross triangular facet. Well-developed terrace lines run along doublure subparallel to posterior and lateral margins.

Judging from some large fragments of free cheeks, it is estimated that this species may have reached a maximum length of about 105 mm, and a maximum width across cephalon of about 60 mm.

Remarks. *P. ? fortis* bears moderately close resemblances to the type species of *Pseudobasilicus*, *P. lawrowi* (Schmidt 1898), from the Middle Ordovician (C₁) of the Leningrad region and Estonia, but differs in exhibiting a slightly more inflated, pear-shaped glabella, a slightly narrower preglabellar area, more prominent lateral cephalic borders, larger genal spines, and less pointed, backwardly curving thoracic pleurae. Also the proportions across the posterior part of the cephalon are rather different, with the glabella occupying about one-quarter of the total cephalic width in *P. lawrowi*, and nearer one-third of the total width in *P. ? fortis*. In consequence the present species is only tentatively assigned to the genus. Schmidt's (1898, 1904)

other two Middle Ordovician species of *Pseudobasilicus*, *P. kuckersianus* and *P. kegelensis*, from horizons C_{II} and D_{II}, respectively, of Estonia, with their much elongated, flattened preglabellar area, seem to be less closely related. Balashova (1971), in recent revision of Schmidt's species, has erected a new genus, *Pseudobasiliella*, for *P. kuckersianus* and *P. kegelensis*. *Pseudobasilicus? brachyrachis* (Törnquist) from the Middle Ordovician of the Siljan district, Sweden (Jaanusson 1953), is also similar to the present species, but it too has several distinguishing points—a more obtuse angle of intersection of anterior branches of the facial suture at the mid-line, lack of prominent lateral cephalic borders, shorter, more rapidly tapering genal spine, and wider pygidial doublure with more acute V-shaped inner edges.

Of South-East Asian forms, *Basiliella satunensis* Kobayashi and Hamada (1964) from Ordovician shales at Satun, southern Thailand, seems to be most closely related. Though fragmentary, the cranidia of the Thai species are very closely similar to those of *P.? fortis*. Kobayashi and Hamada described the species as having anterior branch of facial suture 'a little intramarginal', seemingly on dorsal side, 'then abruptly bent forward to meet its fellow on the axis', presumably marginally. From their statement and illustrations (pl. IX, fig. 1a-b), it is clear they correctly interpreted the suture as extending dorsal-intra-marginally along the border, swinging across the ridge-like edge of the border approaching the mid-line, and descending to meet the other branch on the margin, almost exactly analogous to that seen in *P.? fortis*. But they assigned the species to *Basiliella* Kobayashi, a sub-genus of *Basilicus* Salter, characterized by having a marginal suture in front of the glabella (Jaanusson 1959, p. O 336). The eyes of *B. satunensis* are stated as being placed about mid-glabellar length (Kobayashi and Hamada 1964, p. 208). Yet a poorly preserved imprint of the free cheek (pl. IX, fig. 6) actually shows the posterior edge of the eye lobe running into the posterior border furrow. The large eyes seem to be situated posteriorly with raised palpebral lobes as in *P.? fortis*. Therefore, the Thai species should perhaps like *P.? fortis* be tentatively assigned to *Pseudobasilicus*. The basic differences between the two species lie in the shorter and less slender genal spine, and hypostome with wide diverging inner margins of posterior notch of *P.? satunensis*.

The presence of a raised, median ridge across the preglabellar area of the small specimen of *P.? fortis* (Pl. 53, fig. 13) may invite the suggestion of a distant link with species like *Basiliella carinata* Harrington from the Upper Tremadocian of Argentina (Harrington and Leanza 1957, p. 144).

Pseudobasilicus? sp. A

Plate 55, figs. 1-19

Material. Fragmentary silicified cranidium, large and small free cheeks, an almost complete hypostome, and two fragmentary pygidia from Ordovician limestone at Billabong Creek (SUP 37906-37913); also incomplete hypostome from Quondong Formation, Bowan Park (SUP 37914).

Comparative description. This species is described with particular emphasis on characters which distinguish it from *P.? fortis*, and on additional features not seen in the latter. Small, weakly convex, fragmentary cranidium has less inflated frontal

lobe, narrower, posteriorly tapering wings of fixed cheek, and relatively larger, though less elevated, palpebral lobe (Pl. 55, fig. 1). Large specimen of free cheek (Pl. 55, figs. 2-4) retains part of visual surface of eye, showing on inside surface numerous tiny hexagonal facets; relatively longer (exsag.) and less elevated eye than in *P. ? fortis*. Inner edge of doublure extends in gentle curve outward from just inside posterior margin (Pl. 55, fig. 3); detailed nature of course uncertain because of incomplete silicification, and no evidence of Panderian structures. In small specimens, lateral border narrows posteriorly toward relatively smaller genal spine (Pl. 55, figs. 5-7). Faint terrace lines on doublure, borders, and genal spine.

Hypostome with gently convex, subrounded middle body, subdivided into large anterior, and very small posterior lobes by marked, transversely elongate middle furrows. Small, ovate, forwardly tilted macula situated near lateral border just behind middle furrow. Broad, flattened, lateral, and posterior borders with bluntly pointed postero-lateral prongs to either side of notch, and diagnostic sharp nick half-way along margin of lateral border. Inner, ventral edges of notch sharply crested; sides slope upward and outward on to convex, dorsal surface of posterior part of doublure. Inner edge of doublure turns sharply upward into short, posterior wing directly above and behind macula; inclined inward and backward at about 45° to exsagittal line. Broad, shallow groove running forward along doublure outside posterior wing, continuous into downward and forwardly curving lateral notch between shoulder and anterior wing; possibly formerly occupied by antenna or similar structure. Inner edge of doublure between posterior wing and shoulder slightly upturned. Anterior margin curved gently forward, but with small, shallow notch across mid-line. Backward and upward continuation of anterior margin runs into very broad anterior wing. Anterior wing broad, subtriangular, upwardly and backwardly directed; dorsal edge slightly damaged, but well enough preserved to show, in side view, asymmetrical profile with gentle backward curve anteriorly and sharply deflected postero-dorsal tip. Anastomosing terrace lines directed more or less transversely across middle body and in front of posterior median notch; deflected forwards on either side across lateral borders, shoulders, and lateral notches to intersect anterior margin obliquely.

Pygidium gently convex, with much less well-differentiated axis and pleural regions than in *P. ? fortis*. Only very faint trace of about seven pleural ribs on internal surface of large specimen, 39.5 mm long (sag.) and estimated to have been about 46 mm wide (Pl. 55, fig. 13); evenly curved margin but for slight flattening of posterior margin and very weak upward deflection medially (Pl. 55, fig. 16). Less prominent lateral and posterior borders than in *P. ? fortis*. First pleural furrow very weakly developed. Axis occupies about three-sevenths of total width of pygidium anteriorly. Broad tongue-like appearance of articulating half-ring. Triangular articulating facet with moderately sharply rounded antero-lateral corner. Doublure occupies about one-half width of pleural field anteriorly; inner edge gently curved between fulcrum and posterior end of axis, broadly V-shaped, sharply rounded at posterior end of axis; terrace lines well exhibited subparallel to margin (Pl. 55, figs. 13 and 18). In large specimen, ornamentation of scallop-shaped markings especially on lateral border; irregular to transverse, widely spaced lines inside lateral border (Pl. 55, figs. 15-16). Smaller specimen exhibits anastomosing lines intersecting margin

obliquely, directed forward and outward, and fine pitting (Pl. 55, figs. 17 and 19); terrace lines also run outward on facet.

To sum up, *P.?* sp. A is distinguished from *P.?* *fortis* in the following main characters: (1) a less inflated frontal lobe, narrower wing-like lateral areas of fixed cheeks of cranium, and relatively longer (exsag.) and less elevated eyes, (2) a prominent nick on lateral margin of border of hypostome, and (3) a poorly differentiated axis and pleural regions of pygidium.

Family ILLAENIDAE Hawle and Corda 1847

Genus ILLAENUS Dalman 1827

Subgenus PARILLAENUS Jaanusson 1954

Type species. Illaenus fallax Holm 1882.

Illaenus (Parillaenus)? incertus sp. nov.

Plate 54, figs. 5–18

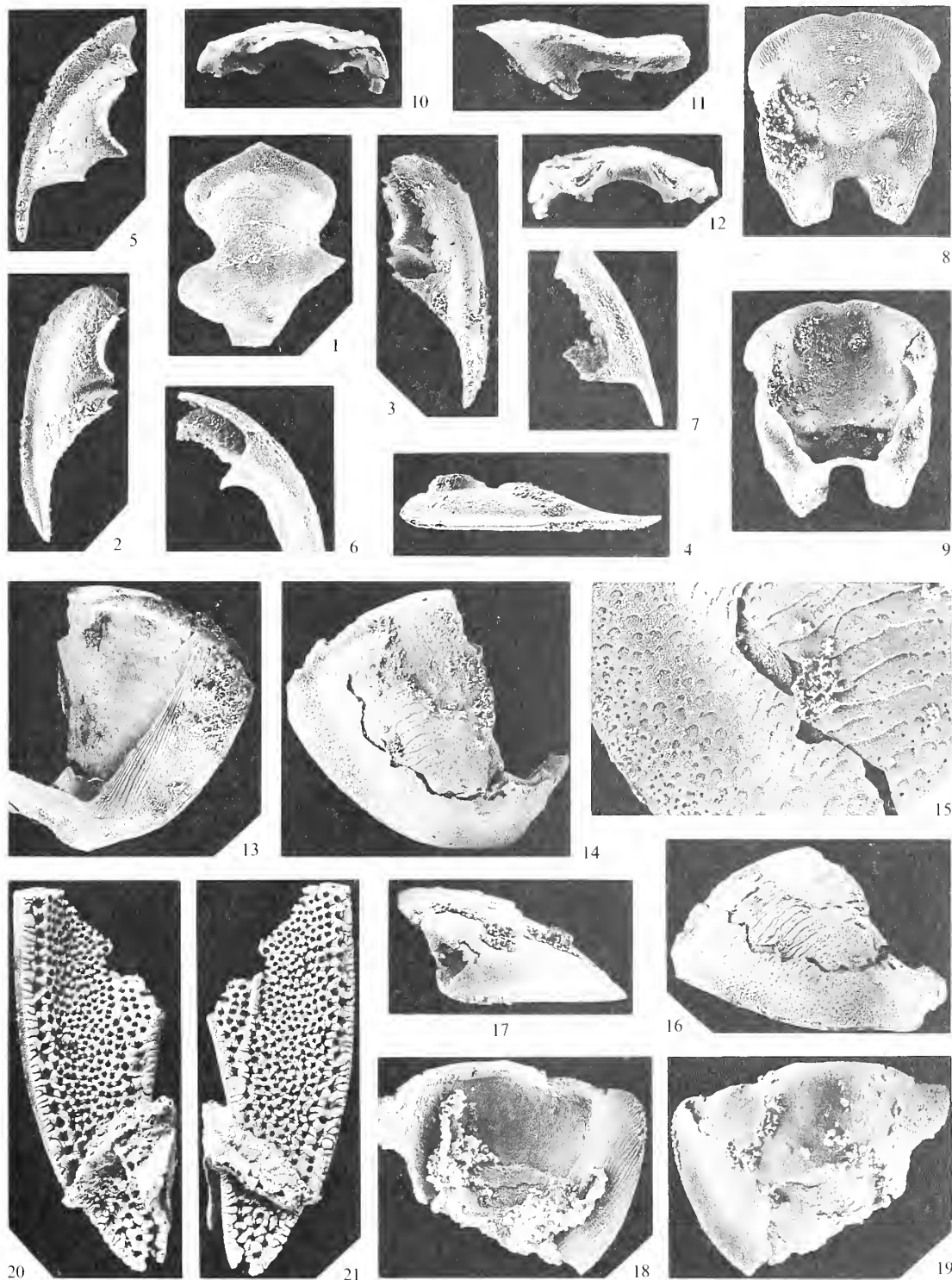
Material. Holotype (SUP 29932a) and nineteen paratypes (SUP 17700, 18928, 18931–18932, 18933a–c, 18934, 19914, 19941, 20905, 20910, 29928b, 29929, 29931a–c, 29932b, 29933) from the ‘calcarenite’ unit of the Ballingoolle Formation, Bowan Park Group (Semeniuk 1970), at Malachi’s Hill.

Description. Cranium moderately convex, subsemicircular in outline, wider than long; widest across posteriorly placed palpebral lobes; glabella in posterior part of cranium bounded by prominent, fairly deep axial furrows as seen in internal moulds, but only weakly developed in external moulds. From posterior margin, axial furrows directed forward and slightly inward to inner edges of pair of large, exsagittally elongate, oval lateral muscle impressions (lunettes); appear to be deflected forward and outward in front of impressions; internal moulds of small specimen (Pl. 54, fig. 17) exhibits weakly impressed axial furrows diverging outwards in front of lateral muscle impressions. Lateral muscle impressions set only slightly in front of palpebral lobes, at about one-third of total cranial length (sag.) from posterior margin. Just in front of anterior edges of lateral muscle impressions, and immediately across axial furrows on glabella, are pair of elongate, obliquely placed

EXPLANATION OF PLATE 55

Figs. 1–19. *Pseudobasilicus?* sp. A from Ordovician limestone at Billabong Creek. 1, Dorsal view of part of cranium; SUP 37906, $\times 3$. 2–4, Dorsal, ventral, and lateral views of part of left free cheek; SUP 37907, $\times 1.5$. 5, Dorsal view of left free cheek of small specimen; SUP 37908, $\times 4$. 6, Dorsal view of anterior part of right free cheek of small specimen; SUP 37909, $\times 4$. 7, Ventral view of posterior part of left free cheek of small specimen; SUP 37910, $\times 4$. 8–12, Ventral, dorsal, anterior, lateral, and posterior views of nearly complete hypostome; SUP 37911, $\times 3$. 13–16, Ventral, dorsal, enlarged dorsal, and posterior views of large fragmentary pygidium; SUP 37912; 13–14, 16, $\times 1$; 15, $\times 3$. Note scallop-shaped ornament on dorsal surface of lateral border. 17–19, Lateral, ventral, and dorsal views of incomplete pygidium; SUP 37913, $\times 2.5$.

Figs. 20–21. Harpid gen. et sp. ind. Dorsal and ventral views of incomplete specimen of fringe from Ordovician limestone at Billabong Creek; SUP 29949, $\times 4$.



WEBBY, *Pseudobasilicus*?, harpid

glabellar muscle scars (basal scars of Jaanusson 1954); they are orientated more or less at right angles to adjacent axial furrows and subparallel to antero-lateral margins of cephalon (Pl. 54, figs. 5 and 8). Glabellar width at level of palpebral lobes about three-sevenths of total cranidial width. Toward posterior margin, tiny median tubercle well exhibited on internal moulds of glabella. Internal mould of posterior margin of glabella shows narrow rolled edge, or incipient doublure. Posterior branch of facial suture runs only short distance backward on to posterior margin; anterior branch of suture has somewhat sigmoidal course, firstly forward and slightly outward, then curving gently inward to meet margin antero-laterally; sharp curve at margin into connective suture which continues in gentle arc flanked by doublure of free cheek and presumably rostral plate. Anteriorly, cranidium strongly curved downward, with greatest curvature towards ventral edge, giving slightly backwardly deflected anterior margin. In anterior aspect, outline made by deflected anterior margin seems to be flattened and horizontal. Anterior part of cranidium exhibits anastomosing terrace lines subparallel to margin, appearing like more or less horizontally arranged contours with slight backward and upward deflection along anterior branch of suture (Pl. 54, fig. 9).

From outline of facial suture and position and size of palpebral lobe, free cheek seems to have been rather small, with eye situated posteriorly. One large fragmentary specimen (Pl. 54, fig. 19) of a free cheek from the same locality and horizon, possibly belonging to the species, shows a moderately large, crescent-shaped eye with numerous tiny facets, and evenly rounded genal angle.

Only broken fragments of rostral plate seen; surface with very coarse transverse terrace lines.

Hypostome (Pl. 54, fig. 20), also from same locality and horizon, provisionally placed in species; relatively large, and exhibits almost straight, unnotched anterior margin, with expanded anterior wing. Anterior lobe of middle body subcircular, moderately convex, separated by deep furrow from lateral border. Lateral margins incompletely preserved. Middle furrow runs backward and inward from deep lateral border furrow, and dies out adjacent to small, oval macula. Posterior lobe of middle body poorly differentiated, especially medially; separated from raised, gently arched posterior border by broad (sag. and exsag.) and deep postero-lateral border furrow. Faint, small pits and subconcentrically, well-spaced lines developed on surface of middle body, and lines run parallel to margin on posterior border.

Thoracic segments unknown, but judging from relative widths of posterior margin of glabella and anterior edge of pygidial axis, narrows only slightly backward along thorax.

Pygidium moderately convex (tr. and sag.), subsemicircular in outline; widest across anterior part, just behind antero-lateral corner; slightly wider than long. Axis occupies about one-third of pygidial width anteriorly; usually only differentiated from pleural areas at anterior margin; axial furrows deeply impressed at margin with small downward and backward deflection of anterior edge. Relatively broad, shallow, diagonal furrow arises at anterior extremity of axial furrow and continues back and out toward lateral margin; isolates from rest of pygidium rather small, narrow, raised first pleural lobe with steep forward and outward facet-like area on antero-lateral corner. Doublure narrow, about one-fifth length (sag.) of

pygidium, evenly rounded laterally and posteriorly, with very slight narrowing in antero-lateral direction; not indented or notched sagittally; terrace lines, usually about 10–12, run subparallel to margin. On undersurface of one well-preserved small specimen (Pl. 54, fig. 18), trace of axial furrows seen extending backward from anterior margin toward large pair of oval, exsagittally elongate 'lateral' muscle impressions; rear edge of these impressions near mid-length of pygidium; axis forms subtriangular area lying inside axial furrows, with lateral muscle impressions apparently situated on outer side of axial furrows, strictly on inner part of pleural field. Axis tapers to point immediately behind rear edge of these muscle impressions, with faint, fine median ridge, seen as furrow on undersurface, continuing to inner edge of doublure. Pattern of muscle scars on axis preserved on internal mould of one well-preserved specimen (Pl. 54, fig. 15). Faint trace of large, crescent-shaped lateral muscle impression (one of a pair) and, on axis, inside and to front of it, six pairs of small muscle scars. First three pairs faint, elongate scars, closely spaced and almost transversely aligned; fourth pair, larger, pear-shaped and placed diagonally just in front of lateral muscle impression; last two pairs, subequal, rounded, set in line (but inside line of fourth pair), opposite anterior part of lateral muscle impression. Dorsal surface usually smooth, but one specimen (upper, Pl. 54, fig. 12) shows fine, widely spaced lines with intervening tiny pits running postero-laterally away from axis.

Remarks. This species may eventually prove to belong to a new genus, but additional, preferably articulated, material must be found and prepared to elucidate details of the rostral plate. It exhibits similarities to both *Illaeus* (*Parillaenus*) and *Bumastus* Murchison, though strictly is not identical with either. The relatively narrow posterior part of the glabella and the less outwardly diverging axial furrows to the front are features more typical of *Illaeus* (*Parillaenus*) than *Bumastus*. Neither genus, nor for that matter any other illaenid, appears to have the same pattern of an elongate, 'basal' glabellar muscle scar situated beside the axial furrow as in *I. (P.)? incertus*.

The even curve of the inner margin of the pygidial doublure, which characterizes the *Parillaenus* group (Jaanusson 1954), is displayed by the New South Wales species, though not with a shallow median furrow on the surface of the doublure as sometimes occurs in the type species, *I. fallax* Holm, from the Kullberg and Chasmops Limestones of Sweden (Warburg 1925). Unfortunately, no pygidial muscle impressions have been recorded from species of *Illaeus* (*Parillaenus*) for comparison. In *Bumastus bouchardi* (Barrande) from the Silurian of Bohemia, Šnajdr (1957) has recorded two pairs of pygidial muscle impressions, a large postero-lateral, and a small, antero-median pair. The large, postero-lateral pair resembles the large, lateral pair of impressions in *I. (P.)? incertus*. But the one small antero-median pair bears little resemblance to the pattern of six small 'axial' pairs of scars of *I. (P.)? incertus*.

The present species also has similarities with forms like *Bumastus* (*Bumastoides*) *aplatus* (Raymond) from the Chazy of New York (Shaw 1968). However, the relatively more widely spaced axial furrows on the cranidium behind the lateral muscle impression, and the relatively wider and more flattened pygidium, with the pygidial doublure exhibiting on its ventral surface a shallow median furrow, readily distinguish the Chazy species.

Features of the cranium of *I. (P.)? incertus*, particularly the moderately small, posteriorly situated eyes and the palpebral lobes placed well out from the axial furrows, suggest a close relationship with *Stenopareia* Holm 1886. But the hypostome and pygidium are markedly different. In the type species of *Stenopareia*, *S. linnarssoni* (Holm 1882) from the Boda Limestone (Middle Ashgill) of the Siljan district, Sweden, the hypostome is short (sag.) and subpentagonal, and the pygidium has strongly truncated antero-lateral angles and a pygidial doublure with a sharply pointed, forwardly directed projection on the mid-line (Holm 1886, Warburg 1925).

Illaeus (Parillaenus)? sp. A

Plate 54, fig. 21

Material. One specimen (SUP 29935) from shales of the Malongulli Formation near Mirrabooka homestead, north of Cheeseman's Creek.

Comparative description. This specimen is somewhat flattened by compression and poorly preserved, but does show a relatively narrower axis at anterior margin of pygidium, and apparently a somewhat broader doublure.

Family HARPIDAE Hawle and Corda 1847
Harpid gen. et sp. ind.

Plate 55, figs. 20-21

Material. Numerous silicified fragments of fringe from upper part of Cliefden Caves Limestone and Ordovician limestone at Billabong Creek. One diagnostic specimen (SUP 29949) from Billabong Creek shows prolongation of fringe and girder.

Description. On lower lamella of fringe, raised girder extends obliquely in to gently curving internal rim of prolongation behind postero-lateral corner of cheek. On upper lamella, narrow, slightly irregular band corresponds to girder beneath, lying between pitted areas of genal roll prolongation and brim prolongation respectively. Genal roll prolongation steeply sloping; brim prolongation concave, becoming flatter posteriorly, with gentle outward slope. Prominent gently curving, convex external rim with adjacent row of coarse pits; pronounced ridge on upper lamella and corresponding weaker 'pseudogirder' on lower lamella inside row of coarse pits; toward tip of prolongation, ridge dies out. External rim has trace of marginal suture dividing it into two; marginal band relatively broad, slightly concave above and below fine median ridge with trace of suture. Numerous, irregular pits covering surface of brim prolongation, with slightly larger pits adjacent to outer ridge, girder and preserved fragment of genal roll prolongation. Approximately eleven rows of pits between girder and external rim. Some fringe fragments show typical harpid feature of fine radiating, somewhat anastomosing ridges across row of pits.

Remarks. Judging from the number of silicified fragments, this harpid species is fairly abundant in the limestones. It probably represents a new Australian genus, bearing resemblances to *Selenoharpes* Whittington (1950b) in having a girder which intersects the internal rim, but differing fundamentally in showing a ridge and

corresponding 'pseudogirder' immediately inside the first row of large pits at the external margin, and narrower prolongations with relatively coarser and fewer rows of pits. A Lower Ordovician harpid has been recorded from Waratah Bay, Victoria (Singleton, in Lindner 1953), and, more recently, Whittington and Hughes (1972) have listed a harpid from the Gordon Limestone of Tasmania.

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LOWER CARBONIFEROUS CONODONT FAUNAS FROM THE EASTERN MENDIPS, ENGLAND

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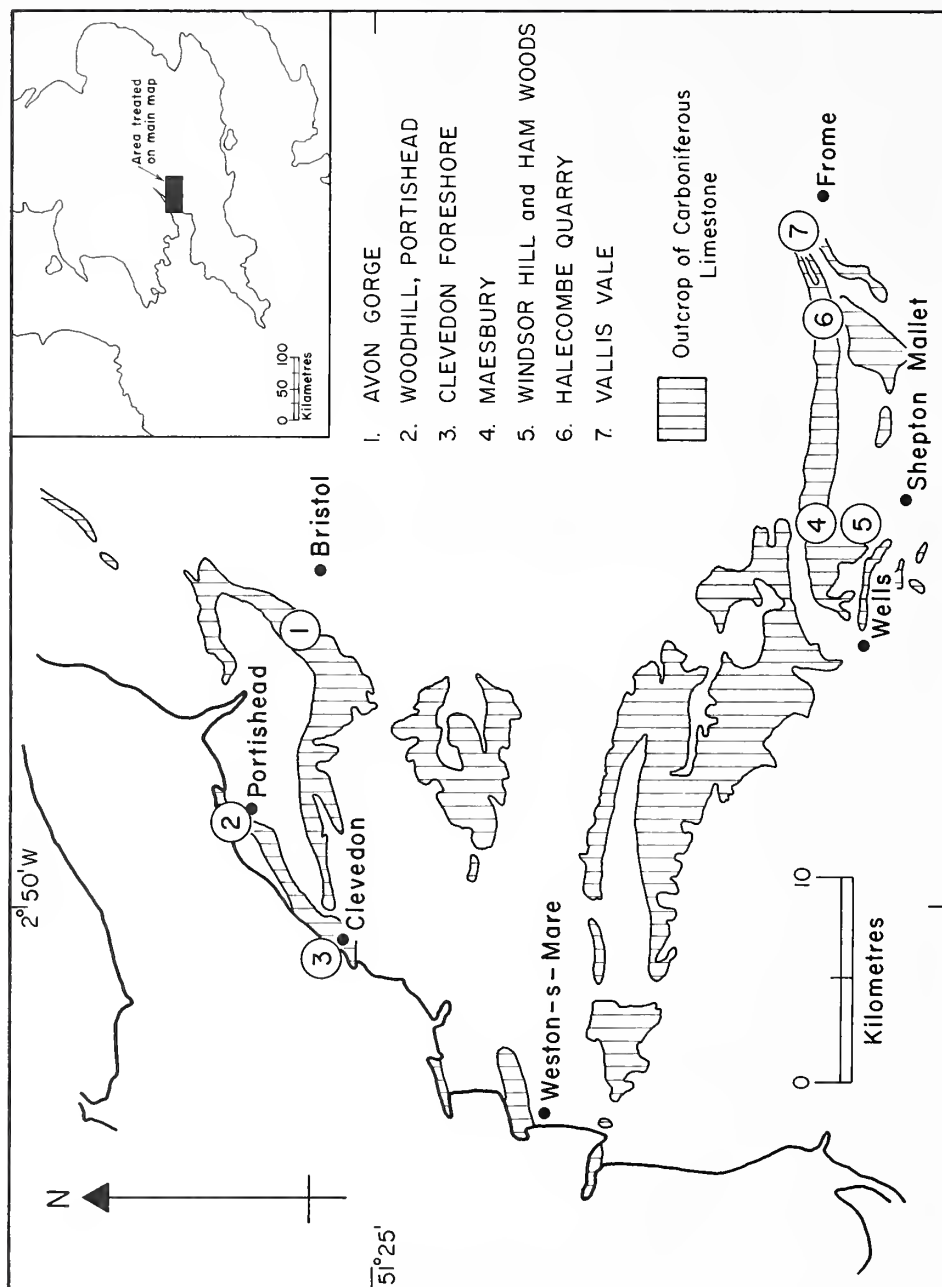
ABSTRACT. In the Mendip Hills, the lower part of the Carboniferous Limestone succession (the Lower Limestone Shale and Black Rock Groups) extends to greater thickness than is found in the Avon Gorge at Bristol. Conodont faunas from this range of the Mendip succession are described here. A distinctive lag-type deposit occurs low in the Lower Limestone Shale Group. Faunas below this lag (with *Patrognathus*, *Pseudopolygnathus dentilineatus*, *Polygnathus symmetricus*) cannot yet be dated precisely. Above, faunas with *Siphonodella*, *Elictognathus*, and *Gnathodus* correlate with those known from the late Kinderhookian of the U.S.A. and probably represent the range of the upper *Siphonodella crenulata*-Zone of Germany. Higher, in the middle part of the Black Rock Group, faunas typical of the German *anchoralis*-Zone appear. Particular interest attaches to the occurrence of *Scaliognathus anchoralis*, *Dolymae bouckaerti*, *Pelekysgnathus bultyncki*, and related forms. These compare closely with faunas recently described from Tn 3c in Belgium. None of the *anchoralis*-Zone species are known from the Avon Gorge succession, which is considered to be incomplete.

THE Carboniferous Limestone of the Bristol area provided the evidence on which Vaughan (1905) based his scheme of coral-brachiopod zones. More recently Kellaway and Welch (1955) have erected a series of lithological units for the Carboniferous Limestone of this area, intended to supersede Vaughan's zones. Neither of these schemes enables correlation to be made on anything more than a local scale. In an attempt to correlate on an international scale, Rhodes, Austin, and Druce (1969) studied the conodont faunas of the Avon Gorge section. However, these authors failed to recover certain important species of conodont, in particular the indices of the *anchoralis*-Zone (Bischoff 1957; Voges 1959, 1960).

Workers using both Vaughan's (1905) zones (e.g. Welch 1932) and the lithological units of Kellaway and Welch (1955) have noted that the strata near the top of the Black Rock Group (Z to C₁) thicken southwards from Bristol into the Mendips (see Kellaway and Welch 1955, pl. 1). It was decided to sample the Lower Limestone Shale and Black Rock Groups in the eastern Mendips to test the possibility that since the succession is thicker there, it might also be more complete, and might therefore produce conodont faunas which are not available in the Avon Gorge.

The sedimentary petrology of the sections sampled for conodonts has been studied in detail, and in addition a brief study has been made of the nature of equivalent levels in the Avon Gorge. The results of these investigations are considered elsewhere (Butler 1972). The sections were divided into sedimentological units, a brief description of each being given in text-figs. 3 to 10, along with details of sampling localities and sample numbers.

In the eastern Mendips the best section in the Lower Limestone Shale Group is that seen in the disused railway cutting at Maesbury (ST 606 475). Here the upper two-thirds of the Group are exposed, together with the transition to the overlying Black Rock Group (Green and Welch 1965). The lower and middle parts of the



TEXT-FIG. 1. Locality map, showing outcrop of the Carboniferous Limestone in the Bristol-Mendip area.

Black Rock Group are seen in disused quarries at Windsor Hill and Ham Woods (ST 615 452) and the middle and upper parts of this group are well exposed in a working quarry at Halecombe (ST 702 475). These sections were sampled systematically for conodonts, 2-kg samples being taken at 3-metre intervals. In addition a number of samples were taken from the middle and upper parts of the Black Rock Group in Vallis Vale (ST 755 490). This section is likely to provide a more permanent record than Halecombe Quarry, which is being actively worked. Isolated samples were also taken from Lower Limestone Shale Group exposures at Portishead (ST 465 775), Clevedon (ST 402 718), and Asham (ST 717 463) and from the Palate Bed in the Avon Gorge (ST 555 746). Faunal lists for these samples are given in an appendix, and the forms recovered are not treated systematically.

Conodont occurrence charts are given in text-figs. 3 to 10. 167 samples were processed and yielded 5324 identifiable specimens. 2491 of these are 'bar' forms. Yields per sample averaged 36 specimens in the Lower Limestone Shale Group and the lower and middle parts of the Black Rock Group. Certain samples gave relatively high yields, over 500 in one case (HW 18). Yields were especially poor in the upper part of the Black Rock Group (unit br 4), only three samples producing conodonts, and in this part of the succession samples were processed from 6-metre intervals only. Samples whose number bears a suffix 'a' come, in each case, from a level $1\frac{1}{2}$ metres above the preceding sample (e.g. HW 18a came from $1\frac{1}{2}$ metres above HW18). Duplicate samples were processed in a number of cases. None showed any marked differences from what was found in the first sample. Acetate peels were made of all rocks sampled for conodonts. The peels, bearing sample numbers, are stored in the Geology Museum, University of Bristol. There is no clear evidence of any link between conodont abundances and particular lithologies.

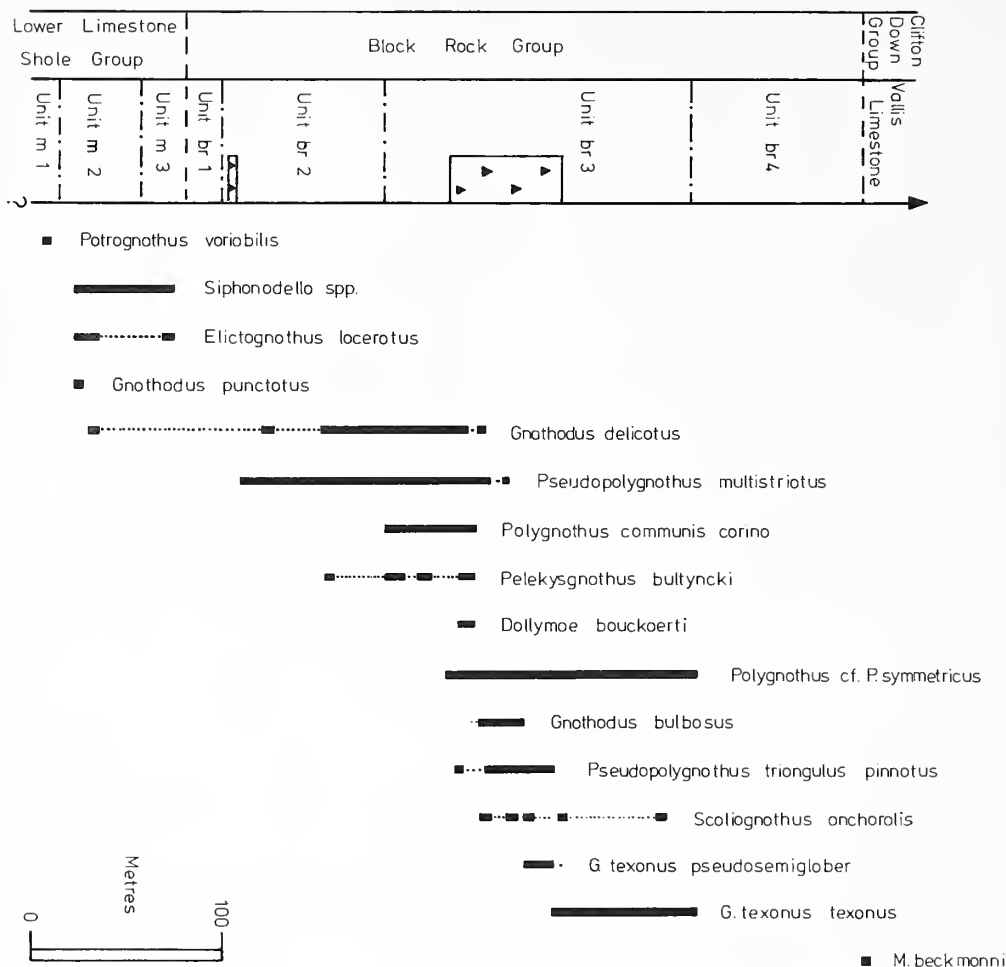
Samples were digested in 10% acetic acid and residues collected by sieving to 125-mesh sieve. Heavy liquid separation was carried out on the dried residues, using the methods described by Collinson (1963).

CONODONT OCCURRENCES IN THE EASTERN MENDIPS

Details of the occurrences of conodonts discussed here are available in text-figs. 3-10.

The Lower Limestone Shale Group. Conodont faunas recovered from the lowest part of the Lower Limestone Shale Group at Maesbury include *Polygnathus symmetricus* Branson and *Pseudopolygnathus dentilineatus* Branson. In addition, two specimens of *Patrognathus variabilis* Rhodes, Austin, and Druce were recovered from sample Ma 4.

At the base of unit m 2 coarse limestones with phosphatic nodules occur, forming a lag-type deposit, and an abrupt change in fauna takes place. The genera *Siphonodella*, *Elictognathus*, and *Gnathodus* first appear here (in sample Ma 7). The interval Ma 7 to Ma 19a is characterized by the presence of *Siphonodella obsoleta* Hass, *S. isosticha* (Cooper), *S. cf. S. isosticha* (Cooper), *S. cooperi* Hass, and *S. cf. crenulata* (Cooper). Two specimens of *Gnathodus punctatus* (Cooper) were recovered from sample Ma 7 and two specimens of *G. delicatus* Branson and Mehl were found in sample Ma 9. *Polygnathus inornatus* Branson ranges from Ma 7 to Ma 19a, and



TEXT-FIG. 2. Chart to show the ranges of selected conodont species in the Carboniferous Limestone of the eastern Mendips. See text-figs. 3 to 10 for full information. Firm lines represent proven ranges, broken lines are extrapolations.

Elictognathus laceratus (Branson and Mehl) ranges from Ma 7 to Ma 19 but appears in only three samples.

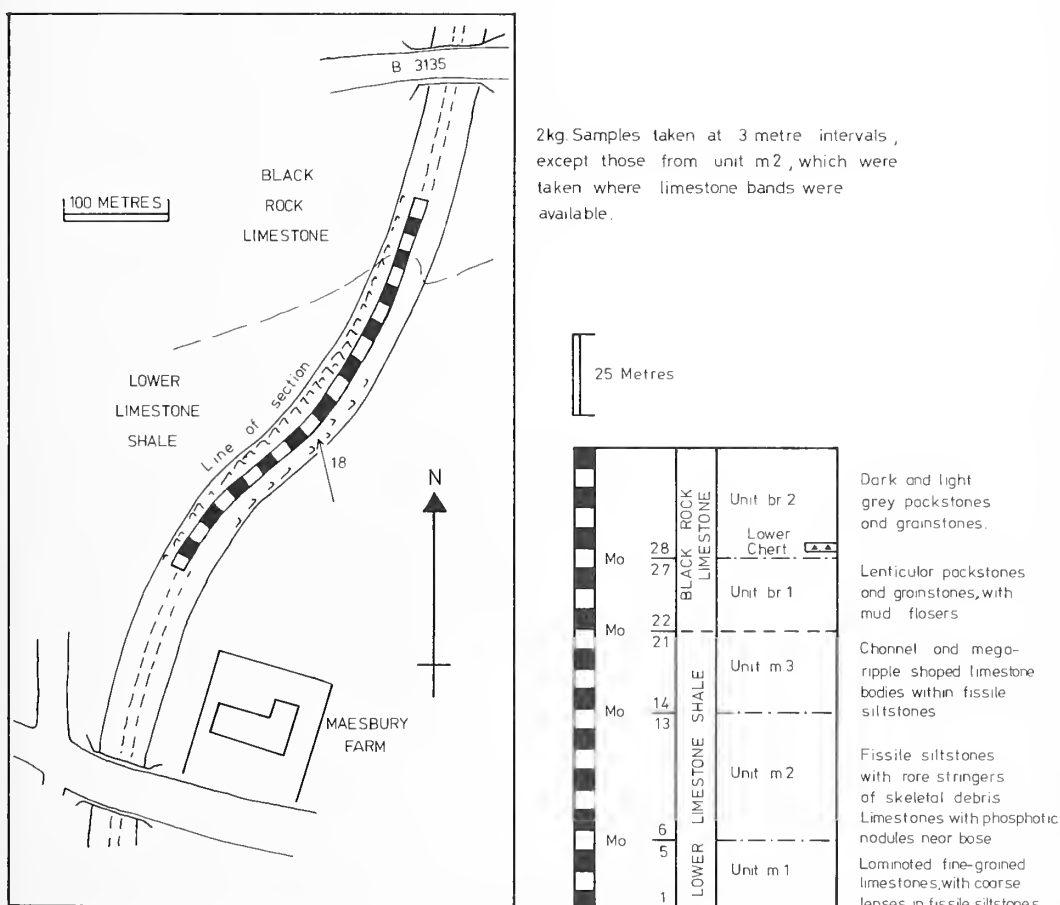
Sample Ma 20 marks another abrupt change in the conodont faunas, siphonodellids and associated forms disappearing. The fauna in this uppermost part of the Lower Limestone Shale Group includes *Polygnathus communis communis* Branson and Mehl and *Spathognathodus stabilis* (Branson and Mehl), and also includes poorly preserved specimens of *Spathognathodus aculeatus* (Branson and Mehl).

The Black Rock Group. The faunal assemblage seen in the uppermost part of the Lower Limestone Shale Group continues into the Black Rock Group. However, *Pseudopolygnathus multistriatus* Mehl and Thomas appears in sample WH 5, immediately above a minor chert development at the base of unit br 2, and *Sp. aculeatus*

is no longer seen. *Gnathodus delicatus* Branson and Mehl occurs in sample WH 12, but is not seen again until sample HW 2, where it becomes abundant. *Pseudopolygnathus primus* Branson and Mehl occurs in unit br 2. *Pelekysgnathus bultyncki* (Groessens) first appears in sample HW 3 and occurs along with *Polygnathus communis carina* Hass in samples HW 8 and HQ 1.

In the lower part of the Main Chert (unit br 3) at Ham Woods Quarry (samples HW 18 and HW 18a) there is an occurrence of abundant representatives of *Dolymae bouckaerti* Groessens. This genus was not recovered from any other section. Associated with *D. bouckaerti* in these samples are *Pe. bultyncki*, *Ps. multistriatus*, and *Gnathodus delicatus*. In addition, a single specimen referable to *Doliognathus* sp. was recovered from HW 18.

Near the upper limit of the range of *P. communis carina*, *Gnathodus bulbosus* Thompson first appears (samples HW 20, HQ 12, and Va 2). *G. bulbosus* rapidly takes over from *G. delicatus* as the dominant gnathodid. At this level in both Ham Woods and Halecombe Quarries specimens referred to *Bactrognathus* cf. *B.*



TEXT-FIG. 3. Location of sampled section in Maesbury railway cutting (ST 606 475) and notes on lithologies.

MAESBURY	Samples	Ma	1	1a	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	
Pseudopolygnathus dentilineatus			1	6																												
Polygnathus symmetricus			3	15	4	25	21																									
Patrognathus variabilis						2																										
Spathognathodus crassidentatus						1	1																									
P. communis communis						4			2	2		11		1					2			19	1			1						
Elictagathus laceratus										2		3										5										
Siphonadella isosticha										7		5	1	1									4	3								
S. cf. S. isosticha										1									1			3										
S. absaleta										1			1						1	1		11										
Polygnathus inornatus										68	3	40	3	10					3	11		11	2									
Spathognathodus stabilis										2												5			4		1					
Gnathodus punctatus										2																						
G. delicatus												3																				
Siphonadella cf. crenulata														2																		
Spathognathodus aculeatus																			1					3								
Siphonadella cooperi																						2	1									
Polygnathus sp.																						1										
Gnathodus sp.indet.												2																				
Siphonadella sp.indet.										8	2	3	3	6					1	3			21	2								
Spathognathodus sp.indet.							1			2		3	3	2	1				2			1	6	2	1	1	1	8				
BARS				6	4	9	6	6	39	8	28	7	14	5					5	5			85	7		13	2	30		1	2	1
TOTAL			-	4	27	8	42	28	8	134	13	98	18	36	6	-	-		13	23	-	1	173	18	4	18	3	40	-	1	2	1

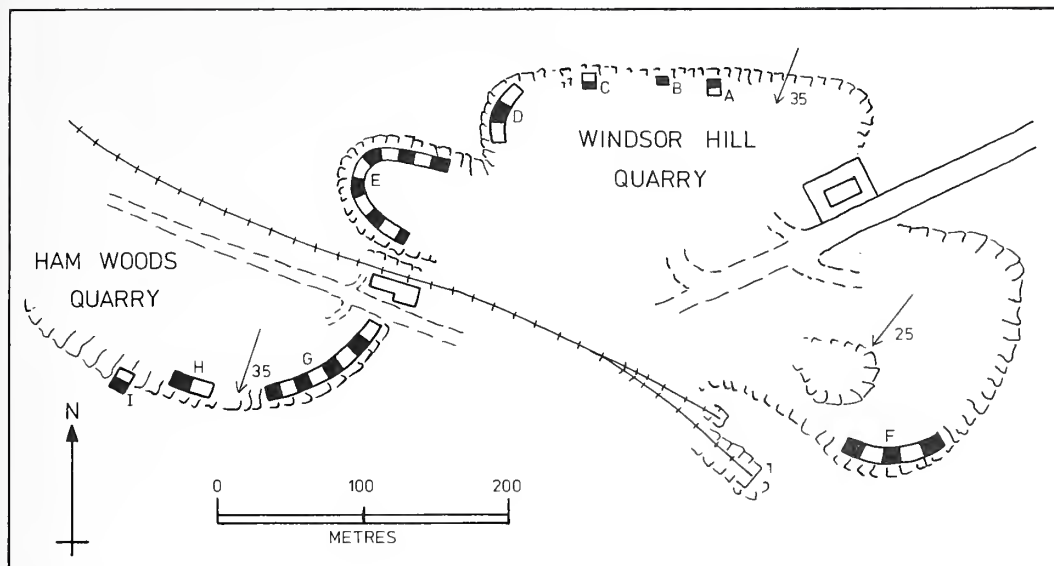
TEXT-FIG. 4. Chart to show conodont occurrences in samples from Maesbury railway cutting. (Sample prefix Ma.)

distortus Branson and Mehl occur (samples HW 21, 22, and HQ 14a). At Halecombe these are followed by the first occurrence of *Scaliognathus anchoralis* Branson and Mehl (in sample HQ 15). *Pseudopolygnathus triangulus pinnatus* Voges first appears in samples HW 23, HQ 16, and Va 1, and is an important constituent of the fauna in the middle part of unit br 3. *Pseudopolygnathus triangulus triangulus* Voges is present in samples throughout the range of *Ps. triangulus pinnatus*, although specimens possibly attributable to this subspecies also occur in samples HW 14 and HQ 14a.

Ps. multistriatus dies out near the beginning of the range of *Ps. triangulus pinnatus* (sample HQ 19). Near the top of the range of *Ps. multistriatus*, *Polygnathus nodomarginatus* Branson makes a brief appearance. *Polygnathus* cf. *P. symmetricus* Branson first occurs here and ranges up into the top of unit br 3, where conodonts become rare.

In the middle part of unit br 3 both at Halecombe and in Vallis Vale (samples HQ 22 and Va 9) *G. bulbosus* disappears and *Gnathodus texanus pseudosemiglaber* Thompson and Fellows first appears. Towards the top of unit br 3 (samples HQ 32 and Va 13) *Gnathodus texanus texanus* Roundy first appears and *Ps. triangulus pinnatus* disappears. *Scaliognathus anchoralis* occurs in sample HQ 33, but is not seen again until HQ 46, where it is present together with *Hindeodella segaformis* Bischoff. A single specimen of *Pelekysgnathus* sp. A Voges was recovered from sample Va 13, and additional specimens of *H. segaformis* were also found in this sample.

Associated with *G. texanus texanus* and *P. cf. P. symmetricus* in the upper part of unit br 3 are common apatognathids and *Spathognathodus scitulus* (Hinde).

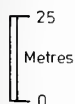


I	HW	23 22	BLACK ROCK LIMESTONE	<div><div>▲▲</div><div>Main Chert</div><div>▲▲</div></div>
H	HW	21 18		
		17		
G	HW	1		
F	WH	21 19		
		18		
E	WH	10		
D	WH	9 7		
C	WH	6 5		
B	WH	4		
A	WH	3 1		<div><div>▲▲</div><div>Lower Chert</div><div>▲▲</div></div>
				Unit br 3
				Unit br 2
				Unit br 1

Dark grey, muddy crinoidal packstones and wackestones

Dark and light grey packstones and grainstones.
Cross-bedding occasionally visible

Lenticular limestone bodies, with mud flasers.



2 kg. Samples taken at intervals of approximately 3 Metres.

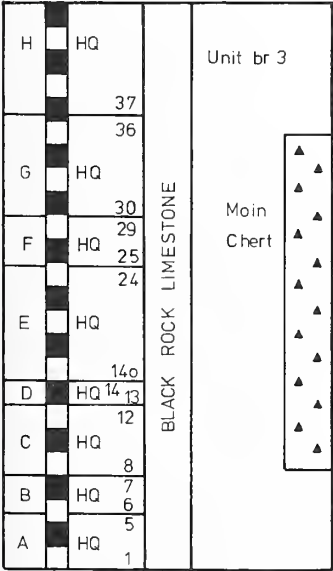
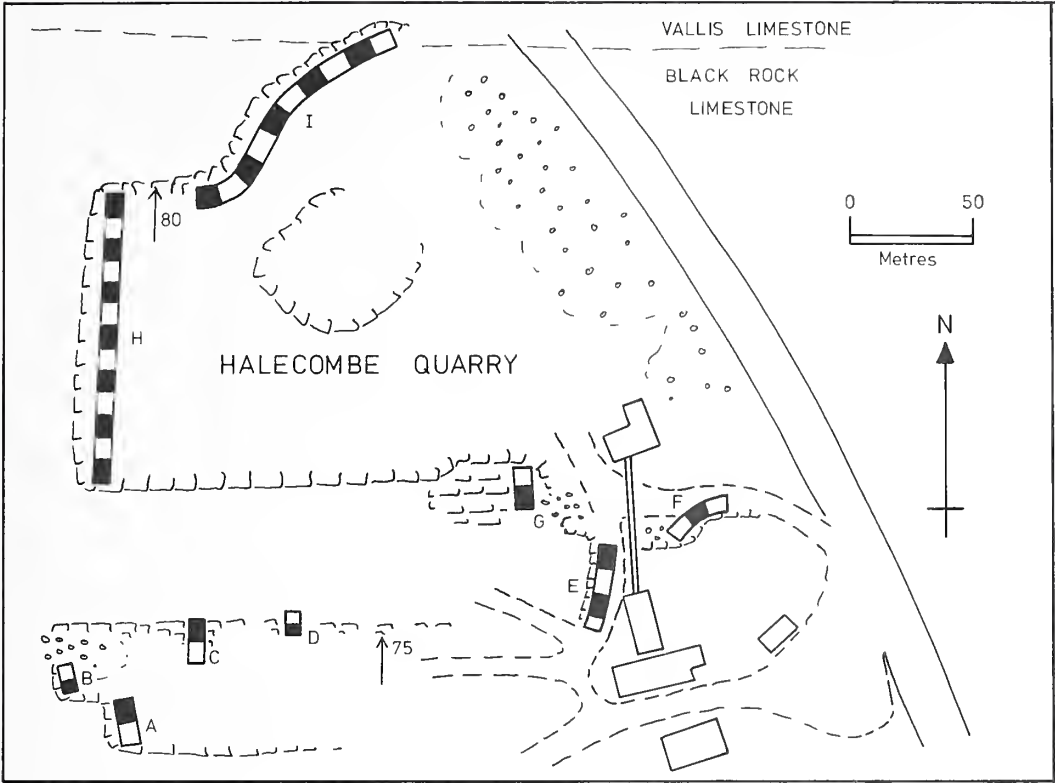
TEXT-FIG. 5. Location of sampled sections in Windsor Hill and Ham Woods Quarries (ST 615 452) and notes on lithologies.

WINDSOR HILL Qy. Samples WH	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Palygnathus communis communis				1	5			2	1	6		7	1				2	3	4	2	
Pseudopalygnathus multistriatus					1			2	2	1	2	4				1	5	13	1	1	
Spathagnathodus crassidentatus					1			1											1		1
Sp.stabilis												1					1	1			
Ps.primus												1					1	4			
Gnathodus delicatus												1									
Spathagnathodus sp.indet.		1					1		1	2	2		2					3	3		
BARS	3	5		3	25	1	5	4	4	10	1	24	3		1	11	17	20	7	3	2
TOTAL	3	6	-	4	32	2	5	10	9	19	3	40	4	-	1	12	26	44	16	6	3

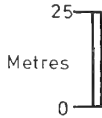
TEXT-FIG. 6. Chart to show conodont occurrences in samples from Windsor Hill Quarry. (Sample prefix WH.)

HAM WOODS Qy. Samples HW	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	18a	19	20	21	22	23
Spathagnathodus crassidentatus	1	2				1		3		6		1				1								2
Sp. stabilis		2	2			1		1		3							2	18	5	1	10			
Pseudopalygnathus multistriatus		4	3			6		2		2	1							5			8			
Ps. postinodasus		1																						
Gnathodus delicatus		2				3				17		8	3	7	9		6	6	116	31	10		1	5
Pelekysgnathus bultyncki			1					2										12						
Palygnathus communis communis		10	6	1	1	20				2		8	1	3	4		4	20	45	9		1	4	
P.communis carina								1		2		5	6	8	11		12	7	68	1				
Gnathodus cf. delicatus										2				1	1	1								
Ps.triangularis cf triangularis															1									
Palygnathus cf. P. symmetricus																	2				16	3		6
Dallymae bauckaerti																		57	6					
Daliagnathus sp.																		1						
P.nadamarginatus																			1					
Gnathodus n.sp.B,THOMPSON 1967																			1		2			2
G.bulbasus																					19	11	28	33
Bactragnathus cf. B.distortus																						1	1	
Ps. triangularis triangularis																								1
Ps. triangularis pinnatus																								23
Dallymae sp.																					1			
Gnathodus sp.indet.																			11			6	2	1
Pseudopalygnathus sp.indet.									1								3							
Spathagnathodus sp.indet.		3	4			6		9	2	4		3						32	12	5	19	1		
BARS	4	60	27		3	34		20	1	19		15	2	1	13	20	11	154	31	17	28	24	24	72
TOTAL	5	84	43	1	4	71	-	38	4	57	1	40	16	27	38	43	51	519	97	33	104	51	55	145

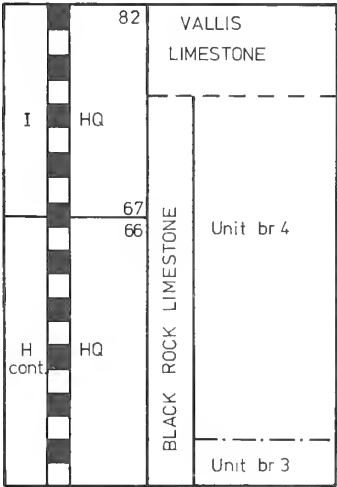
TEXT-FIG. 7. Chart to show conodont occurrences in samples from Ham Woods Quarry. (Sample prefix HW.)



Dork grey, muddy wockstone with Zoophycos. Few microfossils.



Dork grey crinoidol pockstone and wockstone.



Light grey pelletal groinstone, with micritic introclasts.

Light grey crinoid - foraminifer groinstone.

2 kg. Samples taken at intervals of approximately 3 metres.

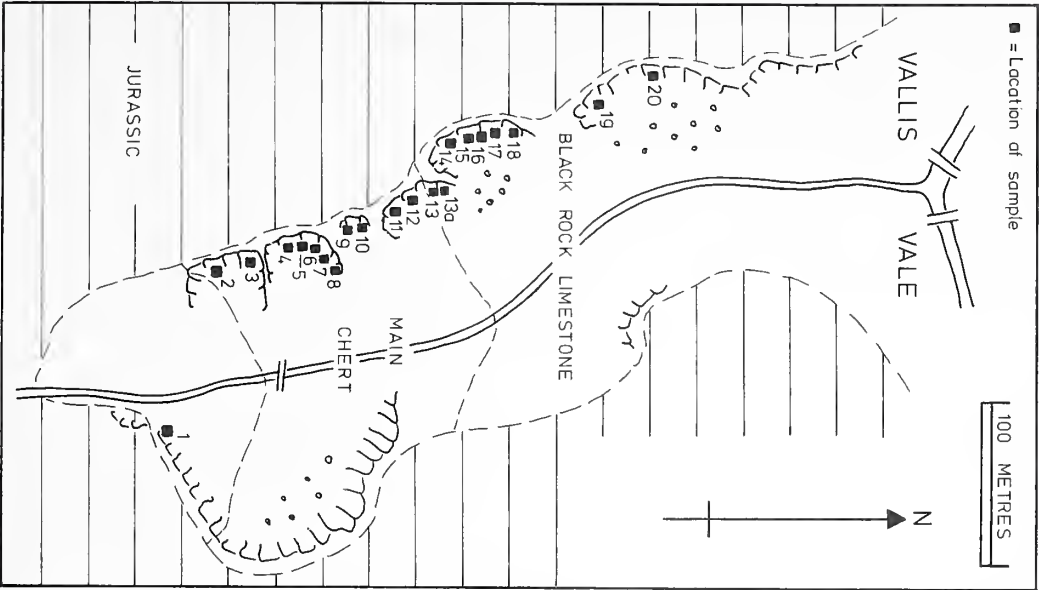
TEXT-FIG. 8. Location of sampled sections in Halecombe Quarry (ST 702 475) and notes on lithologies.

HALECOMBE Qy. Samples HQ	1	2	3	5	6	7	8	9	10	11	12	13	14	14a	15	16	17	18	19	20	21	22	23	24	25
Pelekysgnathus bultyncki	2																								
Pseudapalygnathus multistriatus	2	1														1			1						
Palygnathus communis communis	6				6	4	3	2	9		11			4				1	34		1	86	34	3	6
P.communis carina	6					13	4	1	5																
Gnathadus delicatus	1	1	1		6	6	2	7			1														
G.cf. delicatus						1		1																	
Spathagnathadus stabilis	1	3		1				2	1	7								1		1	11		1	2	
Sp. crassidentatus		1						1	4									5			1				
Palygnathus cf. P. symmetricus								1	2	3				1	1		8	3	11		1	6	1		
Gnathadus bulbosus										1				18	124	11	26	55	25						
Gnathadus n.sp.B, THOMPSON 1967										1					1				2		1	5			
Bactragnathus cf. B. distartus														1											
Ps. triangulus cf. triangulus														1											
Scaliagnathus anchoralis															3			1				1			
Ps. triangulus pinnatus																1	4	5				11	5		
Palygnathus nadamarginatus															1										
Ps. triangulus triangulus																	1								
G. texanus pseudasemiglaber																						5	1		
Gnathadus sp. indet.	1					1		1		5			10	17				3					1		
Pseudapalygnathus sp. indet.	1	1																1	1		1				
Spathagnathadus sp. indet.		1		1				1	5	1	19										1	22		2	2
BARS	29	6	5	2	5	7	4	2	33	9	31		6	32	44	5	21	116	25	1	5	90	31	4	20
TOTAL	49	7	12	3	13	30	19	10	65	13	78	1	6	67	191	18	60	186	103	2	10	239	73	10	30

HALECOMBE Qy. Samples HQ	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
<i>G. texanus pseudasemiglaber</i>	1		4	2																					
<i>Ps. triangularis pinnatus</i>			1			1																			
<i>Ps. triangularis triangularis</i>			3				1																		
<i>Spathagnathadus stabilis</i>	1		3			1				5	2	1		1			2	1	1						
<i>Sp. crassidentatus</i>			1							1				1											
<i>G. texanus texanus</i>						1				5		3				1			1		1		1		
<i>Palygnathus cf. P. symmetricus</i>			2	3			2	3		8	9		2	2	1		22	5		2	1		2		
<i>Scaliagnathus anchoralis</i>								1														1			
<i>Hindeadella segafarmis</i>																						1			
<i>Spathagnathadus scitulus</i>																	1					2	4		
<i>apatagnathids</i>																	5	1		1	2	5	1		
<i>Gnathadus sp. indet.</i>				2																					
<i>Spathagnathadus sp. indet.</i>						1		1				3			1		4								
BARS	2	7	36	24	3	17		4	3	30	6	8		14	2	2	77	8	1	3	17	6	3		
TOTAL	4	7	50	31	4	19	5	8	3	49	20	12	2	19	3	3	109	15	3	6	25	15	7	-	-

HALECOMBE Qy. Samples HQ	52	54	56	58	60	62	64	66	68	70	72	74	75	76	78	80	82								
<i>Mestagnathus beckmanni</i>														2											
<i>Spathagnathadus sp. indet.</i>									1																
BARS													1	3											
TOTAL	-	-	-	-	-	-	-	-	1	-	-	-	1	5	-	-	-								

TEXT-FIG. 9. Chart to show conodont occurrences in samples from Halecombe Quarry. (Sample prefix HQ.)



VALLIS VALE	Samples Va	1	2	3	4	5	6	7	8	9	10	11	12	13	13a	14	15	16	17	18	19	20
Polygnathus communis communis		7	6																			
P. communis carina		12									6	10										
Gnathodus delicatus		4	10																			
G. cf. delicatus		1																				
Spathognathodus stabilis		2																				
Sp. crassidentatus		3	2																			
Rs. triangulus pinnatus		1				3	1			1						6	2					
Polygnathus nodomarginatus		1																				
Gnathodus bulbosus		27	1		36	2																
Pseudopolygnathus multistriatus					3																	
Gnathodus n.sp.B. THOMPSON 1967					1																	
Bactrognathus sp					1																	
Polygnathus cf. P. symmetricus									1	1		1		19	1	7	11	8	14	25		
G. texanus pseudosemiglobus										8	3	2	9	26	1							
G. texanus texanus													2	2	3				9	2		
Pelekygnathus sp.A. VOGES 1959														1								
Hindeodella seggiformis														2								
opatognathids																	1	2	9	4		
Spathognathodus scitulus																		2	1	1		
Gnathodus sp. indet.		6			2	1																
Pseudopolygnathus sp. indet.		3									3											
Spathognathodus sp. indet.											5	3	2	9	4				4	9	3	
BARS		2	23	4		53	8	4	11	6	18	6	82	284	21	5	6	21	23	90		2
TOTAL		32	78	5	-	99	12	4	12	30	35	13	117	370	28	17	19	39	67	133	-	2

2kg. Samples. No regular sampling interval.

TEXT-FIG. 10. Location of samples from Vallis Vale (ST 755 490) and chart of conodont occurrences. (Sample prefix Va.)

Faunas from unit br 4 are particularly poor, only three samples producing any conodonts at all, and samples were processed from 6-metre intervals after HQ 50 (see text-fig. 11). Sample HQ 76 (at the base of the Vallis Limestone) produced two specimens of *Mestognathus beckmanni* Bischoff.

COMPARISONS AND CORRELATIONS WITH NORTH AMERICA AND EUROPE

Conodonts recovered during the course of this study are all referable to the Lower Carboniferous (Dinantian). The first definitive studies of conodonts of this age were carried out in Germany by Bischoff (1957) and Voges (1959). These authors erected a series of conodont zones for this part of the Carboniferous. In recent years it has become clear that although the German sections offer good information on the lowest Carboniferous and also on the *anchoralis*-Zone and higher levels, there is a paucity of information on the intermediate parts of the succession. The reason for this is that the rocks which include the *Siphonodella crenulata*-Zone of Voges (1959), that is the Liegende Alaunschiefer, have not produced good conodont faunas.

In Belgium, conodonts from that part of the succession characterized by the genus *Siphonodella* are still little known, although here again both lower and higher levels are better documented (for example, Conil *et al.* 1964; Conil *et al.* 1969; Austin *et al.* 1970). Groessens (1971) has recently described faunas of *anchoralis*-Zone age from Belgium. These latter faunas compare closely with some recovered during the present study.

In North America Collinson *et al.* (1962) erected a series of conodont zones for the Mississippian, based on evidence from the upper Mississippi Valley. These zones have been recently revised by Collinson *et al.* (1971). Recent work by Thompson (1967) and Thompson and Fellows (1970) has indicated that the upper Mississippi Valley sections are incomplete (see Collinson *et al.* 1971, fig. 2). It is with their more complete sequence of Mississippian rocks from south-western Missouri and Arkansas that the Mendip faunas best compare.

Lowest part of the Lower Limestone Shale Group at Maesbury. The conodonts from this part of the succession do not readily provide for detailed comparison with information from either German or North American sections. Voges (1959) found that *Pseudopolygnathus dentilineatus* has a range from the uppermost Devonian to the base of the *Siphonodella crenulata*-Zone, and possibly into that zone. This species has been reported from North America by several authors (for example Branson 1934; Collinson *et al.* 1962; Klapper 1966; Canis 1968) and has a range from basal Carboniferous, and possibly Upper Devonian, into the *Siphonodella quadruplicata*-*S. crenulata* Zone of Collinson *et al.* (1962). Thompson and Fellows (1970) reported *Ps. dentilineatus* ranging up into their *Gnathodus delicatus*-*Siphonodella cooperi cooperi* Zone. The genus *Patrognathus* has been recorded from the lowest Carboniferous of Belgium by Austin *et al.* (1970), but from an upper part of the Kinderhookian of North America by Klapper (1971). Klapper (1971) recovered the genus from within a range of stratigraphy which also yielded *Siphonodella isosticha* and *S. cooperi*, although siphonodellids and patrognathids were found together in only one sample.

It seems clear that the conodonts recovered from this part of the stratigraphy at Maesbury do not, at present, offer any possibility of precise correlation with other areas.

Faunas with Siphonodella. Siphonodellids first appear at Maesbury in beds which include phosphatic nodules and which are interpreted as lag concentrates. The species of *Siphonodella* present are advanced, in terms of the North American progression of forms (see Collinson *et al.* 1971), and their association with *Gnathodus punctatus* enables comparison to be made with what Thompson and Fellows (1970) regard as the uppermost Kinderhookian faunas. However, the ranges of *Gnathodus punctatus*, *G. delicatus*, *Siphonodella isosticha*, *S. obsoleta*, and *Elictognathus laceratus* are not shown to coincide on table 1 of Thompson and Fellows (1970). Their zonal scheme is not consistent with their own recorded results. An examination of the stratigraphic logs and conodont occurrence charts of these authors reveals that in the Baird Mountain Quarry section (Thompson and Fellows 1970, p. 149) several samples included this association of forms. Their samples 6 to 8 included *Gnathodus punctatus*, *G. delicatus*, *Siphonodella cooperi hassi* (= *S. isosticha*, *fide* Klapper, see systematic part), and *Elictognathus laceratus*, even though these forms do not have corresponding ranges in their table 1. Since these Baird Mountain Quarry samples are placed within the *Siphonodella cooperi hassi*-*Gnathodus punctatus* Zone, it would seem reasonable to correlate samples Ma 7 to Ma 19 with a part of this zone.

This zone of Thompson and Fellows (1970) represents a part of the stratigraphy which is not seen in the upper Mississippi Valley (Collinson *et al.* 1971, fig. 2). The uppermost Kinderhookian of the upper Mississippi Valley was correlated with the Belgian Tn 2b by Sando *et al.* (1969) on the basis of foraminiferids. Groessens (1971) gives an upper limit to the range of *Siphonodella* at the top of Tn 2c in Belgium. In Germany the range of the genus extends into the *anchoralis*-Zone (Voges 1959; Meischner 1971), and a similar situation has been noted in south-west England by Matthews (1969*a, b*). Matthews *et al.* (1972) report the occurrence of siphonodellids in a fauna including *Gnathodus punctatus*, *Dollymae hassi*, and *Polygnathus communis carina* from Devon.

A tentative correlation is here suggested between samples Ma 7 to Ma 19 and some part of the interval Tn 2b to Tn 2c in Belgium.

Uppermost Lower Limestone Shale Group and the lower part of the Black Rock Group. The lowest part of this interval is characterized by the dominance of *Pseudopolygnathus multistriatus* and *Polygnathus communis communis*. This association of forms conforms to faunas lying immediately above the range of *Siphonodella* in North America (for example Rexroad and Scott 1964) with the exception that there they include abundant gnathodids. There appears to be a scarcity of gnathodids throughout the Mendip sections at this time, these forms appearing in only two samples at Maesbury. Two possibilities emerge here: first, the lack of gnathodids at this level in the eastern Mendips could be due to some facies control; or secondly, this association of forms could be present in North America also, but has not been recognized since the successions there are thinner at this level. Further study of this problem is necessary. Whatever the cause of this absence, gnathodids reappear in the middle part of the Black Rock Group.

The first occurrence of *Polygnathus communis carina* is taken by Thompson and Fellows (1970) to define the lower limit of their *Gnathodus semiglaber*-*P. communis carina* Zone. This form first appears in sample HW 8 and is present in sample HQ 1. The first appearance of *Pseudopolygnathus multistriatus* is taken by Thompson and Fellows (1970) to mark the base of the overlying *Bactrognathus*-*Ps. multistriatus* Zone. This form appears earlier than *P. communis carina* in the Mendip successions (in sample WH 5). There does not appear to be any distinction to be made in the Mendip succession of conodonts between assemblages characteristic of the *Gnathodus semiglaber*-*P. communis carina* Zone and those of the *Bactrognathus*-*Ps. multistriatus* Zone of Thompson and Fellows (1970). Nor is it clear where the equivalent of the boundary between the *G. semiglaber*-*P. communis carina* Zone and the underlying *G. punctatus*-*Siphonodella cooperi hassi* Zone should be taken in the Mendips.

Pelekysgnathus bultyncki (Groessens) first appears in sample HW 3, but is present with *P. communis carina* in samples HW 8 and HQ 1. Groessens (1971) shows two maxima in the occurrence of *P. communis carina*, one of which coincides with the first appearance of *Pe. bultyncki*. It would seem reasonable to correlate sample HW 8 with a point near the beginning of the second maximum of *P. communis carina*, that is with the base of Tn 3c of Groessens (1971). In Belgium Groessens has shown that a level characterized by abundant *Dolymae bouckaerti* lies at the top of the range of *Pe. bultyncki*. Above this level *Doliognathus latus* makes a brief appearance and the range of *Scaliognathus anchoralis* begins. This progression of forms compares with that recognized in the Mendip successions. It is possible therefore to correlate with a fair degree of certainty between the eastern Mendips and Groessens's Belgian successions at these levels.

Faujas comparable with the German anchoralis-Zone. The *anchoralis*-Zone was established in Germany by Bischoff (1957). Voges (1959, 1960) revised the zone and selected *Scaliognathus anchoralis*, *Hindeodella segaformis*, and *Doliognathus latus* as indices. Although *Scaliognathus anchoralis* was first described from North America by Branson and Mehl (1941), the *anchoralis*-Zone has not been widely recognized there. It is now clear that discontinuities within the Upper Mississippi Valley sections are in part responsible for this.

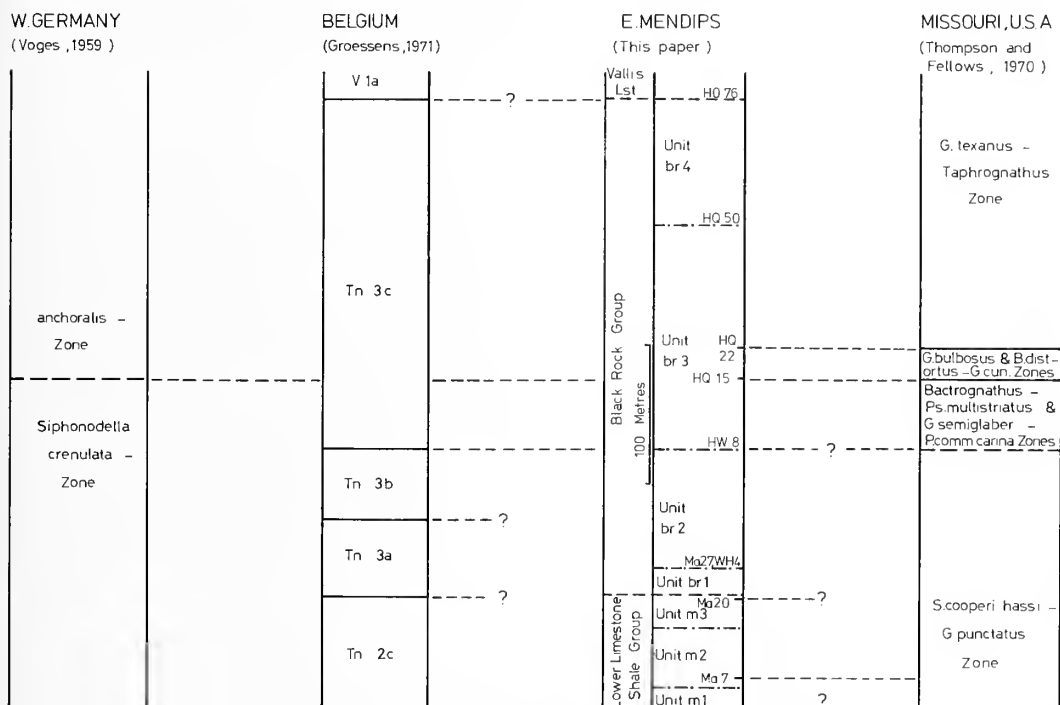
The recognition of a line of development leading to *Scaliognathus anchoralis* suggests that the first occurrence of this form at Halecombe Quarry must be at least as early as any occurrence elsewhere. Correlation is possible with Groessens's (1971) sections and with the base of the *anchoralis*-Zone in Germany.

Again it is necessary to point out some differences in the record of conodont occurrences between the eastern Mendip sections and those of Thompson and Fellows (1970). According to these authors the ranges of *Scaliognathus anchoralis* and *Pseudopolygnathus triangulus pinnatus* do not coincide with that of *Gnathodus bulbosus*. In the eastern Mendips, *Ps. triangulus pinnatus* and/or *Scaliognathus anchoralis* occur together with *G. bulbosus* in certain samples between HQ 15 and HQ 21 and with *G. texanus* subsp. in certain samples within the range HQ 22 to HQ 46. For the reasons given above, it seems unlikely that *Scaliognathus* would appear earlier in Thompson and Fellows's sections than it does in the eastern Mendips. The two first occurrences are therefore tentatively correlated, suggesting an equivalence

between sample HQ 15 and the base of the *Bactrognathus distortus*-*Gnathodus cuneiformis* Zone of Thompson and Fellows (1970).

The sequence of development from *G. bulbosus* to *G. texanus pseudosemiglaber* and *G. texanus texanus*, recognized by Thompson and Fellows (1970, p. 89) can also be seen in the Mendip faunas. The recognition of this sequence enables correlation to be made between sample HQ 22 and the base of the *Gnathodus texanus*-*Taphrognathus* Zone of Thompson and Fellows (1970), although it should be noted that no *Taphrognathus* has been recovered from the eastern Mendips. Below this zone in Thompson and Fellows's scheme lies the *Gnathodus bulbosus* Zone, which must fall within the interval HQ 15 to HQ 22 along with the *B. distortus*-*G. cuneiformis* Zone. As already stated, there seems to be no real distinction in the Mendips between the *G. semiglaber*-*P. communis carina* Zone and the *Bactrognathus*-*Ps. multistriatus* Zone. In addition it does not seem to be possible to separate a *B. distortus*-*G. cuneiformis* Zone from a *G. bulbosus* Zone here. It appears therefore that the four zones suggested by Thompson and Fellows (1970) for this part of the stratigraphy in Missouri and Arkansas resolve themselves into only two distinct divisions in the Mendips.

Groessens (1971) reported *Mestognathus beckmanni* from the uppermost part of Tn 3c and ranging up into the Viséan. Two specimens of *M. beckmanni* were recovered during the present study from a single sample (HQ 76) near the base of the Vallis Limestone. Voges (1959) reported *M. beckmanni* from the *anchoralis*-Zone,



TEXT-FIG. 11. Chart showing suggested correlations between the eastern Mendip composite section and sections in Europe and North America. Eastern Mendip column is drawn to scale, the others are not.

and it is therefore not possible to recognize an equivalent of zones higher than this in the sections studied.

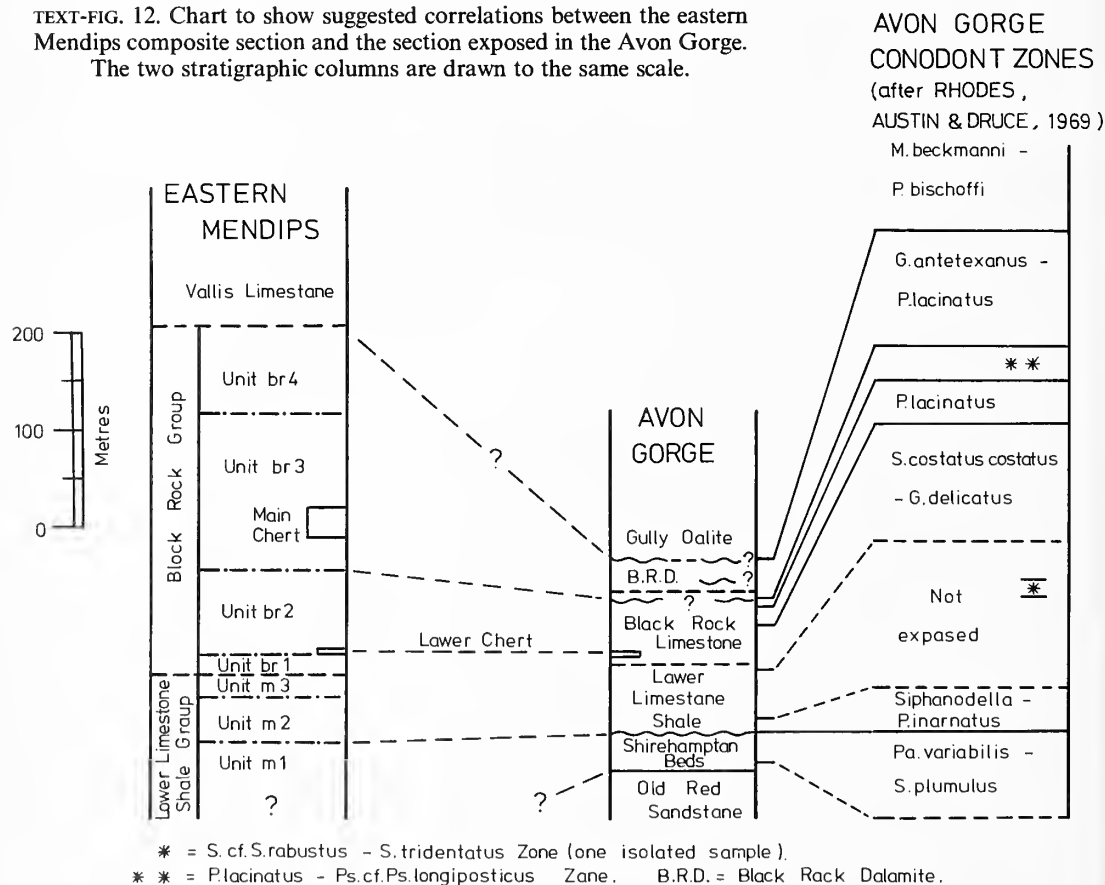
Text-fig. 11 sets out the suggestions made here on correlation with sections in Europe and North America.

COMPARISONS AND CORRELATIONS WITH THE AVON GORGE

Rhodes *et al.* (1969) sampled the Lower Carboniferous succession in the Avon Gorge and compared it with a composite section from the North Crop of the South Wales Coalfield and with scattered sections in northern England and Scotland. They erected a zonal scheme, and suggested that facies-control might explain the absence of certain forms used as zonal indices in Germany and North America. This work has been criticized by Ziegler (1971) on methodological and other grounds. Among other points, Ziegler observes that it is difficult to extract from Rhodes *et al.* (1969) information on the exact occurrences and ranges of species and on the composition of faunas. This being the case, it will be understood that proposals on correlation between the Mendips and the Avon Gorge must be tentative at the present time. The proposals made here are set out in text-fig. 12, and discussed below.

TEXT-FIG. 12. Chart to show suggested correlations between the eastern Mendips composite section and the section exposed in the Avon Gorge.

The two stratigraphic columns are drawn to the same scale.



Faunas from the lowest parts of the Lower Limestone Shale Group (Samples K 1 to K 11 of Rhodes et al.; samples Ma 1 to Ma 6 of this paper). Faunas recovered from this part of the succession by Rhodes *et al.* (1969) include *Patrognathus*, *Pseudopolygnathus vogesi* (= *Ps. dentilineatus*, see systematic part), and also *Clydagnathus* and clydagnathid-like spathognathodids. This association compares in some respects with the Maesbury faunas, where *Patrognathus* was recovered from one sample and *Ps. dentilineatus* occurs in several samples.

It is possible that the absence of the clydagnathid group of conodonts at Maesbury may be explained by restriction of these conodonts to a narrow range of facies. They occur both at Portishead and Clevedon (see Appendix) in facies different from that of the Shirehampton Beds in the Avon Gorge, but it may be worth while to note that in the North Crop, where stromatolitic and oolitic rocks predominate (George 1954), this group of conodonts extends into the Z zone (Black Rock Group) (Rhodes *et al.* 1969).

The Palate Bed in the Avon Gorge (which lies between samples K 11 and K 12 of Rhodes *et al.* 1969) contains a large conodont fauna, including abraded specimens (see Appendix). *Siphonodella duplicata* appears in this bed, but has not been reported from elsewhere in the Bristol district. A discontinuity is present below the Palate Bed in the Avon Gorge. Caliche formation occurred within the underlying Bryozoa Bed, and pebbles of Bryozoa Bed material occur within the Palate Bed. The possibility cannot therefore be ruled out that the lower part of the Maesbury section (unit m 1) might include faunas which have no representation in the discontinuous Avon Gorge stratigraphy.

Faunas with Siphonodella (Samples K 12 and K 17 of Rhodes et al.; Samples Ma 7 to Ma 19a of this paper). Rhodes *et al.* (1969) recovered two specimens of *Siphonodella* from the Avon Gorge. Both were broken, but were identified as advanced forms on the basis of the rostral ridge development (Rhodes *et al.* 1969, p. 55). Patrognathids occur with these siphonodellids in the Avon Gorge. Both at Maesbury and in the Avon Gorge the incoming of siphonodellids is associated with a phosphatic lag deposit. At this level a comparison is therefore possible both in faunal and sedimentological terms.

The presence of patrognathids along with the siphonodellids in the Avon Gorge section could be due entirely to reworking associated with the Palate Bed, which (see Appendix) certainly includes reworked patrognathids. It is also possible that facies differences play some part in this. This problem may become clearer when the full distribution of *Patrognathus* is known.

It should be noted that in a later paper, Austin *et al.* (1971, text-fig. 2) extend the range of *Siphonodella* below the Bryozoa Bed. There is no justification for this on the basis of any published information. In the Avon Gorge a covered interval is present above sample K 17 of Rhodes *et al.* (1969). In their paper these authors give this interval as 25 ft (7.5 m) (Rhodes *et al.* 1969, fig. 59). This gap has been recognized by other workers and is usually given a value of some 200 ft (60 m). Thus, Kellaway (1971) gives the total thickness of the Lower Limestone Shale Group in the Avon Gorge as 350 ft (107 m) compared with the 175 ft (53.5 m) given by Rhodes *et al.* (1969). This covered interval may, in part, explain the rarity of siphonodellids in the Avon Gorge reported by Rhodes *et al.* (1969).

Faunas from the uppermost part of the Lower Limestone Shale Group and those from the lower part of the Black Rock Group (Samples K_2 1 to Z 37 of Rhodes *et al.*; Samples Ma 20 to Ma 28; WH 1 to WH 21; HW 1 to HW 22; HQ 1 to HQ 14a; Va 1 to Va 2 of this paper). Faunas recovered from this part of the succession by Rhodes *et al.* (1969) compare well with those from the Mendips. In the lower part of this interval the faunas are dominated by *Pseudopolygnathus multistriatus* (see systematic description for synonymy) and *Polygnathus communis communis*. *Gnathodus delicatus* appears some way above the base of the Black Rock Limestone (Z zone). It should be noted here that Rhodes *et al.* (1969) did not in fact recover *Gnathodus delicatus* from their *Spathognathodus costatus costatus*-*Gnathodus delicatus* Zone in the Avon Gorge. The first occurrence of *G. delicatus* there is given by Rhodes *et al.* (1969, p. 97) as sample Z 28, and this may tentatively be correlated with the point where gnathodids become abundant in the Mendips, that is sample HW 2 at Ham Woods Quarry.

The lower chert horizon noted in the Mendips is represented in the Avon Gorge (sample Z 13 of Rhodes *et al.* 1969, fig. 60). However, the Main Chert is not present there, nor are any of the conodonts found at this level in the Mendip succession. *Polygnathus communis carina* was not reported from the Avon Gorge and no conodonts of the kind of *Pelekyognathus bultyncki* or *Dolymae bouckaerti* were recorded. Since *P. communis carina* first appears in sample HW 8 in the Mendips, it seems likely that the interval Z 28 (the first appearance of *G. delicatus*) to Z 37 (first appearance of *G. bulbosus* in Z 38, see below) in the Avon Gorge lies below the level of HW 8 in the Mendips, but above that of HW 2.

An equivalence appears therefore to have been established between the uppermost part of the Black Rock Limestone (Z zone) in the Avon Gorge and a level less than half-way up this division in the Mendips. It seems that a considerable discontinuity may exist at the top of the Black Rock Limestone in the Avon Gorge, as has already been suggested by Mitchell (1971, 1972) on the basis of coral faunas.

Faunas comparable with the German anchoralis-Zone (Samples Z 38 to C 14 of Rhodes *et al.*; Samples HW 23; HQ 15 to HQ 82; Va 3 to Va 20 of this paper). Rhodes *et al.* (1969) did not record any trace of anchoralis-Zone faunas (with the exception of one specimen of *Pseudopolygnathus triangulus* cf. *pinnatus*, which is removed from this species altogether in the systematic part of this paper, see below). However, an examination of their faunas from the Black Rock Dolomite in the Avon Gorge has revealed that certain gnathodids characteristic of the anchoralis-Zone equivalents in the Mendips do in fact occur here. Thus, *G. bulbosus* occurs in sample Z 38 and *G. texanus pseudosemiglaber* occurs in sample C 4. S. C. Matthews (pers. comm.) has recovered *Ps. triangulus pinnatus* from the Black Rock Dolomite in the Avon Gorge.

It appears therefore that although the Mendip succession is much the thicker at this level, and the Avon Gorge succession broken, there might nevertheless be some isolated remnants of the fuller succession of faunas to be found in the Black Rock Dolomite at Bristol. All of this question will be clearer when the conodont faunas of the Black Rock Dolomite have been restudied.

Sparse faunas with *Mestognathus beckmanni* were recorded from the Gully Oolite of the Clifton Down Group in the Avon Gorge by Rhodes *et al.* (1969), and

they may perhaps be compared with those recovered from sample HQ 76 in the Mendips. This would indicate that the base of the Gully Oolite in the Avon Gorge is no lower than the top of the Black Rock Group in the eastern Mendips, which is consistent with the proposals advanced by Kellaway and Welch (1955). Mitchell (1972) has recently suggested that the Tournaisian-Viséan boundary should lie at, or below, the base of the Gully Oolite in the Avon Gorge. The conodont faunas recovered from the eastern Mendips during this study do not contradict this suggestion when compared with those recovered from Belgium by Groessens (1971).

SYSTEMATIC PALAEOLOGY

The entire conodont collection has been deposited in the Leeds Office of the Institute of Geological Sciences. Four-figure numbers prefixed LZA identity 32-cavity slides in the collection. Individual cavities are identified by a suffix to the four-figure number. Each figured specimen occupies its own cavity. Bar-type conodonts are included in the collection, but since they have in almost every case no stratigraphic significance, they are not treated in the systematics. The sole exception is *Hindeodella segaformis*.

The synonymy lists carry annotations according to the system proposed by Richter (1948).

Genus BACTROGNATHUS Branson and Mehl 1941

Bactrognathus cf. *B. distortus* Branson and Mehl 1941

Plate 58, figs. 11-13

Remarks. This form possesses a posterior lateral process, suggesting comparison with the genus *Bactrognathus*. The prominent hornlike denticle is similar to that described for *B. distortus* Branson and Mehl by Rexroad and Scott (1964). These authors figure a lateral view of *B. distortus* which is similar to that of the present specimens (cf. Rexroad and Scott 1964, pl. 3, fig. 9). The distal part of the posterior lateral process of *B. distortus* is, however, normally redirected towards the posterior, giving a Z-shaped appearance in oral view.

In lateral view the main bar resembles that of *Pelekysgnathus bultyncki* (Groessens) and in oral view the species has much in common with immature forms of *Scaliognathus anchoralis* Branson and Mehl, which, however, have two posterior lateral processes (cf. Pl. 58, figs. 12, 13, and figs. 21, 22).

Material. 3 specimens, from 3 samples.

Genus DOLIIGNATHUS Branson and Mehl 1941

Doliognathus sp.

Plate 58, figs. 17, 18

Remarks. A single specimen referable to this genus was recovered in association with *Pelekysgnathus bultyncki* (Groessens) and *D. bouckaerti* Groessens. It resembles early forms of *Pe. bultyncki*, displaying a short posterior bar behind the prominent hornlike denticle, but has a small node on the inner side of this denticle.

The basal cavity has a corresponding lobe underneath this lateral node. Although this specimen is an immature form, it is considered to resemble the genus *Doliognathus* Branson and Mehl. The lateral view of a specimen assigned to *D. latus* Branson and Mehl by Groessens (1971, pl. 2, fig. 1) is similar in appearance.

Material. 1 specimen.

Genus DOLLYMAE Hass 1959
Dollymae bouckaerti Groessens 1971

Plate 58, figs. 19, 20, 25, 26

1959 *Dollymae* sp. B Voges, p. 276, pl. 33, figs. 15–17.

*1971 *Dollymae bouckaerti* Groessens, p. 14, pl. 1, figs. 6–8.

Remarks. Specimens found during the present study demonstrate similar morphological variations to those described by Groessens (1971). The diagnosis given by Groessens (1971, p. 14) runs as follows: 'A species of the genus *Dollymae* with a straight blade and two lateral processes, each ornamented by a single node or row of nodes. The basal cavity occupies the whole of the aboral surface of the platform and includes a median groove.'

In agreement with Groessens (1971, p. 15) this species is considered to have been derived from his own *Spathognathodus bultyncki* (referred to *Pelekygnathus* below) by an expansion of the basal cavity and the development of nodes on the resulting lateral processes.

Material. 63 specimens, from 2 samples.

Dollymae sp.

Remarks. A single specimen referable to the genus *Dollymae* Hass was recovered from sample HW 20. This specimen was broken, only part of the platform and lateral process from one side being found. The specimen shows the development of a broad basal cavity, with a platform ornamented by a laterally directed arc-shaped row of denticles. The platform ornamentation does not fall within the range of variation of that of *D. bouckaerti* Groessens.

Material. 1 specimen.

Genus ELICTOGNATHUS Cooper 1939
Elictognathus laceratus (Branson and Mehl 1934)

Plate 59, figs. 25, 28

*1934 *Solenognathus lacerata* Branson and Mehl, p. 271, pl. 22, figs. 5, 6.

1970 *Elictognathus laceratus* (Branson and Mehl); Thompson and Fellows, p. 81, pl. 5, figs. 20, 21 (with synonymy).

Remarks. Klapper (1966) and Thompson and Fellows (1970) have discussed the range of variation in ornament exhibited by this species. Specimens recovered from Maesbury are simple forms, similar to Branson and Mehl's holotype.

Material. 10 specimens, from 3 samples.

Genus GNATHODUS Pander 1856

Remarks. In recent years much confusion has arisen in the classification of gnathodids, particularly in that of *G. texanus* Roundy. It is now becoming clear that part of the reason for this is that the record of gnathodids from the upper Mississippi Valley is not complete (compare Rexroad and Scott 1964 and Thompson and Fellows 1970). In addition, the stratigraphy immediately below the *anchoralis*-Zone in Germany has not produced many conodonts. It now appears that the gnathodids referred to as *G. antetexanus* Rexroad and Scott lie below the *anchoralis*-Zone and that the German *anchoralis*-Zone gnathodids (including the *G. texanus* group of Voges 1959) are not represented in the upper Mississippi Valley sections.

In the eastern Mendips, *G. delicatus* Branson and Mehl dominates faunas immediately below the *anchoralis*-Zone and faunas in the lower part of this zone are dominated by *G. bulbosus* Thompson.

Gnathodus bulbosus Thompson 1967

Plate 56, figs. 12, 15, 16, 19–24, 27

- *1967 *Gnathodus bulbosus* Thompson, p. 37, pl. 3, figs. 7, 11, 14, 15, 18–21; pl. 6, figs. 2, 7.
- v1969 *Gnathodus punctatus* (Cooper); Rhodes, Austin, and Druce, p. 105, pl. 18, figs. 1, 10, 11.
- v1969 *Gnathodus punctatus*–*Gnathodus semiglaber* transition; Rhodes, Austin, and Druce, pl. 30, figs. 2, 8.
- 1970 *Gnathodus bulbosus* Thompson; Thompson and Fellows, p. 84, pl. 1, figs. 3, 6, 8, 9, 12, 13.

Remarks. Thompson (1967, p. 37) restricted this species to those forms whose carina is bulbous where it protrudes beyond the posterior end of the platform. Specimens he illustrated are characterized by high peg-like nodes at the anterior end of the platform, appearing almost to 'pinch' the carina. In the present study, many specimens possess further nodes lying in rows parallel to the carina in the posterior part of the platform. These are considered to lie within the range of variation of *G. bulbosus*.

As suggested by Thompson and Fellows (1970, p. 89) *G. texanus* Roundy appears to have developed from *G. bulbosus* by a reduction of the platform and the expansion of the peg-like inner node into a short parapet.

Material. 417 specimens, from 15 samples.

Gnathodus delicatus Branson and Mehl 1938

Plate 56, figs. 3–5, 7–11, 13, 14

- *1938 *Gnathodus delicatus* Branson and Mehl, pl. 34, p. 145, figs. 25–37.
- 1967 *Gnathodus* sp. cf. *bilineatus* (Roundy); Thompson, p. 37, pl. 3, figs. 8, 10, 12, 17.
- v1969 *Gnathodus semiglaber* Bischoff; Rhodes, Austin, and Druce, p. 106, pl. 30, fig. 1.
- 1970 *Gnathodus* sp. cf. *bilineatus* (Roundy); Thompson and Fellows, p. 84, pl. 1, figs. 5, 10.
- v1972 *Gnathodus delicatus* Branson and Mehl; Matthews, Sadler, and Selwood, pp. 559–560, pl. 110, figs. 5, 7–9 (with synonymy).

Remarks. This species is considered to include all those gnathodids which possess platforms ornamented by rows of nodes sub-parallel to the carina, but without the low broad outer platform characteristic of *G. bilineatus* (Roundy). Forms towards

the top of the range of the species show the development of a distinct parapet, situated anteriorly on the inner side, the rows of nodes posterior to it being less well developed. These forms resemble those called *G. antetexanus* Rexroad and Scott and *G. typicus* Cooper but are here considered to lie within the range of variation of *G. delicatus*. A transition exists between *G. delicatus* and forms with a bulbous platform on the inner side, referable to *G. semiglaber* Bischoff. Matthews *et al.* (1972) have drawn attention to forms of *G. delicatus* which resemble *G. punctatus* (Cooper). The specimen illustrated here in Plate 56, figs. 10, 11 is of this type.

Material. 275 specimens, including 8 cf. determinations, from 27 samples.

Gnathodus punctatus (Cooper 1939)

Plate 56, figs. 1, 2

*1939 *Dryphenotus punctatus* Cooper, p. 386, pl. 41, figs. 42, 43; pl. 42, figs. 10, 11.

v1972 *Gnathodus punctatus* (Cooper); Matthews, Sadler, and Selwood, pp. 560-562, pl. 109, figs. 5, 13; pl. 110, figs. 1-4, 11-15 (with synonymy).

Remarks. Matthews *et al.* (1972) have described several variants of this species. The two specimens recovered during the present study both lie within variant 5 of these authors. A specimen illustrated by Rhodes *et al.* (1969) as *G. delicatus* is considered here to lie within the range of variation of *G. punctatus* (variant 1 of Matthews *et al.* 1972, and cf. Plate 56, figs. 10, 11 of this paper). Specimens referred to *G. punctatus* by Rhodes *et al.* (1969) are placed in *G. bulbosus* (see above). *G. punctatus* has a curved inner parapet, convex to the carina, and is therefore distinguished from *G. bulbosus*, which has a peg-like node on the inner side.

Material. 2 specimens, from 1 sample.

EXPLANATION OF PLATE 56

Specimens dusted with ammonium chloride. All $\times 30$.

Figs. 1, 2. *Gnathodus punctatus* (Cooper). Aboral and oral views of LZA 6008/1 (sample Ma 7).

Figs. 3-5, 7-11, 13, 14. *Gnathodus delicatus* Branson and Mehl. 3, 4, Aboral and oral views of LZA 6060/1 (HW 10). 5, LZA 6010/1 (Ma 9). 7, 8, Oral and aboral views of LZA 6086/1 (HQ 10). 9, LZA 6080/1 (HQ 3). 10, 11, Aboral and oral views of LZA 6063/1 (HW 13). 13, 14, Aboral and oral views of LZA 6068/10 (HW 18).

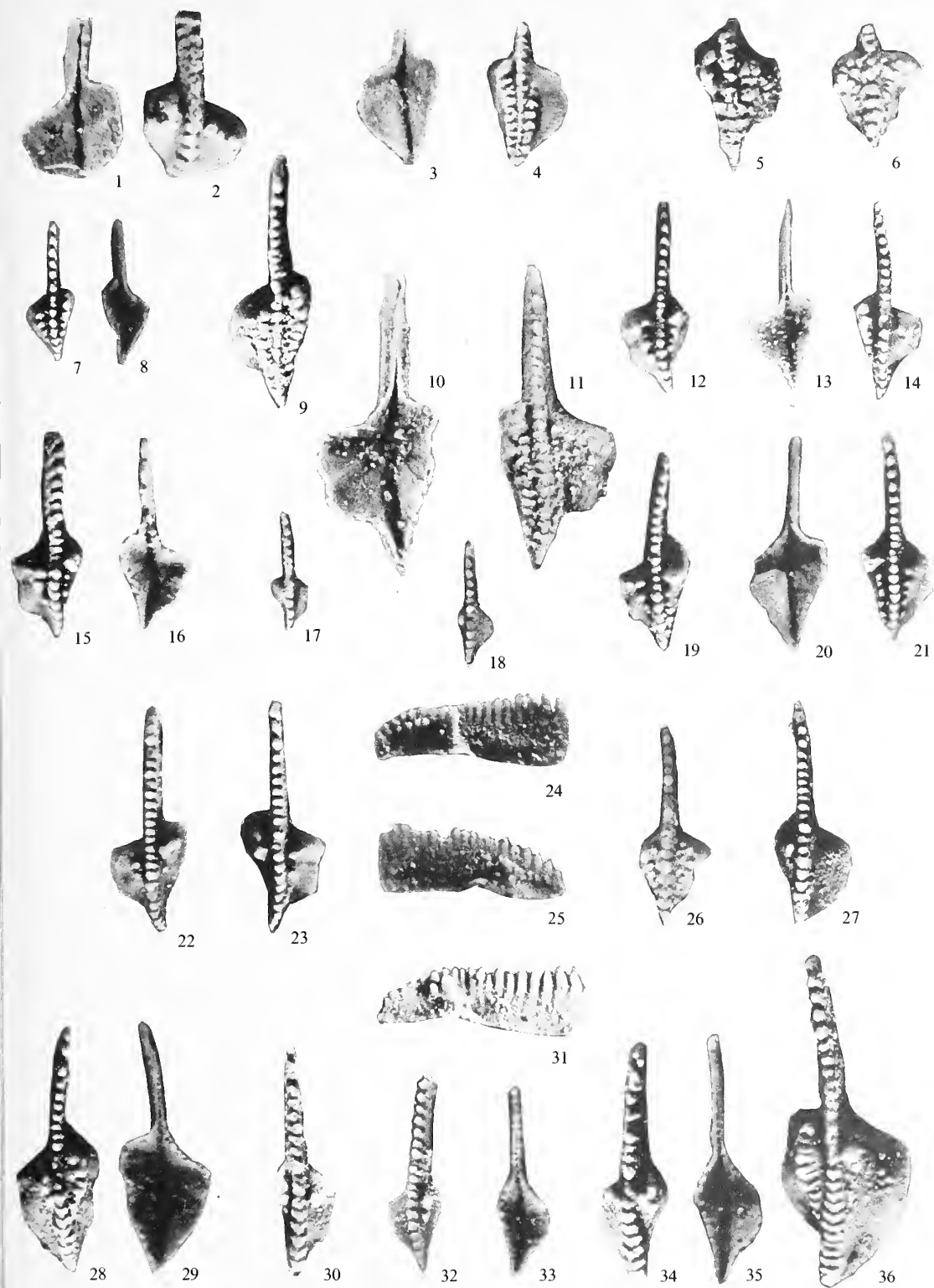
Figs. 6, 25, 26. *Gnathodus* n. sp. B Thompson, 1967. 6, LZA 6077/4 (HW 23). 25, 26, Lateral and oral views of LZA 6093/4 (HQ 15).

Figs. 12, 15, 16, 19-24, 27. *Gnathodus bulbosus* Thompson. 12, LZA 6093/6 (HQ 15): specimen transitional from *G. delicatus*. 15, 16, Oral and aboral views of LZA 6093/1 (HQ 15). 19, LZA 6093/9 (HQ 15). 20, 21, Aboral and oral views of LZA 6100/1 (HQ 19). 22, LZA 6093/2 (HQ 15). 23, LZA 6093/5 (HQ 15). 24, LZA 6093/3 (HQ 15). 27, LZA 6098/1 (HQ 18).

Figs. 17, 18. *Gnathodus* sp. (juv?). 17, LZA 6093/7 (HQ 15). 18, LZA 6093/8 (HQ 15).

Figs. 28, 29, 36. *Gnathodus texanus pseudosemiglaber* Thompson and Fellows. 28, 29, Oral and aboral views of LZA 6112/3 (HQ 29). 36, LZA 6150/1 (Va 13).

Figs. 30-35. *Gnathodus texanus texanus* Roundy. 30, LZA 6118/5 (HQ 35). 31-33, Lateral, oral, and aboral views of LZA 6118/1 (HQ 35). 34, 35, Oral and aboral views of LZA 6155/1 (Va 17).



BUTLER, Carboniferous conodonts

Gnathodus texanus Roundy 1926

Remarks. Thompson and Fellows (1970) have recognized two subspecies of *G. texanus* Roundy. Both have been recovered from the eastern Mendips.

Gnathodus texanus pseudosemiglaber Thompson and Fellows 1970

Plate 56, figs. 28, 29, 36

- ?1967 *Gnathodus texanus* Roundy; Wirth, p. 213, pl. 23, fig. 18 (only).
- v. 1969 *Gnathodus antetexanus* Rexroad and Scott; Rhodes, Austin, and Druce, pl. 18, fig. 13 (only).
- *1970 *Gnathodus texanus pseudosemiglaber* Thompson and Fellows, p. 88, pl. 2, figs. 6, 8, 9, 11-13 (with synonymy).
- ?1970 *Gnathodus typicus* Cooper; Marks and Wensink, p. 264, pl. 4, figs. 1, 4 (only).

Remarks. Thompson and Fellows (1970, p. 89) suggest that this form arises from *G. bulbosus* and in turn gives rise to *G. texanus texanus* Roundy. This view is supported by evidence from the eastern Mendips. Specimens recovered are similar to those illustrated by Thompson and Fellows (1970).

Material. 62 specimens, from 11 samples.

Gnathodus texanus texanus Roundy 1926

Plate 56, figs. 30-35

- *1926 *Gnathodus texanus* Roundy, in Roundy, Girty, and Goldman, p. 12, pl. 2, figs. 7, 8.
- 1970 *Gnathodus texanus texanus* Roundy; Thompson and Fellows, p. 89, pl. 2, figs. 15, 16 (with synonymy).
- ?1970 *Gnathodus typicus* Cooper; Marks and Wensink, p. 264, pl. 4, figs. 2, 3 (only).

Remarks. Specimens recovered from the eastern Mendips conform to the description given by Thompson and Fellows (1970, p. 89). As these authors suggest, the subspecies seems to develop from *G. texanus pseudosemiglaber* by a reduction of the outer platform.

Material. 31 specimens, from 12 samples.

Gnathodus n. sp. B Thompson 1967

Plate 56, figs. 6, 25, 26

- 1967 *Gnathodus* n. sp. B Thompson, p. 43, pl. 4, figs. 1-4.

Remarks. This species is characterized by a platform ornamented by scattered low nodes or rows of nodes. It may deserve to be included within the range of variation of *G. delicatus*.

Material. 16 specimens, from 9 samples.

Genus HINDEODELLA Ulrich and Bassler 1926

Hindeodella segaformis Bischoff 1957

Plate 58, fig. 29

- *1957 *Hindeodella segaformis* Bischoff, p. 28, pl. 5, figs. 40, 41, 43.
- 1959 *Hindeodella segaformis* Bischoff; Voges, p. 285.

- 1964 *Hindeodella segaformis* Bischoff; Burton, range chart, facing p. 74.
 1965 *Hindeodella segaformis* Bischoff; Budinger, p. 66, pl. 5, figs. 19-21 (with synonymy).
 1967 *Hindeodella segaformis* Bischoff; Zikmundová, pl. 2, fig. 3; pl. 3, figs. 2a, 2b.
 1969a *Hindeodella segaformis* Bischoff; Matthews, pl. 47, figs. 10, 11.
 1970 *Hindeodella segaformis* Bischoff; Marks and Wensink, p. 265, pl. 1, fig. 2.

Material. 3 specimens, from 2 samples.

Genus MESTOGNATHUS Bischoff 1957
Mestognathus beckmanni Bischoff 1957

Plate 58, figs. 1, 2

- *1957 *Mestognathus beckmanni* Bischoff, p. 37, pl. 2, figs. 4, 5, 6, 8, 9.
 1960 *Mestognathus beckmanni* Bischoff; Ziegler in Kronberg, Pilger, Scherp, and Ziegler, p. 14, pl. 3, fig. 1.
 v1969 *Mestognathus beckmanni* Bischoff; Rhodes, Austin, and Druce, p. 150, pl. 15, fig. 7.
 1971 *Mestognathus beckmanni* Bischoff; Groessens, pl. 2, fig. 8.

Material. 2 specimens, from 1 sample.

Genus PATROGNATHUS Rhodes, Austin, and Druce 1969
Patrognathus variabilis Rhodes, Austin, and Druce 1969

Plate 59, figs. 1, 2

- v*1969 *Patrognathus variabilis* Rhodes, Austin, and Druce, p. 179, pl. 2, figs. 8-11.
 1970 *Patrognathus variabilis* Rhodes, Austin, and Druce; Austin, Conil, Rhodes, and Streel, pl. 1, fig. 7.

Remarks. Klapper (1971) has distinguished two species of *Patrognathus*, based on the size of the basal cavity. The two specimens recovered from the Maesbury section have widely-flared basal cavities and can therefore be included in *P. variabilis*.

Material. 2 specimens, from 1 sample.

Genus PELEKYSGNATHUS Thomas 1949

Remarks. This genus was originally described from Upper Devonian rocks. Voges (1959) reported its occurrence in rocks of *anchoralis*-Zone age, and further records from Carboniferous rocks of this age have come from New Mexico (Burton 1964) and Belgium (Groessens 1971). Klapper (1966) has discussed the difficulty of distinguishing *Pelekysgnathus* from *Icriodus* in the Upper Devonian. Forms recovered from the eastern Mendips are here referred to as *Pelekysgnathus*, following the lead of Voges (1959). The relationship of these to any Devonian forms, whether *Pelekysgnathus* or *Icriodus*, is not understood.

Pelekysgnathus bultyncki (Groessens 1971)

Plate 58, figs. 8-10, 14-16

- *1971 *Spathognathodus bultyncki* Groessens, p. 115, pl. 1, figs. 2-5.

Remarks. Groessens's diagnosis (1971, p. 15) runs as follows: 'A species of *Spathognathodus* with a straight, or slightly arched, blade. The denticles are upright in the anterior part, and progressively show more posteriorward inclination towards the

posterior end of the blade. A prominent posteriorly pointing denticle is present in the posterior part of the blade. The basal cavity is situated at the posterior end of the blade and is rounded posteriorly and pointed anteriorly.'

It is considered here that the features described by Groessens are more consistent with the genus *Pelekysgnathus* than with *Spathognathodus*.

Early forms possess denticles behind the main cusp, but these are not present in later specimens (cf. Groessens 1971, pl. 1, figs. 2-4). The origin of the species is not clear.

Pe. bultyncki appears to have formed the stock from which both *Dollymae bouckaerti* and *Scaliognathus* developed. Expansion of the basal cavity and the development of nodes on the oral surface of the expansion seem to have led to *D. bouckaerti*. A range of forms showing this transition is available in sample HW 18 (slide LZA 6070). *Scaliognathus anchoralis* appears to have been derived by the development of lateral processes, the basal cavity remaining relatively restricted. *Bactrognathus* cf. *B. distortus* is considered to be a transitional form, with only one lateral process. In addition, the specimen of *Doliognathus* sp. (Pl. 58, figs. 17, 18) is close to *Pe. bultyncki* but has a single rudimentary lateral bar.

Material. 17 specimens, from 4 samples.

Pelekysgnathus sp. A Voges 1959

Plate 58, figs. 3-5

1959 *Pelekysgnathus* sp. A Voges, p. 287, pl. 33, fig. 44.

1971 ?*Pelekysgnathus* sp. A Voges; Groessens, pl. 2, fig. 3.

Remarks. Klapper (1966) has stated that this form, because of its double row of nodes, should be placed in the genus *Icriodus*. It has been retained in *Pelekysgnathus* for the present, however, until its relationship to other forms is understood. It appears to be related to *Pe. bultyncki*. In lateral view the two species are almost identical (see Pl. 58).

Material. 1 specimen.

Genus POLYGNATHUS Hinde 1879

Polygnathus communis Branson and Mehl 1934

Remarks. Hass (1959) subdivided *P. communis* on the basis of platform ornament. In the eastern Mendips the zonally important form *P. communis carina* Hass has been recovered, in addition to the long-ranging *P. communis communis* Branson and Mehl.

Immature specimens of this species have relatively large basal cavities and larger forms have relatively small cavities. The actual size of the basal cavity appears to remain constant throughout growth.

Polygnathus communis carina Hass 1959

Plate 59, figs. 10-13, 26

*1959 *Polygnathus communis* var. *carina* Hass, p. 391, pl. 47, figs. 8, 9.

- 1969 *Polygnathus communis dentatus* Druce, p. 95, pl. 18, figs. 13, 14.
 v1972 *Polygnathus communis carina* Hass; Matthews, Sadler, and Selwood, pp. 563-564, pl. 111, figs. 6, 7, 13 (with synonymy).

Remarks. Variants of *P. communis* showing the development of nodes or ridges on the anterior part of the platform or platform margin are placed within this subspecies.

Material. 162 specimens, from 16 samples.

Polygnathus communis communis Branson and Mehl 1934

Plate 59, figs. 8, 9, 15-17

- *1934 *Polygnathus communis* Branson and Mehl, p. 293, pl. 24, figs. 1-4.

Remarks. Some members of this subspecies have exceptionally long blades and abbreviated platforms. In these specimens the basal cavity often lies on the aboral surface in a position anterior to the blade-platform junction. These forms resemble *P. varcus* Stauffer.

Material. 455 specimens, from 55 samples.

Polygnathus inornatus Branson 1934

Plate 59, figs. 6, 7, 19, 20

- *1934 *Polygnathus inornata* Branson, p. 309, pl. 25, figs. 8, 26.
 1971 *Polygnathus inornatus* Branson; Klapper, p. 6 (with synonymy).

Remarks. Klapper (1971, p. 7) discussed the distinction between this species and *P. inornatus sensu* Branson and Mehl 1934. All specimens recovered from the Mendips lie within the range of variation of *P. inornatus* Branson, including forms which might previously have been called *P. lobatus* Branson and Mehl. The species is distinguished from *P. symmetricus* Branson by its well-defined subcircular basal cavity. In juvenile forms, the basal cavity resembles that of *P. communis*. A short free blade is common in this species.

Material. 151 specimens, from 9 samples.

The *Polygnathus symmetricus* Branson Group

Remarks. A number of polygnathids figured by other workers resemble *P. inornatus* in their platform development but differ in that they possess an elongate basal cavity. Klapper (1966) placed specimens with this type of cavity in *P. symmetricus* Branson, and his lead is followed here.

Within this group of polygnathids are recognized two subgroups. The first has been recovered from the lowest part of the Lower Limestone Shale Group seen at Maesbury and has been found in the Shirehampton Beds at Stoke Bishop (Bristol) by S. C. Matthews (pers. comm.). This subgroup closely resembles the specimens of *P. symmetricus* recovered from the Hannibal Shale by Branson and Mehl (1934) and is included within that species.

The second subgroup includes a broader range of polygnathids found higher up the stratigraphy, around the equivalent of the base of the *anchoralis*-Zone. These

were reported from Missouri by Thompson (1967) and Thompson and Fellows (1970). Some representatives are also available in the Avon Gorge (see Rhodes *et al.* 1969). These forms are included here as *P. cf. P. symmetricus*, since they have the characteristic basal cavity but are generally asymmetrical. This subgroup appears to develop from *Pseudopolygnathus multistriatus* by reduction of the size of the basal cavity and a change in the platform ornament. *Polygnathus nodomarginatus* Branson is considered to be a transitional form. Members of this subgroup show characteristic pseudopolygnathid asymmetry in juveniles, the platform on the right-hand side tending to be better developed than that on the left.

Juvenile forms of both subgroups have basal cavities which are deep and widely excavated along the underside of the platform, resembling those of spathognathodids.

Polygnathus nodomarginatus Branson 1934

Plate 57, figs. 2, 3

- *1934 *Polygnathus nodomarginatus* Branson, p. 310, pl. 25, fig. 10.
- 1956 *Polygnathus nodomarginatus* Branson; Bischoff and Ziegler, p. 156, pl. 12, fig. 6.
- 1956 *Polygnathus inornata* Branson; Bischoff and Ziegler, p. 157, pl. 12, fig. 5.
- v1969 *Pseudopolygnathus nodomarginatus* (Branson); Rhodes, Austin, and Druce, p. 212, pl. 9, figs. 1-4; pl. 12, figs. 6-8, 10.
- v. 1969 *Pseudopolygnathus cf. longiposticus* Branson and Mehl; Rhodes, Austin, and Druce, p. 210, pl. 30, figs. 11-16 (only).
- v. 1969 *Pseudopolygnathus triangulus cf. pinnatus* Voges; Rhodes, Austin, and Druce, p. 216, pl. 30, fig. 19.

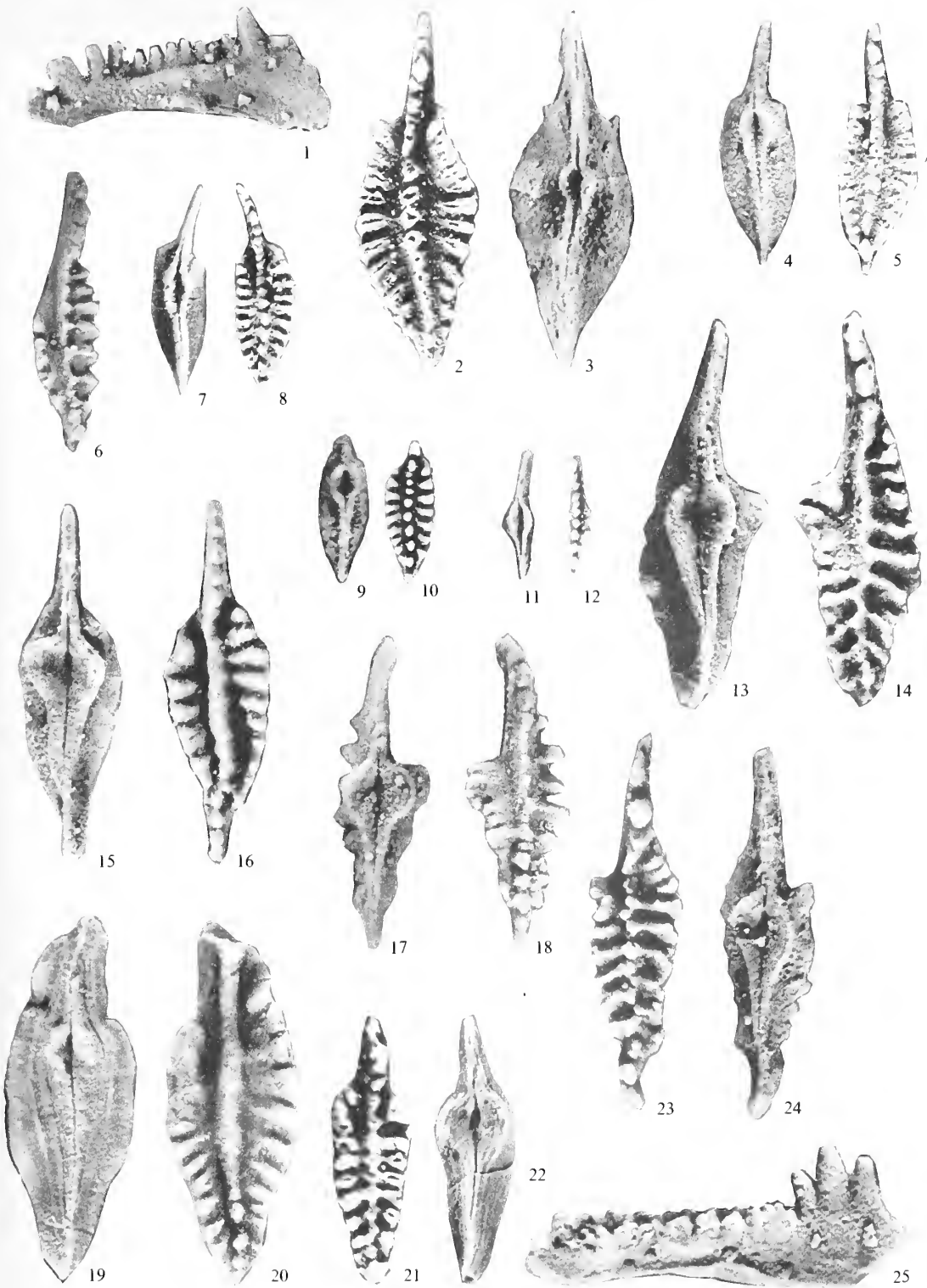
Remarks. This species is considered to be closely related to *Pseudopolygnathus multistriatus* Mehl and Thomas. The form appears briefly near the top of the range of *Ps. multistriatus* and some specimens have basal cavities similar to that of this pseudopolygnathid. The platform ornament is coarse, but polygnathid-like. Members of this species show a characteristic asymmetry, the right-hand side of the platform often extending farther anteriorly than the left.

Material. 3 specimens, from 3 samples.

EXPLANATION OF PLATE 57

Specimens dusted with ammonium chloride. All $\times 30$.

- Fig. 1. *Pseudopolygnathus postinodosus* Rhodes, Austin, and Druce. LZA 6052/1 (sample HW 2).
- Figs. 2, 3. *Polygnathus nodomarginatus* Branson. Oral and aboral views of LZA 6093/12 (HQ 15).
- Figs. 4, 5, 7, 8, 11, 12, 19, 20. *Polygnathus cf. P. symmetricus* Branson. 4, 5, Aboral and oral views of LZA 6098/11 (HQ 18). 7, 8, Aboral and oral views of LZA 6119/1 (HQ 36). 11, 12, Aboral and oral views of LZA 6118/6 (HQ 35). 19, 20, Aboral and oral views of LZA 6077/3 (HW 23).
- Figs. 6, 9, 10, 15, 16, 23-25. *Pseudopolygnathus multistriatus* Mehl and Thomas. 6, LZA 6046/9 (WH 17). 9, 10, Aboral and oral views of LZA 6100/2 (HQ 19). 15, 16, Aboral and oral views of LZA 6078/1 (HQ 1). 23, 24, 25, Oral, aboral, and lateral views of LZA 6047/2 (WH 18).
- Figs. 13, 14, 17, 18. *Pseudopolygnathus primus* Branson and Mehl. 13, 14, Aboral and oral views of LZA 6047/1 (WH 18). 17, 18, Aboral and oral views of LZA 6046/1 (WH 17).
- Figs. 21, 22. *Pseudopolygnathus dentilineatus* Branson. Oral and aboral views of LZA 6003/1 (Ma 2).



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Polygnathus symmetricus Branson 1934

Plate 59, figs. 22, 23

- *1934 *Polygnathus symmetrica* Branson, p. 310, pl. 25, fig. 11.
 1966 *Polygnathus symmetrica* Branson; Klapper, p. 21, pl. 4, figs. 7, 9; pl. 6, figs. 1, 5 (with synonymy).
 1968 *Polygnathus symmetrica* Branson; Straka, p. 35, pl. 1, figs. 6, 9 (only).

Remarks. This species is common at the base of the Lower Limestone Shale Group in the Mendips. Immature forms have a basal cavity which is spathognathodid-like, underlying the entire platform, and a symmetrical platform.

Material. 68 specimens, from 5 samples.

Polygnathus cf. *P. symmetricus* Branson 1934

Plate 57, figs. 4, 5, 7, 8, 11, 12, 19, 20

The following are regarded as falling within this subgroup:

- 1967 *Polygnathus mehli* Thompson, p. 47, pl. 2, figs. 1-6.
 1969 *Polygnathus bischoffi* Rhodes, Austin, and Druce, p. 184, pl. 13, figs. 8-11.
 1969 *Polygnathus lacinatus asymmetricus* Rhodes, Austin, and Druce, p. 188, pl. 11, figs. 1-4.
 1969 *Polygnathus lacinatus circaperipherus* Rhodes, Austin, and Druce, p. 189, pl. 11, figs. 12-15.
 1969 *Polygnathus lacinatus lacinatus* Huddle; Rhodes, Austin, and Druce, p. 189, pl. 11, figs. 8-10.
 1969 *Polygnathus lacinatus prelobatus* Rhodes, Austin, and Druce, p. 190, pl. 11, figs. 5-7, 11.
 1970 *Polygnathus bischoffi* Rhodes, Austin, and Druce; Marks and Wensink, p. 268, pl. 1, fig. 18.

Remarks. Included in this subgroup are all those 'late' polygnathids having a narrow platform and elongate basal cavity. Immature members of this species have spathognathodid-like basal cavities, similar to those seen in *P. symmetricus*. The platform in immature forms is, however, often asymmetrical, with the right-hand side consistently better developed than the left (see Pl. 57, fig. 12).

The subgroup appears to develop from *Pseudopolygnathus multistriatus*, and forms with basal cavities resembling those of this pseudopolygnathid are found.

Material. 217 specimens, from 39 samples.

Genus PSEUDOPOLYGNATHUS Branson and Mehl 1934

Pseudopolygnathus dentilineatus Branson 1934

Plate 57, figs. 21, 22

- *1934 *Pseudopolygnathus dentilineata* Branson, p. 317, pl. 26, fig. 22.
 1966 *Pseudopolygnathus dentilineata* Branson; Klapper, p. 14, pl. 5, figs. 10, 11 (with synonymy).
 v. 1969 *Pseudopolygnathus expansus* Rhodes, Austin, and Druce, p. 209, pl. 5, figs. 2, 4.
 v. 1969 *Pseudopolygnathus vogesi* Rhodes, Austin, and Druce, p. 216, pl. 5, figs. 1, 3, 5-8.
 1970 *Pseudopolygnathus dentilineatus* Branson; Thompson and Fellows, p. 99, pl. 5, figs. 1, 5.

Remarks. As suggested by Klapper (1966, p. 15), *Ps. dentilineatus* is characterized by a basal cavity which, in mature specimens, is as wide as the platform. The basal cavity tends to be subcircular and widely flared, and is therefore distinct from that of *Ps. multistriatus*, which is narrow and attenuate posteriorly.

Material. 7 specimens, from 2 samples.

Pseudopolygnathus multistriatus Mehl and Thomas 1947

Plate 57, figs. 6, 9, 10, 15, 16, 23–25

- *1947 *Pseudopolygnathus multistriata* Mehl and Thomas, p. 16, pl. 1, fig. 36.
- 1967 *Pseudopolygnathus multistriata* Mehl and Thomas; Thompson, p. 49, pl. 4, figs. 15, 16, 19, 20 (with synonymy).
- 1968 *Pseudopolygnathus multistriata* Mehl and Thomas; Canis, p. 547, pl. 73, figs. 13, 16.
- v1969 *Pseudopolygnathus multistriatus* Mehl and Thomas; Rhodes, Austin, and Druce, p. 211, pl. 5, figs. 14–16; pl. 6, fig. 2.
- v. 1969 *Pseudopolygnathus dentilineatus* Branson; Rhodes, Austin, and Druce, p. 208, pl. 5, figs. 9–13; pl. 6, fig. 8.
- v. 1969 *Pseudopolygnathus primus* Branson and Mehl; Rhodes, Austin, and Druce, p. 214, pl. 6, figs. 4, 5, 7, 11, 12 (only).

Remarks. Mature specimens of this form possess an elongate basal cavity which is not as wide as the platform. Late forms may have a much-reduced basal cavity. Hass (1959, pl. 47) figured an ontogenetic series of *Ps. lanceolata* (now placed in synonymy with *Ps. multistriatus*). Specimens found during the present study conform to this series, certain immature forms having nodes on the right-hand side only, and resembling *Spathognathodus aculeatus* (Branson and Mehl). Members of this species are again more fully developed on the right-hand side. The basal cavity may be relatively large in immature specimens. In certain forms the blade does not continue into the carina on the platform, but tends towards the nodes on the right-hand side of the platform (see Pl. 57, fig. 23). These forms bear some resemblance to the genus *Clydagnathus* Rhodes, Austin, and Druce.

Material. 73 specimens, from 25 samples.

Pseudopolygnathus postinodosus Rhodes, Austin, and Druce 1969

Plate 57, fig. 1

- v*1969 *Pseudopolygnathus postinodosus* Rhodes, Austin, and Druce, p. 213, pl. 6, fig. 6.

Remarks. This form lacks a platform, but the lateral view is similar to that of *Ps. multistriatus* (compare Pl. 57, fig. 1 with Pl. 57, fig. 25).

Material. 1 specimen.

Pseudopolygnathus primus Branson and Mehl 1934

Plate 57, figs. 13, 14, 17, 18

- *1934 *Pseudopolygnathus prima* Branson and Mehl, p. 298, pl. 24, figs. 24, 25.
- v1969 *Pseudopolygnathus primus* Branson and Mehl; Rhodes, Austin, and Druce, p. 214, pl. 6, fig. 10 (only).
- 1970 *Pseudopolygnathus primus* Branson and Mehl; Thompson and Fellows, p. 101, pl. 5, figs. 15, 16, 18, 19 (with synonymy).

Remarks. The characteristics of this species are taken as follows: The platform possesses a pronounced lateral lobe on either the inner or outer side, separated from the carina by a depression. The basal cavity is not as wide as the platform in mature forms. Immature forms again show a more fully developed right-hand side, irrespective of whether this is the inner or outer side. As Klapper (1966, p. 14) has

pointed out, some specimens of *Ps. primus* resemble *Ps. triangulus pinnatus* Voges (see Pl. 57, fig. 18). This latter species possesses a smaller basal cavity, and tends to have a broad, flat platform.

Material. 6 specimens, from 3 samples.

Pseudopolygnathus triangulus Voges 1959
Pseudopolygnathus triangulus pinnatus Voges 1959

Plate 58, figs. 23, 24, 27, 28, 30, 31, 33, 34

- *1959 *Pseudopolygnathus triangula pinnata* Voges, p. 302, pl. 34, figs. 59–66.
- 1964 *Pseudopolygnathus triangula pinnata* Voges; Higgins, Wagner-Gentis, and Wagner, pl. 4, fig. 16.
- 1967 *Pseudopolygnathus triangula pinnata* Voges; Boogaert, p. 285, pl. 3, figs. 9, 10 (with synonymy).
- 1969 *Pseudopolygnathus triangula pinnata* Voges; Matthews (1969a), p. 271, pl. 48, figs. 3, 4, 8, 10, 11.
- 1969 *Pseudopolygnathus triangula pinnata* Voges; Matthews (1969b), pl. 51, fig. 8.
- non v 1969 *Pseudopolygnathus triangulus* cf. *pinnatus* Voges; Rhodes, Austin, and Druce, p. 216, pl. 30, fig. 19 (= *Polygnathus nodomarginatus* Branson).
- 1970 *Pseudopolygnathus triangulus pinnatus* Voges; Marks and Wensink, p. 269, pl. 1, fig. 17.
- 1970 *Pseudopolygnathus triangulus pinnatus* Voges; Thompson and Fellows, p. 102, pl. 6, figs. 6, 11, 12.

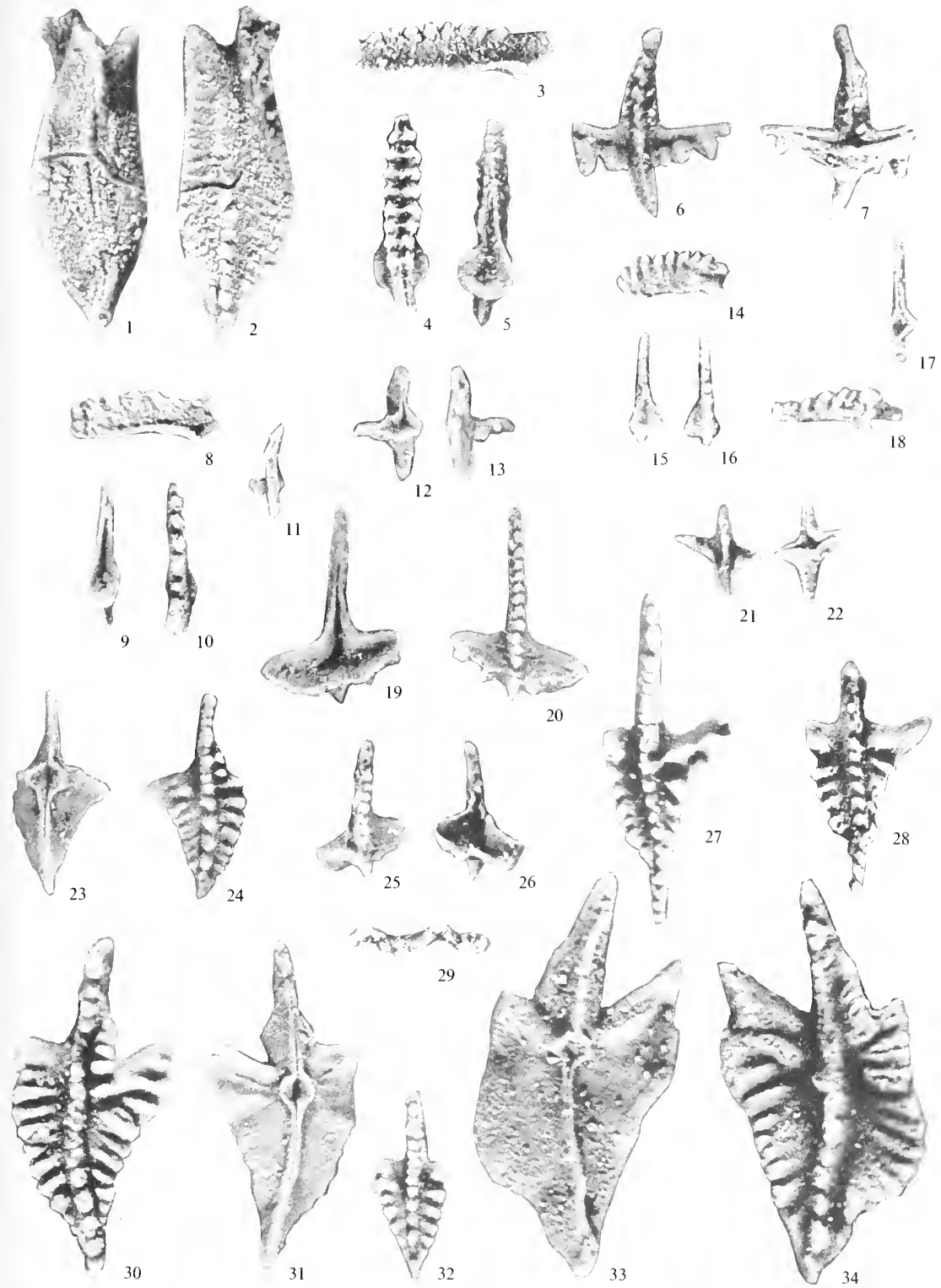
Remarks. Specimens found during the present study show a similar range of variation to that illustrated by Voges (1959). Members of this subspecies again show the tendency for the right-hand side to be more fully developed than the left. A row of platform denticles is often present extending along the blade towards the anterior on the right-hand side, regardless of which side includes the pinnation (compare Pl. 58, fig. 30 with Pl. 58, fig. 34).

Material. 65 specimens, from 14 samples.

EXPLANATION OF PLATE 58

Specimens dusted with ammonium chloride. All $\times 30$.

- Figs. 1, 2. *Mestognathus beckmanni* Bischoff. Aboral and oral views of LZA 6135/1 (sample HQ 76).
- Figs. 3–5. *Pelekysgnathus* sp. A Voges 1959. Lateral, oral, and aboral views of LZA 6150/2 (Va 13).
- Figs. 6, 7, 21, 22. *Scaliognathus anchoralis* Branson and Mehl. 6, 7, Oral and aboral views of LZA 6104/2 (HQ 22). 21, 22, Oral and aboral views of LZA 6093/11 (HQ 15).
- Figs. 8–10, 14–16. *Pelekysgnathus bultyncki* (Groessens). 8–10, Lateral, aboral, and oral views of LZA 6078/2 (HQ 1). 14–16, Lateral, aboral, and oral views of LZA 6068/6 (HW 18).
- Figs. 11–13. *Bactrognathus* cf. *B. distortus* Branson and Mehl. 11, LZA 6092/1 (HQ 14a): specimen later accidentally destroyed. 12, 13, Aboral and oral views of LZA 6075/1 (HW 21).
- Figs. 17, 18. *Doliognathus* sp. Aboral and oblique lateral/oral views of LZA 6068/3 (HW 18).
- Figs. 19, 20, 25, 26. *Dollymae bouckaerti* Groessens. 19, 20, Aboral and oral views of LZA 6068/11 (HW 18). 25, 26, Oral and aboral views of LZA 6068/8 (HW 18).
- Figs. 23, 24, 27, 28, 30, 31, 33, 34. *Pseudopolygnathus triangulus pinnatus* Voges. 23, 24, Aboral and oral views of LZA 6077/2 (HW 23). 27, LZA 6104/1 (HQ 22). 28, LZA 6106/1 (HQ 23). 30, 31, Oral and aboral views of LZA 6077/1 (HW 23). 33, 34, Aboral and oral views of LZA 6098/2 (HQ 18).
- Fig. 29. *Hindeodella segaformis* Bischoff. LZA 6129/1 (HQ 46).
- Fig. 32. *Pseudopolygnathus triangulus triangulus* Voges. LZA 6111/1 (HQ 28).



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Pseudopolygnathus triangulus triangulus Voges 1959

Plate 58, fig. 32

- *1959 *Pseudopolygnathus triangula triangula* Voges, p. 304, pl. 35, figs. 7-13.
- 1969 *Pseudopolygnathus triangula triangula* Voges; Matthews (1969a), p. 271, pl. 48, figs. 2, 7.
- 1970 *Pseudopolygnathus triangulus triangulus* Voges; Thompson and Fellows, p. 103, pl. 7, figs. 6, 7 (with synonymy).

Remarks. Specimens recovered are similar to those figured by Voges (1959, pl. 35). Voges (1959, table 1) gave this subspecies a lower range than that of *Ps. triangulus pinnatus*. In the eastern Mendips the two forms have almost identical ranges.

Material. 8 specimens (including 2 cf. determinations), from 6 samples.

Genus SCALIOGNATHUS Branson and Mehl 1941

Scaliognathus anchoralis Branson and Mehl 1941

Plate 58, figs. 6, 7, 21, 22

- *1941 *Scaliognathus anchoralis* Branson and Mehl, p. 102, pl. 19, figs. 29-32.
- 1964 *Scaliognathus anchoralis* Branson and Mehl; Burton, range-chart, facing p. 74.
- 1967 *Scaliognathus anchoralis* Branson and Mehl; Zikmundová, pl. 1, figs. 1, 2, 4.
- 1968 *Scaliognathus anchoralis* Branson and Mehl; Schulze, p. 220, pl. 20, fig. 32 (with synonymy).
- 1969 *Scaliognathus anchoralis* Branson and Mehl; Matthews (1969a), p. 272, pl. 49, figs. 1-10.
- 1969 *Scaliognathus anchoralis* Branson and Mehl; Matthews (1969b), pl. 51, figs. 1, 2.
- 1970 *Scaliognathus anchoralis* Branson and Mehl; Marks and Wensink, p. 269, pl. 4, fig. 12.
- 1970 *Scaliognathus anchoralis* Branson and Mehl; Thompson and Fellows, p. 103 (with additional synonymy).
- 1971 *Scaliognathus anchoralis* Branson and Mehl; Groessens, pl. 1, figs. 9, 10.

Remarks. The species is one of the indices of the German *anchoralis*-Zone. It has, in the past, been reported mainly from 'basinal' sequences, and there have been suggestions (e.g. Rhodes *et al.* 1969, p. 65) that facies-control resulted in virtual exclusion of this species from the 'shelf' limestone successions. It now seems clear that the species is present in the limestone sequences and that its absence at many places is due in part to discontinuities within the successions.

The species appears to have developed from *Pelekysgnathus bultyncki* (Groessens) by the development of lateral processes at the posterior end (see discussion under *Pe. bultyncki*, above).

Material. 7 specimens, from 5 samples.

Genus SIPHONODELLA Branson and Mehl 1944

Remarks. The suggestions put forward by Klapper (1971) on the systematic palaeontology of this genus are accepted here.

Siphonodella cooperi Hass 1959

Plate 59, figs. 39, 40

- *1959 *Siphonodella cooperi* Hass, p. 392, pl. 49, figs. 35, 36.
- 1971 *Siphonodella cooperi* Hass; Klapper, p. 10, pl. 1, figs. 13-15; pl. 2, figs. 1-3 (with synonymy).

Remarks. This species is distinguished from *S. isosticha* (Cooper) by the ornament of transverse ridges on the outer side of the platform. Most specimens of *S. isosticha* also show faint ridges on the outer side, but some are considered to be sufficiently well developed in this respect to justify inclusion within *S. cooperi*.

Material. 3 specimens, from 2 samples.

Siphonodella cf. *crenulata* (Cooper 1939)

Plate 59, figs. 36, 37

Remarks. Matthews and Butler (in press) discuss occurrences of siphonodellids with platform outlines resembling those of *S. crenulata* (Cooper), but without the characteristic ornament of this species.

Material. 2 specimens, from 1 sample.

Siphonodella isosticha (Cooper 1939)

Plate 59, figs. 21, 30, 31

*1939 *Siphonognathus isosticha* Cooper, p. 409, pl. 41, figs. 9, 10.

1971 *Siphonodella isosticha* (Cooper); Klapper, p. 10, pl. 1, fig. 16 (with synonymy).

Remarks. Klapper (1971, p. 10) made clear the definition of *Siphonodella isosticha* and reillustrated Cooper's holotype. In this species the longest rostral ridge terminates at the outer margin. The inner platform is weakly nodose and the outer margin may be unornamented or have weak transverse ridges. This redefinition makes it clear that *Siphonodella cooperi hassi* Thompson and Fellows is synonymous with *S. isosticha*.

Material. 21 specimens, from 6 samples.

Siphonodella cf. *S. isosticha* (Cooper 1939)

Plate 59, fig. 38

1971 *Siphonodella* cf. *S. isosticha* (Cooper); Klapper, p. 12, pl. 1, figs. 17–20 (with synonymy).

Remarks. Klapper (1971, p. 12) applied this name to those siphonodellids with weak ornament but with rostral ridges terminating on the platform without reaching the margin.

Material. 5 specimens, from 3 samples.

Siphonodella obsoleta Hass 1959

Plate 59, figs. 33, 34

*1959 *Siphonodella obsoleta* Hass, p. 392, pl. 47, figs. 1, 2.

1971 *Siphonodella obsoleta* Hass; Klapper, p. 12, pl. 1, fig. 25 (with synonymy).

v1972 *Siphonodella obsoleta* Hass; Matthews, Sadler, and Selwood, p. 565, pl. 111, figs. 4, 5 (with additional synonymy).

Remarks. This species is characterized by the presence of a long outer rostral ridge, extending to the posterior part of the platform before meeting the margin. The

platform is relatively long and narrow. As Klapper (1971, p. 12) has pointed out, the species may have more than two rostral ridges. Certain specimens here have an additional ridge (see Pl. 59, fig. 33).

Material. 15 specimens, from 5 samples.

Genus SPATHOGNATHODUS Branson and Mehl 1941
Spathognathodus aculeatus (Branson and Mehl 1934)

*1934 *Spathodus aculeatus* Branson and Mehl, p. 186, pl. 17, figs. 11, 14.

Remarks. Matthews (in Matthews and Naylor 1973) gives full systematic treatment to this species. Specimens recovered during the present study are not well enough preserved or numerous enough to justify lengthy discussion.

Material. 4 specimens, from 2 samples.

Spathognathodus crassidentatus (Branson and Mehl 1934)

Plate 59, figs. 18, 24, 29

*1934 *Spathodus crassidentatus* Branson and Mehl, p. 276, pl. 22, fig. 17.

1966 *Spathognathodus crassidentatus* (Branson and Mehl); Klapper, p. 23, pl. 5, figs. 15–17 (with synonymy).

1970 *Spathognathodus crassidentatus* (Branson and Mehl); Thompson and Fellows, p. 111, pl. 7, figs. 8, 14.

EXPLANATION OF PLATE 59

Specimens dusted with ammonium chloride. All $\times 30$.

Figs. 1, 2. *Patrognathus variabilis* Rhodes, Austin, and Druce. Lateral and oral views of LZA 6005/2 (sample Ma 4).

Figs. 3, 14, 32. *Spathognathodus stabilis* (Branson and Mehl). 3, LZA 6150/3 (Va 13). 14, LZA 6104/3 (HQ 22). 32, LZA 6118/3 (HQ 35): variant approaching *S. crassidentatus*.

Figs. 4, 5. *Spathognathodus scitulus* (Hinde). Aboral and lateral views of LZA 6129/2 (HQ 46).

Figs. 6, 7, 19, 20. *Polygnathus inornatus* Branson. 6, 7, Aboral and oral views of LZA 6019/8 (Ma 19). 19, 20, Oral and aboral views of LZA 6012/2 (Ma 11).

Figs. 8, 9, 15–17. *Polygnathus communis communis* Branson and Mehl. 8, 9, Oral and aboral views of LZA 6019/11 (Ma 19). 15–17, Lateral, aboral, and oral views of LZA 6100/3 (HQ 19).

Figs. 10–13, 26. *Polygnathus communis carina* Hass. 10, 11, Oral and aboral views of LZA 6083/4 (HQ 7). 12, 13, Oral and aboral views of LZA 6083/3 (HQ 7). 26, LZA 6083/1 (HQ 7).

Figs. 18, 24, 29. *Spathognathodus crassidentatus* (Branson and Mehl). 18, LZA 6098/3 (HQ 18). 24, 29, Oral and lateral views of LZA 6086/2 (HQ 10).

Figs. 21, 30, 31. *Siphonodella isosticha* (Cooper). 21, LZA 6019/3 (Ma 19). 30, 31, Oral and aboral views of LZA 6019/1 (Ma 19).

Figs. 22, 23. *Polygnathus symmetricus* Branson. Aboral and oral views of LZA 6005/1 (Ma 4).

Figs. 25, 28. *Elictoognathus laceratus* (Branson and Mehl). 25, LZA 6019/12 (Ma 19). 28, LZA 6019/13 (Ma 19).

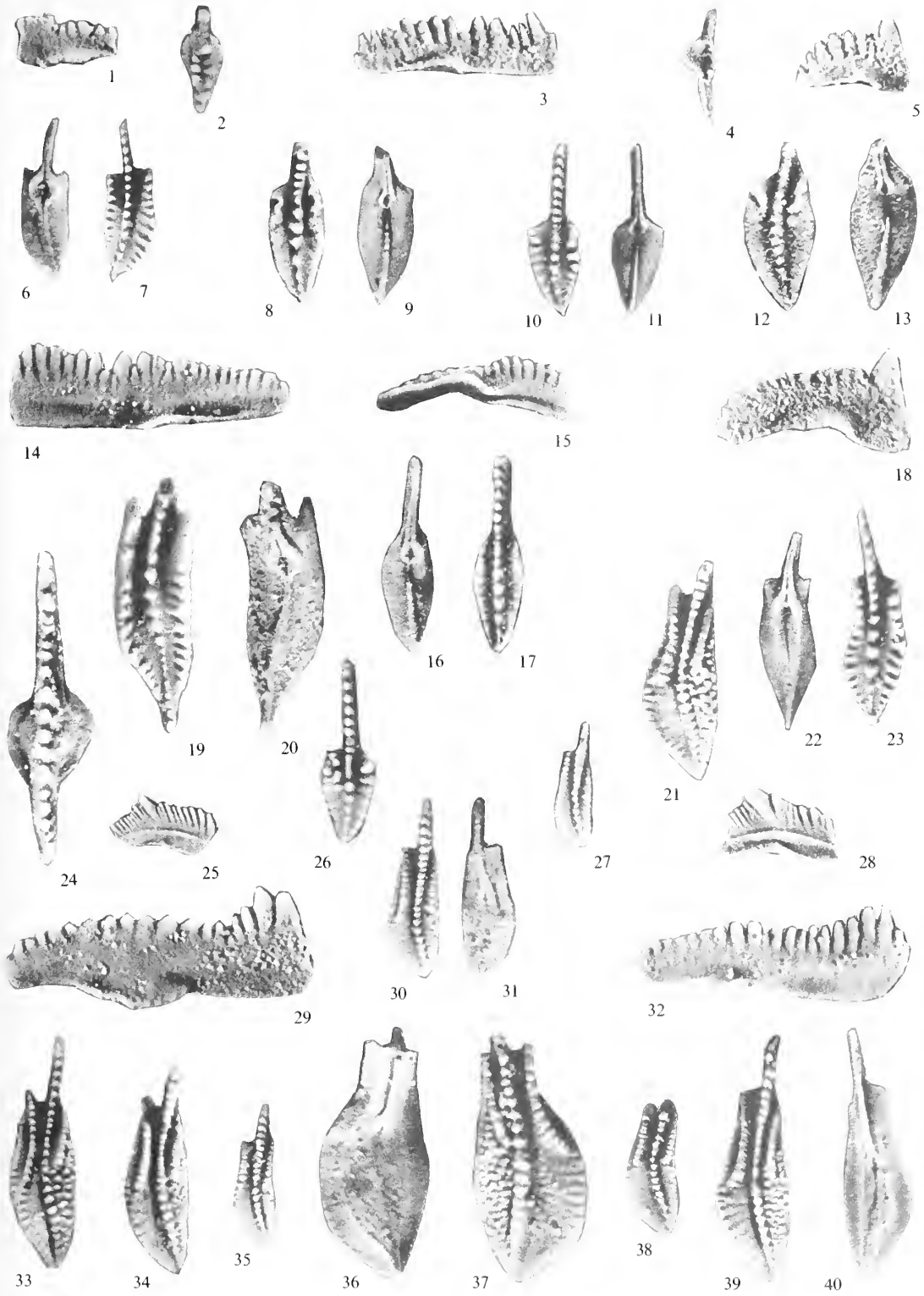
Figs. 27, 35. *Siphonodella* sp. (juv?). 27, LZA 6019/7 (Ma 19). 35, LZA 6019/4 (Ma 19).

Figs. 33, 34. *Siphonodella obsoleta* Hass. 33, LZA 6019/2 (Ma 19). 34, LZA 6014/1 (Ma 15).

Figs. 36, 37. *Siphonodella* cf. *crenulata*. Aboral and oral views of LZA 6012/1 (Ma 11).

Fig. 38. *Siphonodella* cf. *S. isosticha*. LZA 6019/5 (Ma 19).

Figs. 39, 40. *Siphonodella cooperi* Hass. Oral and aboral views of LZA 6019/6 (Ma 19).



BUTLER, Carboniferous conodonts

Remarks. This species was restricted by Klapper (1966, p. 23) to those forms having two main denticles at the anterior end of the blade and a slightly arched profile. Specimens with a similar profile but a single major anterior denticle are also included in the species here (see Pl. 59, fig. 18). A fuller synonymy list is available in Matthews (in Matthews and Naylor 1973).

Material. 40 specimens, from 20 samples.

Spathognathodus scitulus (Hinde 1900)

Plate 59, figs. 4, 5

- *1900 *Polygnathus scitulus* Hinde, p. 343, pl. 9, figs. 9–11 (only).
- 1963 *Spathognathodus scitulus* (Hinde); Rexroad and Collinson, p. 20, pl. 2, figs. 14, 19, 29–31 (with synonymy).
- v1969 *Spathognathodus scitulus* (Hinde); Rhodes, Austin, and Druce, p. 232, pl. 8, figs. 9–11.

Remarks. This spathognathodid has a distinctively flared basal cavity on the outer side. Few denticles are present and these expand rapidly in size from the posterior end to the anterior. In some specimens one or two ridges develop on the oral surface of the flared cavity.

Material. 11 specimens, from 6 samples.

Spathognathodus stabilis (Branson and Mehl 1934)

Plate 59, figs. 3, 14, 32

- *1934 *Spathodus stabilis* Branson and Mehl, p. 188, pl. 17, fig. 20.

Remarks. Matthews (in Matthews and Naylor 1973) supplies a full description and synonymy list for this species, and no attempt will be made to duplicate this here. Specimens similar to that illustrated as *Spathognathodus* sp. A by Groessens (1971, pl. 2, fig. 7) occur in many samples from *anchoralis*-Zone levels in the Mendips. They are considered to lie within the range of variation of *Sp. stabilis*.

Material. 174 specimens, from 49 samples.

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APPENDIX

List of conodont faunas from isolated Lower Limestone Shale Group samples. ($\frac{1}{2}$ -kg samples processed.)

1. The Palate Bed, from the Avon Gorge (ST 555 746): ?*Elictognathus* sp. (3 specimens), *Clydagnathus* spp. (10), *Patrognathus variabilis* Rhodes, Austin, and Druce (3), *Polygnathus inornatus* Branson (33), *P. scobiniformis* Branson (4), *Pseudopolygnathus dentilineatus* Branson (7), *Siphonodella duplicata* (Branson and Mehl) (3), *Spathognathodus plumulus* Rhodes, Austin, and Druce (11), *Sp. stabilis* Branson and Mehl (1), Bars (24). Slide LZA 6161.
2. Phosphatic lag deposit on Clevedon Foreshore (ST 402 718): *Clydagnathus* sp. (2), *Patrognathus variabilis* Rhodes, Austin, and Druce (1), *Polygnathus inornatus* Branson (8), *Pseudopolygnathus dentilineatus* Branson (1), *Spathognathodus plumulus* Rhodes, Austin, and Druce (1), Bars (10). Slide LZA 6164.
3. Bed with *Vaughania* on Portishead Foreshore (ST 465 775): *Spathognathodus plumulus* Rhodes, Austin, and Druce (3). Slide LZA 6165.
4. Small quarry north of road at Asham (ST 717 463). Oolite: *Patrognathus variabilis* Rhodes, Austin, and Druce (2), *Polygnathus symmetricus* Branson (20), *Pseudopolygnathus dentilineatus* Branson (4), *Spathognathodus stabilis* Branson and Mehl (1), Bars (15). Slide LZA 6162.
5. Sample from stream section at Asham (ST 717 464): *Pseudopolygnathus dentilineatus* Branson (2), Bars (2). Slide LZA 6163.

THE STRUCTURAL EVOLUTION OF THE BIVALVE SHELL

by JOHN D. TAYLOR

ABSTRACT. Direct study of the course of evolution of bivalve shell structures has been prevented by the lack of well-preserved lower Palaeozoic material. The 'primitive' molluscan shell structure probably consisted of an outer aragonitic prismatic layer, the prisms being polygonal in transverse and columnar in longitudinal sections. The middle and inner shell layers consisted of nacreous structures. Morphologically similar structures are produced inorganically from the solidification of metals containing impurities. It is suggested that the prism/nacre combination originally arose spontaneously as a result of the precipitation of calcium carbonate with protein (impurity). The subsequent elaboration of the shell structure combinations took place along seven major morphological trends. The main structural changes have been: the modification and loss of the outer prismatic layer; the elaboration of the middle layer from nacre into various other types of dendritic growth such as calcitic foliated or aragonitic crossed-lamellar structures; and the loss of organized structure to produce a homogeneous granular structure. In all the series there has been a progressive loss of layers from the 'primitive' three to a more 'advanced' two or even one.

In recent years there has been considerable interest in the calcified structures of invertebrates and the structure of the molluscan shell, particularly that of the Bivalvia, has received much attention (Bøggild 1930; Taylor *et al.* 1969, 1973; Wise 1970, 1971). It is now known that the shells consist of a number of distinct structures and the micro-morphology and distribution of these structures amongst the various taxa is becoming well known. Although the arrangement of the structures in each of the bivalve superfamilies is obviously related to their phylogenetic history, it is difficult to see how the various structures are related to each other and how they might have evolved. Whilst it has been possible to study the shell structure of some fossil bivalves, the preservation problems caused by the usually aragonitic shells have meant that except in very few cases it has not been possible to extend these studies very far back into the Palaeozoic. This is in contrast to the Brachiopoda, where the frequently good preservation of the calcitic shell has enabled the shell structure of Cambrian forms to be examined (Williams 1968). This lack of information from the lower Palaeozoic is particularly unfortunate because many bivalve lineages are of considerable antiquity and it seems that most of the major radiation of shell structure types took place in the Ordovician (Pojeta 1971).

If it is accepted that the Bivalvia are a monophyletic group, then all of the shell structure types observed in Recent bivalves must have evolved from a single shell structure combination. A study of the distribution of shell structures in all living superfamilies (Taylor *et al.* 1969, 1973) included the discovery of some transitional combinations, which, together with evidence of relationships derived from other available characters makes possible the tentative presentation of an attempt to demonstrate the course of evolution of bivalve shell structures. The original stimulus for this idea was the discovery of a metallurgical analogy (described below) which even if not directly applicable to calcification in bivalves, at least provides a model which (to the author at least) has made the relationships of the various shell structures comprehensible.

THE SHELL STRUCTURES

The various bivalve shell structures have been described in detail by Taylor *et al.* 1969, Wise 1970, 1971, and only the main points relevant to this paper are discussed below.

Prismatic structures

Simple prismatic structures, whether calcite or aragonite have been shown by various workers (Taylor *et al.* 1969) to resemble the group growth of spherulites seen in inorganic samples (Grigor'ev 1965). Recent further work has shown the spherulitic nature of the first calcification on the periostracum surface (Pl. 60, figs. 1 and 2). Although the crystallographic *c* axis is generally parallel to the long axis of the prisms, the alignment is not always exact and each of the small crystallites making up the prism has a slightly different orientation, usually divergent from the morphological long axis. In some species the arrangement of the crystallites may be fanlike.

The composite prismatic structure has the longest morphological and the crystallographic *c* axes aligned more or less parallel to the outside of the shell, but in many respects closely resembles the simple prismatic structure.

Nacreous structures

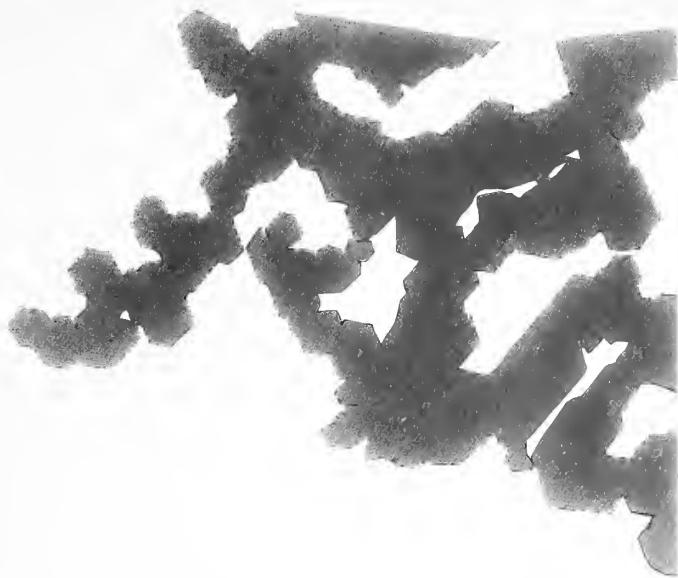
Sheet nacre consists of tablet-shaped crystallites laid down in laminae; the crystallographic *b* axis of the tablets is generally oriented in the growth direction of the shell and the *c* axis is normal to the plane of the tablet. Areas of nacre appear to behave as a single crystal and the crystallites link up to produce large dendritic growth patterns (text-fig. 1). Often large growth spirals are formed arising from screw dislocations (Wada 1961). In columnar or lenticular nacre (Taylor *et al.* 1969; Wise 1970) the tablets are arranged into columns, the growth axis of the columns corresponding to the *c* axis of the aragonite. These columns apparently arise by screw dislocations at the growing tip (see Erben 1971, p. 59, pl. 2, fig. 5) and are another form of dendritic growth.

Foliated structure

This structure is always composed of calcite and consists of long lath-like crystallites arranged in side-to-side contact and into overlapping sheets. In general the crystallographic *c* axis is aligned in the growth direction but local differences in alignment of areas of crystallites are common. This structure has long been considered as dendritic growth (Watabe and Wilbur 1961) and as shown in Pl. 60, fig. 4, this interpretation is reasonable.

Crossed-lamellar structure

This is one of the most common shell structures. It consists of elongate needle-like crystallites which are arranged into lamellae. In adjacent lamellae the morphological alignment of the crystallites differs by about 98° . The crystallographic *c* axis lies within the plane of each lamella, but the orientation of the *c* axis varies by approximately $8-10^\circ$ between adjacent lamellae. Although the structure shows strong



TEXT-FIG. 1. Dendritic growth pattern of aragonite nacre crystallites on the inner surface of the inner layer of *Neotrigonia dubia*. Traced from electron-micrographs, $\times 9000$.

superficial resemblance to twinning there is no evidence of any twin relationship between the lamellae. Each of the two orientations shown by crystallites in the lamellae show complex branching patterns (text-fig. 2) and it is possible that some sort of dendritic growth mechanism is operative. Much work on the mode of secretion of this structure, similar to that on prisms by Nakahara and Bevelander (1971) is needed.

Complex crossed-lamellar structure

This structure appears genetically related to crossed-lamellar structure and can probably be best thought of as being the intergrowth pattern resulting from crossed-lamellar structure in two alignments at right angles to each other. As a result there are four orientations of crystallites. Occasionally the texture resembles that of the patellacean gastropods, interpreted as spherulitic by McClintock (1967).

Homogeneous structure

This is a name given to a fine-grained structure with no particular crystal form; it can be



TEXT-FIG. 2. Tangential section of the outer crossed-lamellar layer of *Hippopus hippopus* showing the dendritic nature of each of the lamellar orientations. Traced from photomicrographs.

derived from any of the other shell structures by a diminution in grain size and a breakdown of structural arrangements. Further detailed study will probably reveal different types of homogeneous structures but these are not yet apparent.

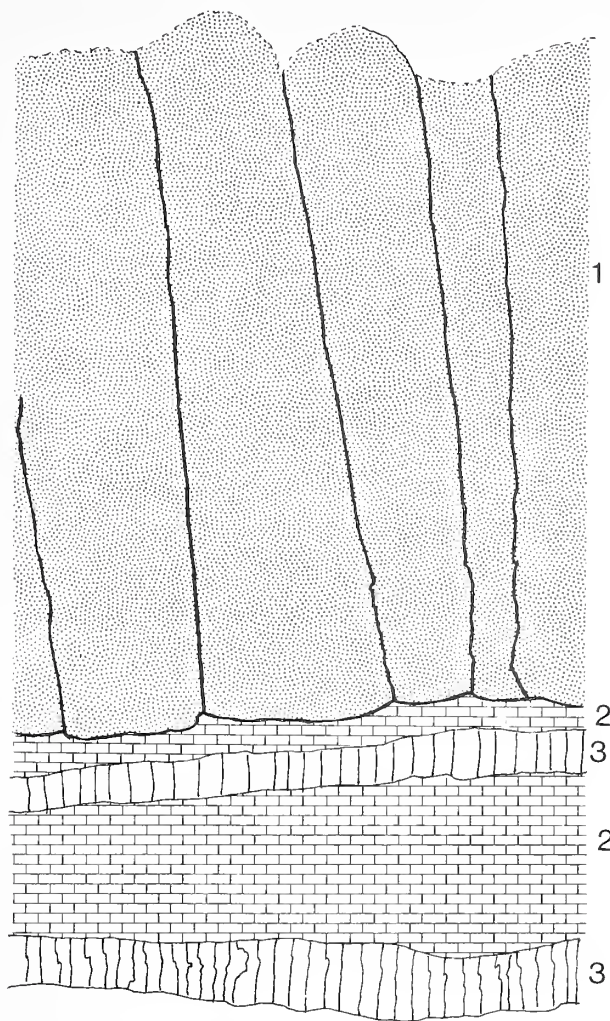
Homologies between layers

Although homologies between shell layers from various taxa should be made with caution (Taylor *et al.* 1969) it is reasonable in most cases to use the trace of the pallial myostracum as a marker horizon. This separates the inner from the middle and outer layers or just the outer layer, depending on how many layers are present. In some Pteriomorphia the pallial myostracum is absent and in others it represents secondary pallial attachment and thus great care must be taken if homologies are attempted between this group and the rest of the bivalves.

The 'primitive' shell structure

Before discussing the evolution of the bivalve shell structure it is necessary to attempt to establish the nature of the 'primitive' shell structure. McAlester (1965, 1966) has demonstrated, mainly through the evidence of pedal muscle scars, how the bivalve *Babinka* may be derived from a monoplacophoran ancestor. At the time, McAlester thought that this may have been a special character of the Lucinacea and he suggested a polyphyletic origin for the bivalves. However, it is now known that several other bivalve groups may be similarly derived from a monoplacophoran ancestor (N. J. Morris, pers. comm.) and the monophyletic derivation of all bivalves from this source is a reasonable proposition. It would thus seem reasonable to regard the structure of the Monoplacophora as being the ancestral structure to that of the Bivalvia. The work of Schmidt (1959) and Erben *et al.* (1968) has shown that, with the exception of *Tryblidium*, the shell structure of Monoplacophora is, and was, aragonitic and consisted of an outer simple prismatic layer and nacreous inner layers (text-fig. 3). The prisms of the outer layer lie with their long axes normal to the outer shell surface, are polygonal in horizontal section, and bounded by a sheath of protein matrix (see also figs. 1–8 in Menzies 1968). The inner nacreous layer is divided by a thin sheet of blocky prisms such as are normally secreted beneath muscle attachment areas. Another sheet of these prisms occurs on the innermost part of the shell. Similar sheets of myostracal prisms have been described from the inner shell layer of some Mytilacea (Taylor *et al.* 1969, pl. 25, fig. 2) and it was suggested that they were formed during times of temporary attachment of the mantle to the shell.

Several bivalve superfamilies have a structural combination of aragonite simple prisms with inner and middle nacreous layers. Although the number of living superfamilies having this combination is only five out of thirty-nine, they usually belong to lineages which extend far back into the Palaeozoic, whereas many of the other superfamilies not having this structure have arisen in the late Palaeozoic or Mesozoic. The superfamilies having this 'ancestral' condition are the Pholomyadacea, Pandoracea, Poromyacea, Unionacea, and Trigonacea. Moreover the combination of calcite prisms and nacre, as found in the Pteriacea, Pinnacea, Mytilacea, and Ambonychiacea (extinct) which all originated in the Palaeozoic, is not very different. It has often been stated that the Nuculacea show the most 'primitive' structure (Oberling 1964), but it will be shown later in this paper that it represents an early modification.



TEXT-FIG. 3. Section through shell of *Neopilina galathea* Lemche. Traced from Erben *et al.* (1968, pl. 3). 1 = simple prisms; 2 = nacre; 3 = myostracal prisms.

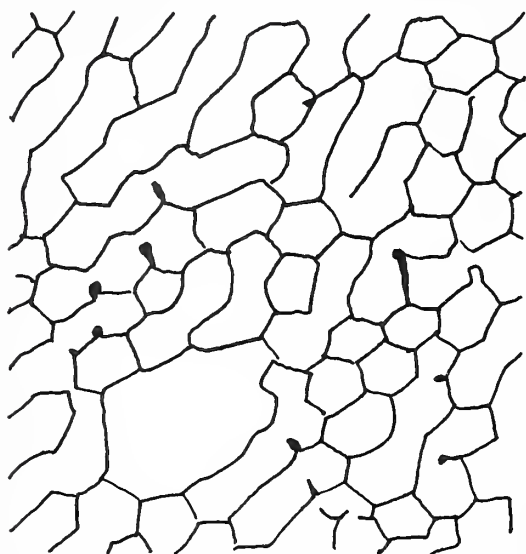
Other evidence of the 'primitive' nature of the simple prisms and nacre combination is seen in its occurrence in the Archaeogastropoda (Wise 1970; Erben 1971; Taylor unpub.) in *Nautilus* and ammonites (Grégoire 1962; Mutvei 1964; Erben *et al.* 1969). In these groups the simple prisms are not as well defined as in the Bivalvia but their spherulitic nature is clear. The nacreous layers usually consist of columnar nacre.

The 'primitive' shell structure may thus be fairly reasonably defined. Assuming a monophyletic origin for the Bivalvia, the problem is how have all the other shell structure combinations arisen from this 'primitive' combination? There is apparently little similarity between the more advanced crossed-lamellar and complex

crossed-lamellar shells and the primitive nacreo-prismatic forms and after some years' consideration of the problem no link could be seen. The situation was changed by the discovery of a metallurgical analogy which caused a reorientation of thought resulting in the present tentative proposal of an evolutionary series of shell structure combinations. This does not mean that the metallurgical analogy is suggested as the mechanism for calcification in bivalves but merely that its consideration has been instructive. A model need not be correct to be useful.

THE CELL-DENDRITE ANALOGY

During the solidification of impure melts in quiescent conditions microsegregations of the impurity may occur. A microstructure which often arises is that of cellular structure, where at the growth surface most of the impurity segregates into



TEXT-FIG. 4. Cellular impurity structure as found in metals. Traced from Chadwick (1967, figs. 4-6(d)).

the walls of a polygonal cell structure (text-fig. 4) (Chalmers 1958). In section the cells are columnar and the impurity appears as a thin line separating adjacent cells (Chadwick 1967). This microstructure may arise if there is a zone of constitutional supercooling (i.e. supercooling developed as a result of compositional changes in the liquid during freezing) at the solid/liquid interface. The usual explanation of the development of the cellular structure (Chalmers 1958; Tiller 1963; Chadwick 1967) is that small irregularities of the solid protruding into the supercooled liquid grow faster than the surrounding solid; the protuberances reject impurities in directions both normal to the tip and laterally. If this process occurs over the entire solid/liquid interface then eventually a hexagonal structure will be produced. The stages in the

development of the cell structure show a progression from a planar interface to a 'pox' structure, then elongate cells and finally regular polygonal cells (Tiller 1963).

If the speed of crystal growth is increased, the temperature gradient decreased (Chalmers 1958) or the degree of constitutional supercooling increased (Chadwick 1967), then the cellular structure may break down into dendritic growth. The criteria for dendritic growth are that the crystals should be branched or that the axis of the growing domain should coincide with a crystallographic axis (Chalmers 1958).

It is uncertain how far this analogy can be taken with reference to shell microstructure, but there are obvious resemblances between this metallurgical example and the microstructure of simple prisms (cells) and nacre (dendrites). There does

not seem to be any reason why the precipitation of calcium carbonate with an impurity (organic matrix) should not produce similar structures, perhaps for similar reasons. The hypothesis put forward here is that the microstructure of simple prisms and nacre corresponding to cells and dendrites originally arose spontaneously as a consequence of the precipitation of calcium carbonate contemporaneously with organic matrix under a certain set of physico-chemical conditions. Subsequently, because of some selective advantage in this structural combination, perhaps strength (Taylor and Layman 1972), this arrangement became stabilized. Further elaboration of the depositional conditions resulted in the formation of the other shell structures, such as foliated or crossed-lamellar structures, both of which appear to have dendritic growth patterns. These are both in a position homologous with the middle nacreous layers and could arise by changes in the dendritic growth patterns of the nacreous structure. The elaboration of shell structures took place at different rates and in different ways in various groups of bivalves. The details of these changes are discussed below.

EVOLUTIONARY TRENDS IN SHELL STRUCTURE COMBINATIONS

The evidence for the evolution of the various shell layer combinations was obtained by superimposing shell structure data upon a phylogeny derived from all available characters and geological history (Taylor *et al.* 1973, fig. 33). It has been possible in this way to demonstrate seven separate trends in shell structure evolution; these are shown in text-fig. 5. Examples of living taxa having a particular structural combination in each series are indicated. The trends and examples are not phylogenetic lineages but represent possible morphological grades arranged in order of increasing advancement.

As previously stated some superfamilies are relatively little altered from the ancestral condition; these include the Pholadomyacea, Unionacea, Trigonacea, some Pandoracea, some Poromyacea, and the early shell of the Clavagellacea.

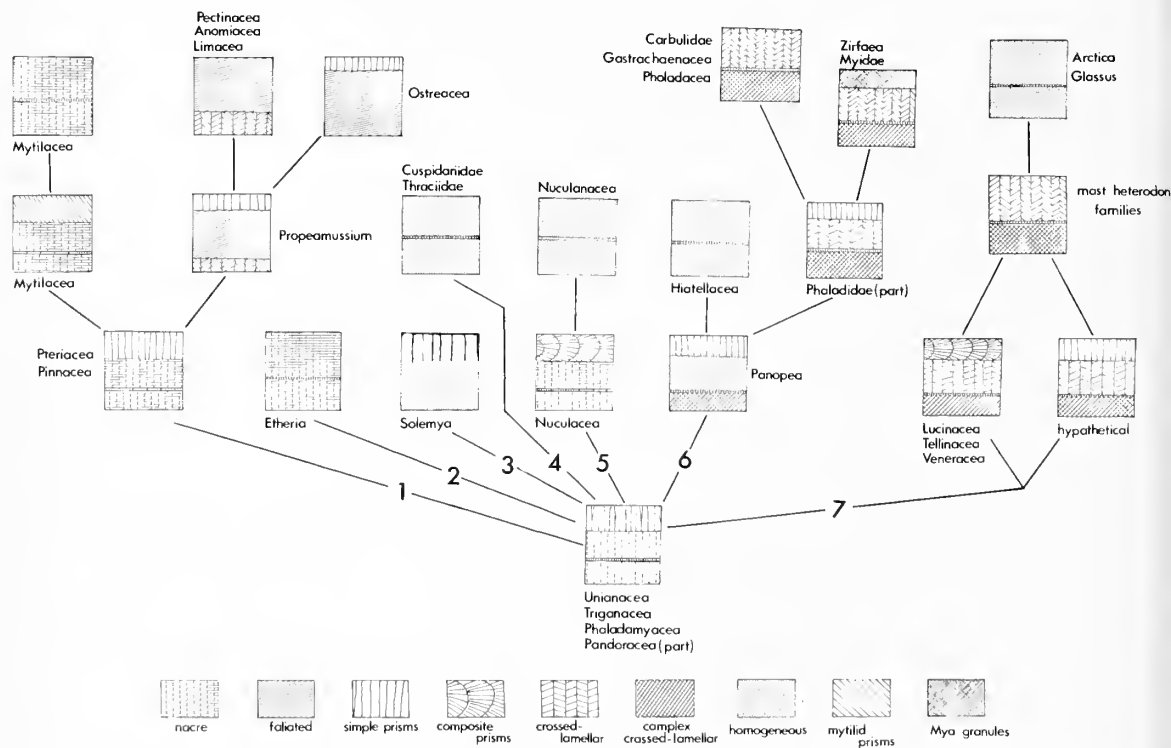
Trend 1

The first step in this sequence (text-fig. 5) was that the outer, simple prismatic layer, aragonite in the ancestral condition, became calcite; this state is found today in the superfamilies Pinnacea, Pteriacea, and in the extinct Ambonychiacea. Although there has been much research into the calcite-aragonite problem in molluscs (Lowenstam 1954, 1964; Dodd 1963; Hall and Kennedy 1967; Kennedy *et al.* 1969) we still know very little about how and why an organism can produce aragonite, or calcite, or both, in the same shell. The temperature effect originally proposed by Lowenstam (1954) has so far only been successfully demonstrated in *Mytilus* (Dodd 1963); other examples are of doubtful validity (Kennedy *et al.* 1969; Taylor *et al.* 1969). The only generalizations one can make are that bivalves which normally employ a calcitic outer layer are all epifaunal and the slightly lower solubility of calcite may have some advantage in this situation. This is not to say that a temperature effect does not exist but that it is *non proven* in most cases.

An early divergence of this trend may have been to the Mytilacea where the outer calcitic prisms are very fine, needle-like, and inclined towards the shell margin.

A possible mode of formation of similar structures in mammalian enamel has been proposed by Osborn (1970). A further development in this series was the loss of the outer calcitic prismatic layer to leave the two underlying nacreous layers. This condition is found in some tropical Mytilacea (Hudson 1968; Taylor *et al.* 1969) and has been related to a temperature effect.

Another offshoot from the calcite prisms/nacre combination gave rise to the sequence which includes the Pectinacea and Ostreacea. The probable first stage in evolution was the transformation of the middle nacreous layer to foliated structure which is calcite, i.e. one type of dendritic growth to another. The changes in microstructure accompanying this transformation may merely be a result of the mineralogical change rather than any direct genetic effect upon shell structure. Although the initial causes of the change are unknown, there are some mechanical properties of the foliated shell, such as the resistance to fracture under impact, which may have some selective advantage (Taylor and Layman 1972). It is uncertain whether the condition found in oysters of calcite prisms (right valve only) and foliated structure, is more 'primitive' or 'advanced' than the combination found today in *Propeamussium* of calcite prisms, foliated structure and a thin crossed-lamellar layer. However, the combination found today in the Pectinacea, Limacea, and Anomiacea of foliated structure and crossed-lamellar structure is a further development from



TEXT-FIG. 5. Diagram showing the postulated evolutionary radiation of shell layers into seven major trends from the ancestral 'primitive' condition. The names in the trends represent living taxa having the particular shell structure combination. The series do *not* necessarily imply a phylogeny.

the 'Propeamussium' condition involving the complete loss of the outer prismatic layer. In most of the Ostreacea the outer prismatic layer is found only as a very thin layer on the upper valve; in the Pycnodontidae it is absent altogether. It seems more likely that the oyster structure is a development from the 'Propeamussium' condition by the loss of the inner crossed-lamellar layer.

Trend 2

This is a simple case merely involving the loss of the aragonitic, outer, simple prismatic layer, leaving nacreous structure as the outer layer. This condition is found today in the oyster-like unionacean *Etheria*.

Trend 3

This sequence is again little changed from the ancestral condition and is found today only in *Solemya*, in which the outer layer consists of simple aragonite prisms and the inner of a very thin homogeneous layer. The prisms of the outer layer are very irregular and have thick interprismatic walls. The prism outlines at the growth surface are frequently elongate and irregular. The inner homogeneous layer is very thin and is probably derived from the structural breakdown of nacreous structure.

Trend 4

In this series the end members are represented today by the Cuspidaridae and the Thracidae; in both of these families the shell consists almost entirely of homogeneous layers. It is fairly certain that both of these groups have descended from a prismato-nacreous ancestor and certainly in the Cretaceous some *Thracia*-like bivalves have a prismato-nacreous shell. A possible transitional stage is seen in the Recent *Poromya granulata* in which the outer layer is now homogeneous, but the two inner layers are nacreous. Perhaps a last vestige of prismatic structure is seen in Recent *Thracia*, where although most of the shell is homogeneous, the very outermost part of the outer layer shows spherulitic structures resembling the initial stages of a prismatic layer (Pl. 60, fig. 3).

Trend 5

In this sequence the simple prismatic layer changes to the composite prismatic layer such as found in the Nuculacea. This change is apparently a fairly simple one involving merely the development of a reflected mantle margin, causing the prisms to become aligned parallel with the outside of the shell rather than normal to it (text-fig. 5). This may have happened as a result of the development of the marginal denticles characteristic of the Nuculacea, which probably allow better valve closure against predators. The Nuculanacea were probably derived from a *Nucula*-like ancestor, but at the present day they have a two-layered shell, both layers consisting of homogeneous structure. However, a Jurassic nuculanid *Ryderia graphica* has a shell structure of composite prisms and nacreous structure similar to that of the Nuculacea (Cox 1959; Taylor *et al.* 1969). The change probably consisted of the loss of the outer layer and the breakdown of the two nacreous layers to homogeneous structure.

Trend 6

In this sequence the first stage we see is that represented today by *Panopea* and the evidence from this genus has been of key importance in the interpretation of the evolution of shell layers. *Panopea* has an outer aragonitic simple prismatic layer (albeit irregular), a middle homogeneous layer, and, within the pallial line, an inner layer which is sometimes homogeneous but at other times may be built from spherulite-like structures, resembling complex crossed-lamellar structure. A further modification of this series along one offshoot is the loss of the outer prismatic layer leaving a shell consisting of two homogeneous layers as in *Hiatella* and *Panomya*.

Another divergent trend resulted in the development of a middle crossed-lamellar layer with the retention of the outer, simple prismatic layer; this condition is found in some Pholadacea. The inner layer may consist of homogeneous or complex crossed-lamellar structure. In other Pholadacea and the Gastrochaenacea, the outer simple prismatic layer has been lost and the shell consists of crossed-lamellar and complex crossed-lamellar layers.

In *Mya*, *Platydont*, and *Zirfaea* the outer layer consists of a grey, granular structure which may be derived from a modification of the outer simple prismatic layer but this is not certain. The other layers are as in the Pholadacea.

Trend 7

This sequence contains, with the exception of the Myoida, all of the rest of the heterodont bivalves, which are by far the most numerous of Recent bivalves. However, more problems are posed in this sequence than in any other, the main difficulty being that no transitional structures such as those of trend 6 have been found. Thus, we are left with rather a large discontinuity between the ancestral structures and what is considered the most 'primitive' structural combination in the sequence. However, as possibly similar changes have taken place in trend 6, there is no reason to suppose that they may not have taken place in this one. In accordance with the sequence of events in trends 5 and 6 we may suppose that the three-layered shell consisting of composite prisms, crossed-lamellar, and complex crossed-lamellar structures might be the most 'primitive' condition now seen in this sequence. This particular combination is found today in the Lucinacea, Tellinacea, and some Veneracea; of these the Lucinacea are an ancient superfamily and can be followed through the Babinkacea back to the lower Ordovician (McAlester 1965). Included at this

EXPLANATION OF PLATE 60

Fig. 1. Inner surface of the periostracum and edge of prismatic layer in *Anodonta cygnea* showing the initial spherulites (arrowed) on the periostracum surface. The spherulites increase in size and eventually impinge to form the polygonal outlines of prismatic structure. Scanning electron-micrograph, $\times 550$.

Fig. 2. As Fig. 1, but detail of an individual spherulite showing the structure of fine radiating needles. $\times 1300$.

Fig. 3. Initial spherulites in the outermost part of the outer layer of *Thracia phaseolina*. This is all that remains of prismatic structure in this family. Scanning electron-micrograph, $\times 1100$.

Fig. 4. Polished, etched section of foliated structure of *Pecten maximus*, showing the dendritic nature of the folia growth. Acetate peel, $\times 150$.



1



2



3



4

TAYLOR, structure of bivalve shell

level is a hypothetical structural combination similar to that described above, but with an aragonite simple prismatic outer layer rather than a composite prismatic one. This has never been found in any fossil or living bivalve, but the evidence from trend 6 suggests that it may once have occurred in trend 7. In trend 5 the derivation of composite prisms from simple prisms by changes in the shape of the shell margin has been discussed.

As in the other trends the next stage in the evolutionary sequence from the most primitive observed is the loss of the outer prismatic layer, whether it be composite or simple, to form a two-layered shell consisting of crossed-lamellar and complex crossed-lamellar structures. This structural combination is found in many heterodont bivalve superfamilies such as the Carditacea, Crassatellacea, Chamacea, Cardiacea, Mactracea, etc., and also in the Arcacea and the Limopsacea, both at present classified in the Pteriomorphia. A further development is the breakdown of the crossed-lamellar and complex crossed-lamellar structures to form homogeneous structure. This may occur in one or both layers and many minor variations (not illustrated here) are found, particularly in the Veneracea (Taylor *et al.* 1973, text-fig. 18). A totally homogeneous shell is found in the Gaimardiacea and some Arctica-cea (*Arctica* and *Calypstogena*).

DISCUSSION

In the evolution of the various structural series three main types of structural change have probably taken place. These may be: (a) loss of layers, (b) orientation changes, (c) complete structural changes.

(a) *Loss of layers.* This is the most commonly occurring of the structural trends and occurs in all of the recognized sequences, the main consequences being the reduction in the number of shell layers from a 'primitive' three to a more 'advanced' two. This usually involves the loss of the outer prismatic layer, whether formed from composite or simple prisms. In some sequences inner layers may be lost, for example in trend 1, but this is apparently associated with changes in the position of pallial attachment to the shell.

(b) *Orientation changes.* The only major example of this type of change is the formation of composite prisms from simple prisms by changes in the shape of the shell margin as discussed above.

(c) *Complete structural changes.* Other more major changes may arise as a result of mineralogical transformation such as the change from aragonitic nacre to calcitic foliated structure, as seen in trend 1. The differences in structure observed may be merely a result of the fact that trigonal calcite will not produce the same crystallization structures as orthorhombic aragonite, rather than there being a major change in the secretory regimes. Both nacre and foliated structure are regarded as types of dendritic growth form.

The origin of crossed-lamellar and complex crossed-lamellar structures and their appearance in the various morphological trends is much more difficult and no sensible explanation can be provided with present knowledge. What is certain is that crossed-lamellar structure arose in a position homologous with the middle nacreous layer of the 'primitive' condition. We have no surviving intermediate stages in the

transformation, but crossed-lamellar structure appears to be a form of dendritic growth and might be derived by an elaboration of nacre dendrites. Similarly, the formation of complex crossed-lamellar structure is also not understood, but it has evolved in a position homologous with the inner nacreous layer of primitive forms. (Dr. Donald Boyd (University of Wyoming) has recently found what appear to be transitional stages in *Schizodus*, in which a crossed-lamellar layer is present in the middle of an otherwise prismatic-nacreous shell.)

Various mechanisms could be invoked to explain the formation of crossed-lamellar structure including: type and composition of the organic matrix, physico-chemical conditions in the extra-pallial fluid, piezo-electric effects, or an alternating electric charge at the valve margins. None of these suggestions has, as yet, any experimental support. Workers adhering to the template theory of calcification would stress the importance of compositional differences in the shell matrix as evidence.

One of the most widely recurring of the morphological changes is the apparent breakdown of distinct crystalline morphology to form homogeneous structure. This structure can arise from simple prisms, composite prisms, crossed-lamellar, complex crossed-lamellar, and nacreous structures, with, in each case, a morphologically similar result, that is a fine-grained, irregularly granular structure. The reasons for this structural change are again not readily apparent, but speed of crystallization may be responsible; growth may be more rapid in homogeneous shells.

One feature obvious from text-fig. 5 is the independent origin of crossed-lamellar structure in several unrelated groups of bivalves; it occurs in the Pectinacea-Limacea-Anomiacea, the Myacea-Pholadacea-Gastrochaenacea, and thirdly in trend 7 where it occurs in the Arcoida and nearly all families of Heterodonta. The independent occurrence of this structure presumably arose by the evolution of similar depositional conditions at the shell-mantle interface, resulting in convergence of depositional morphologies. This convergence is not really all that surprising, for crossed-lamellar structure has also been independently evolved in both the Gastropoda and Scaphopoda.

In a study of various types of nacre, Wise (1970) has attempted to demonstrate an evolutionary significance in his categories 'Vertikalschichtung', 'Treppen', and 'Backsteinbau'. The amount of vertical component in the nacreous structure of the middle shell layers seems to be more closely related to the geometry of the shell, rather than the antiquity of the lineage. Thus bivalves with a low expansion rate (high convexity) will have better developed columnar nacre than forms with a higher expansion rate.

Although this discussion has largely been concerned with the carbonate part of the shell, the shell is of course a two-phased material, the other phase being the organic matrix and both phases have evolved together. Ghiselin *et al.* (1967) and Degens *et al.* (1967) have discussed the phylogeny of the amino-acid composition of the shell matrix proteins in bivalves. Although their conclusions are based upon very limited sampling of taxa, their groupings are generally similar to the shell structure trends recognized here.

Many workers consider the shell matrix to have a very active role in molluscan calcification but, although extensively studied (see Wilbur and Simkiss 1968), the evidence is extremely ambiguous and often based upon preconceived ideas taken

from work on calcification in bone (Glimcher 1960). Recent ideas on the role of the matrix have been well reviewed by Towe (1972). It may be that the matrix has a more passive role in calcification, such as providing a quiet environment, free of Brownian movement, in which crystal nucleation and growth can easily occur. It has been argued that there is a correlation between shell structure type and the composition of the matrix, thereby suggesting a direct control by the matrix on structure (see review, Wilbur and Simkiss 1968). Although to some extent this correlation is true, there are important exceptions. For example, it has been shown by Degens *et al.* (1967), that the shell matrix composition of the Arcacea and Limopacea which have crossed-lamellar shells is more closely similar to that of the Pteriomorphia having foliated and prismatic-nacreous shells, than to other taxa having crossed-lamellar shells. Although it might be argued that different types of matrix can produce the same result, the control would seem to lie in other factors. The evolution of shell matrix composition could possibly be correlated with other factors such as shell strength and thus have a relation with the mode of life and shell structure.

HISTORY OF CALCIFICATION IN BIVALVES

Possibly the first calcification in the ancestral molluscs arose as a result of spontaneous precipitation into a mucoid coating lying between the mantle and an outer tanned protein sheet, the periostracum. It is conceivable that those forms with a thicker, more rigid calcified shell were selectively favoured, with a resultant evolution towards a much more heavily calcified shell. In this early state, it is probable that the shell would show no organized structure but consist of an intergrowth of crystals with no particular orientation. Structures such as this are formed by spontaneous precipitation in pulmonate egg shells (into a mucopolysaccharide matrix) (Taylor, unpub.) and in some foraminifera (Towe and Cifelli 1967, pl. 98). Structures almost identical to these can be produced inorganically by growing crystals in gels, by methods similar to those of Henisch (1970). From this early state, how might the most 'primitive' structure we have recognized, simple prisms and nacre in the Monoplacophora, have arisen? By analogy with the metallurgical example described above it is suggested that an increase in calcium carbonate saturation, an increase in crystallization rate, or an increase in impurity (protein) could have collectively or singly produced the spontaneous precipitation of the cellular, polygonal structure of simple prisms. Further from the mantle margin an increased crystallization rate or an increased saturation resulted in the breakdown of the cellular structure to form laminar dendrites (nacre). This cell/dendrite combination may have originally appeared spontaneously, but possibly because of some selective advantage conferred upon the animal became fixed in the population as prisms and nacre. Further elaboration of shell structures mainly concerned the modifications of dendritic growth in the middle layer and the loss of the outer prisms. Thus both foliated and crossed-lamellar structures are regarded as varieties of dendritic growth which have been elaborated from nacreous structure. The mechanisms by which they have arisen are, however, unknown.

The modifications of shell structure could have arisen spontaneously in a section

of the population and subsequently become fixed in a lineage as a result of some selective advantage. This advantage could be a more efficient calcification mechanism involving closer control by the animal. The change from aragonitic to calcitic prisms and from aragonitic nacre to calcitic foliated structure could have originally arisen as a result of colder environmental temperatures, calcite being easier to precipitate in colder water. Or perhaps slight biochemical differences in the extrapallial fluid may be sufficient to cause the precipitation of the more stable polymorph (Wilbur and Simkiss 1968).

Although a relation of shell structure with phylogeny is evident, it has been shown (Taylor and Layman 1972) that there is a strong correlation between structure and the mode of life of the animal concerned. It can thus be argued that the shell structure combinations have been evolved in response to functional demands, although the selective advantages conferred are in most cases unknown. In common with other anatomical characters of the Bivalvia, shell structures exhibit a mosaic evolution. In different phylogenetic lineages various shell structural combinations are evolved at different rates presumably in response to increasing specialization to various diverse modes of life.

Many of the conclusions reached in this paper are speculative, but in view of the paucity of well-preserved shell structure material in the lower Palaeozoic we must rely upon circumstantial or indirect evidence to reconstruct the original radiation pattern of the shell structure combinations.

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THE PROBLEMATICAL PRECAMBRIAN FOSSIL *CHUARIA*

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ABSTRACT. *Chuar* *circularis* from the late Precambrian of the Grand Canyon was regarded by Walcott as a primitive brachiopod. It has subsequently been referred to as an alga, a chitinous foraminiferid, a gastropod, a hyolithid operculum, a trilobite egg, and an acritarch. It is here suggested that *Chuar* is a compressed, unusually large planktonic organism (generally 2 to 5 mm diameter). *Chuar* *wimani*, *Fermoria*, and unnamed material from Canada, Sweden, France, Siberia, India, Iran, and Australia show no systematic differences from *C. circularis* and are considered synonymous. *Chuar* is compared with *Leiosphaeridia* and classified with this as an sphaeromorphid acritarch. All recorded occurrences of *Chuar* are in late Precambrian strata, less than 1000 m.y. old: it may be regarded as a new stratigraphic index fossil.

Chuar is a small carbonaceous disc-like fossil which has been found in a number of regions of late Precambrian rocks. It has been assigned to both plant and animal kingdoms and at different times to several phyla of the latter. Recent collections from the type-locality in the Grand Canyon allow a more detailed examination and have resulted in a more definite conclusion regarding its nature.

Chuar appears to have first been noted in the Kwagunt Valley of the Grand Canyon by White (in Powell's 1876 monograph on the Uinta Mountains). Powell regarded it as a primordial fossil like *Lingulella* and *Obolella*, and assigned the sediments in the floor of the Grand Canyon and some of its tributary canyons to the Silurian, doubtless using Silurian in the old Murchison sense as pre-Devonian sediments. No name for the fossil was proposed by Powell at that time.

During the winter of 1882–1883, Walcott investigated what later became known as the Chuar and Unkar Groups of Powell's Grand Canyon Series (Walcott 1895). He spent a considerable part of his time in a search for fossils from these rocks, and 'but for the discovery of a small Discinoid shell, a couple of specimens of a Pteropod allied to *Hyolithes triangularis*, and an obscure *Stromatopora*-like group of forms, the two and one-half month's search for fossils in these groups would have been without result' (Walcott 1883, p. 441). These same fossils were later noted by Walcott (1886, p. 43) who wrote that in the '... Chuar strata the presence of a fauna is shown by a minute Discinoid or Patelloid shell, a small *Lingula*-like shell, a species of *Hyolithes* and a fragment of what appears to have been the pleural lobe of the segment of a trilobite belonging to a genus allied to the genera *Olenellus*, *Olenoides*, or *Paradoxides*'.

In a more definitive study of Precambrian life, Walcott described and figured the shell-like fossil as *Chuar* *circularis* (Walcott 1899, pp. 234–235, pl. 27, figs. 12 and 13; cf. Pl. 61, fig. 1 herein) and referred it to the discinoid type of brachiopod. His figures were drawings, not photographs, and whilst they could be interpreted as horny brachiopods there is nothing in them diagnostic of this phylum. He also suggested that they might be opercula of hyolithids. At the same time Walcott also decided that the *Hyolithes* of 1883 and the trilobite fragment of 1886 were of inorganic origin though he figured them, again by drawings. The *Lingula*-like shell of 1886

was not mentioned and so presumably was included within the specimens referred to *C. circularis*. Walcott (1899, p. 235, pl. 27, fig. 9) also noted an enigmatic object showing some similarity to the brachiopod *Acrothele* in a limestone 150 ft above the shale containing *Chuar*. The specimen (USNM 33801) has been re-examined and could be a *Chuar*, but it provides too little information to make any further inquiry profitable. No further specimens have been found. It could just as easily be a fragment of an oolite in the highly recrystallized and dolomitized oolitic limestone.

Walcott's type was listed in a catalogue of the U.S. National Museum type fossils (Schuchert 1905). However, the taxon was not noted in most standard works of fossils: it was not listed in the Zoological Record, nor mentioned in Zittel or in the summaries of American fossils by Grabau and Shimer, or Shimer and Schrock. The name does not appear in Walcott's classic work on the Cambrian brachiopods. Neave (1939) listed *Chuar* and noted an assignment to Problematica.

In view of the above it is surprising to find that Wenz (1938, pp. 85-86) placed *Chuar* in a new family Chuariidae which was assigned, with some doubt, to the superfamily Tryblidiacea (Gastropoda), specifically rejecting the possibility that it might be an orbiculoid brachiopod. Later, Schindewolf (1956, p. 463) dismissed *Chuar* as inorganic, probably a concretion.

Chuar has been mentioned in several volumes of the *Treatise on Invertebrate Paleontology* but in each case only to mention that the genus did not belong to the group concerned in that volume. In the Gastropoda volume (Knight *et al.* 1960, p. I 324) *Chuar* was listed as a generic name improperly regarded as Gastropoda and Monoplacophora and was considered to be a 'carbon scale'. In the Miscellanea volume, Häntzschel (1962, p. W 232) followed Schindewolf's view of 1956 and classed *Chuar* with 'Fossils probably of inorganic origin' and claimed it, without citing supporting evidence, as 'certainly inorganic'. The Brachiopoda volume (Williams *et al.* 1965) surprisingly made no mention of *Chuar* but listed the probably identical fossil *Fermoria* as a synonym of *Protobolella*, though this in turn was regarded as a 'generic name erroneously attributed to Brachiopoda'. In the Foraminifera volume (Loeblich and Tappan 1964, p. C 786) *Chuar* was listed as a 'generic name erroneously applied to Foraminifera'.

In palaeobotanical literature, David White suggested (1928a, p. 389) that the genus represented some sort of alga 'named, though apparently not published, by Doctor Walcott, *Chuar*'. White had evidently missed the 1899 paper and as a result Andrews (1955, p. 131) listed the genus with the wrong date. White (1928b) also reported finding additional specimens in the upper division of the Chuar Group, and he was the first to suggest that they were algae or at least alga-like. White's specimens have not been located. White also referred to a specimen from the Bass Limestone (at the base of the underlying Unkar Group) but this has apparently not been preserved and no further information is available. Recently both Glaessner (1966) and Cloud (1968) noted *Chuar* as an alga. Rowell (1971) did not mention *Chuar* in his recent review of Precambrian brachiopods, but Hofmann (1971) referred Precambrian fossils from Canada to Walcott's genus.

In a preliminary review of the situation Ford and Breed (1969, pp. 119-120) left it uncertain whether *Chuar* was 'Chitinous Foraminifera or algal in nature' and

required larger samples for further study. These samples have since been collected. Ford and Breed (1972a) have described the stratigraphy of the Chuar Group, and together with Mitchell (1972) have demonstrated a probable age of less than 1000 m.y.

COMPARATIVE FOSSILS

1. *Chuar* *wimani* Brotzen 1941

Wiman (1894) found discs similar to *Chuar* *circularis* in the Late Precambrian Visingsö Formation of Sweden. These were figured but neither described nor named by Wiman, and it was not until 1941 that Brotzen referred them to Walcott's genus, but, on account of their smaller size, erected a new species *C. wimani*. He regarded them as chitinous foraminiferids. Eisenack (1951, p. 192), however, referred them to *Leiosphaera*, a well-known early acritarch. (*Leiosphaera* was later emended to *Leiosphaeridia* by Eisenack.) Subsequently Eisenack (1966) revised this opinion on the basis of chemical tests and supported Brotzen's interpretation. On the basis of colour, composition, and wall-thickness Eisenack compared *C. wimani* with the chitinous foraminiferid *Archeochitina gotlandica* from the Silurian Visby Marl of Gotland. Meanwhile Timofeev (1960) had examined the type material by crushing and dissolving it for a study of nanno-plankton, and later (1966) compared some of the smaller 'sporomorphs' to those described from the Brioverian of France (Roblot 1964). Some of the fragments of pellicles of *Laminarites* described by Timofeev (1960) could well be pieces of *Chuar*, as noted by Eisenack (1966). Eisenack hinted that the smaller objects might well be young *C. wimani*. Both Wiman and later Regnell (1955, p. 555) considered a possibility that the fossils might be trilobite eggs but this suggestion seems to have found little favour.

One of us (T. D. F.) has been able to study the remaining specimens of the type *C. wimani*, mounted on three glass slides (Pl. 62, figs. 2, 3, 5, 6). One of these is a serially sectioned specimen which may be that prepared for Eisenack (1966, p. 52). The findings are reported below in the description of *Chuar*.

Timofeev (1970) has drawn attention to the existence of giant sphaeromorphid microplankton, similar to *C. wimani*, which he has found whilst dissolving rock samples from the Riphean (Upper Precambrian) of Siberia. No description has been published, but he included photographs of two specimens of *C. wimani* from Sweden renamed *Kildinella magna*.

Timofeev (1969, pl. 6, fig. 3) also figured and briefly described a further rather indeterminate specimen from the Visingsö Series as *Trachysphaeridium vetterni* sp. nov., though Eisenack (1966, p. 53, fig. 1) had previously figured it as *C. wimani*.

2. *Chuar* sp. Hofmann 1971

Small round to oval 'brachiopod-like shells' were found by Allan (1913, pp. 174, 192) in a 50 cm shale layer 16 m below the top of the Hector Formation (Late Precambrian) of Banff National Park in Canada. These show, very poorly, irregular creases in the centre and more strongly developed concentric wrinkles around the margin.

Hofmann (1971, p. 24, pl. 11, figs. 5-7) briefly described topotype material (GSC types 24409, 24410) and referred them to *Chuar*, though remaining uncommitted

as to their nature, 'perhaps compressed planktonic spheroids, Foraminifera . . . or small medusoids similar to ones illustrated by Wade (1969)'.

Further specimens have been collected from the type locality and the present writers support Hofmann's assignment to *Chuaria*.

3. *Fermoria* Chapman 1935

The only other named fossil which seems to be comparable to *Chuaria* is *Fermoria*, first described from the late Precambrian of India and more recently from Iran (Pl. 63, figs. 1, 2).

Small carbonaceous disc-like fossils were found in the Suket Shales of the Vindhyan System of India by Jones (in Holland 1909, p. 66), who commented that they might be compared with either *Obolella* or *C. circularis*. Other suggestions (see Pascoe, 1959, p. 498) were that they belonged to *Acrothele*, known to occur in the Cambrian of the Salt Ranges. However, Chapman (1935) assigned the specimens to two new genera and four new species, *Protobolella jonesi*, *Fermoria minima*, *F. granulosa*, and *F. capsella*.

Sahni (1936) thought that there was insufficient evidence for the separation of these and placed them all in the synonymy of *F. minima*, though at the same time erecting a new generic name *Vindhyanella* for one of the specimens figured as *Protobolella jonesi* by Chapman (1935, pl. 2, fig. 1), though he admitted that the specimen was lost!

In 1954 Sahni and Shrivastava briefly described and named a single, larger, new fossil found with *Fermoria* as *Krishnaniania acuminata*. Their illustration (1954, fig. 4) is entirely unconvincing regarding the filaments they claim to be attached, and the writers support Glaessner (1962) in regarding it simply as a large *Fermoria*.

Misra and Dube (1952) recorded new material with *Fermoria* which they regarded as mostly inorganic pellets. Misra (1957) restated this, noting that some alleged *Fermoria* were chlorite aggregates in schist, and others were haematite spots in sandstone. Misra's plate 7, however, shows forms which could easily be badly preserved algal bodies like *Chuaria*.

Pascoe (1959, facing p. 498) figured specimens up to 4 mm diameter. He also commented that *Fermoria* left a white ash when incinerated and was therefore a plant, but at the same time he felt it possible that *Fermoria* could be an archaic form of brachiopod though with 'no reliable feature definitely attributable to this class'.

A few specimens of *Fermoria* from the Geological Survey of India collections have been examined. They are from Neemuch, Madhya Pradesh (24° 24' north, 74° 54' east), in the Vindhyan System. They occur either isolated or as small clusters of smooth carbonaceous discs on fissile olive-coloured shale. Taking these in conjunction with the various descriptions of other specimens, the writers have no doubt that *Fermoria* should be regarded as synonymous with *Chuaria*.

Fermoria has also been found in Iran, apparently in large numbers at several localities (Pl. 63, figs. 1, 2). Assereto (1963, pp. 507–508, fig. 2) and Stöcklin *et al.* (1964, p. 14, pl. 1, figs. 3–5) have recorded *Fermoria* in the Chapoghlu Shales (late Precambrian) of northern Iran. They figured specimens up to 3 mm diameter crowded together.

A few specimens of *Fermoria* from Iran have been examined, and a number of

unpublished photographs by R. Assereto of other specimens have been available for comparison. Though mostly lacking in carbonaceous matter, the impressions on fine-grained olive-grey shale are so close to *Chuaria* as to leave no doubt that here again, organisms identical to *Chuaria* were present. Whole surfaces of chips of shale are covered with impressions, and clusters of at least fifty are indicated. They are commonly 2–3 mm in diameter. There is little indication of overlap, but concentric wrinkles are frequent particularly near the margins.

Recent interpretations of *Fermoria* have either been non-committal or that it is algal. In the *Treatise* volume on Brachiopoda (Williams *et al.* 1965, p. H 864) *Fermoria* is noted only as a synonym of *Protobolella*, which in turn is listed among the generic names erroneously ascribed to Brachiopoda. Häntzschel (1962, p. W 240) listed *Fermoria* amongst unrecognizable genera.

Glaessner (1966, p. 41) was non-committal and noted both *Fermoria* and *Chuaria* under the heading of 'other algae', thus supporting Howell (1956, p. 110), who also included *Corycium enigmaticum* in this group of uncertain algae. Ohlson (1961), though, regarded the latter as mud-pellets armoured with aegagropilous algal debris. Cloud (1968) also listed *Fermoria* as 'possibly algal but needs restudy'.

4. Unnamed fossils

In describing medusoids from the Central Mt. Stuart Beds of the Central Australian Late Precambrian, Wade (1969, p. 356, pl. 69, figs. 5–7) noted 'numerous minute unidentifiable organisms' in maroon sandstones with minor shales. Latex casts have been examined (Pl. 63, fig. 3) and the impressions clearly show the concentric wrinkles characteristic of *Chuaria*, though they are somewhat larger, ranging between 5 and 8 mm. As noted above, Hofmann (1971, p. 24) compared them with the Canadian specimens of *Chuaria*.

SYSTEMATIC DESCRIPTION

Group ACRITARCHA Evitt 1963

Subgroup SPHAEROMORPHITAE Downie, Evitt, and Sarjeant 1963

'group' MEGASPHAEROMORPHIDA Timofeev 1969

Family LEIOSPHAERIDAE Eisenack 1959

Genus CHUARIA Walcott 1899

Diagnosis. Flattened carbonaceous spheroids, now discs, from 0.5 mm to 5 mm in diameter, commonly 2–2.5 mm, showing wrinkles and cracks irregularly or concentrically arranged owing to crushing; no surface ornament; no pores; openings restricted to gaps where spheroid burst open in a few specimens; translucent resinous yellow in prepared specimens.

Chuaria circularis Walcott 1899

Plates 61–63

1899 *Chuaria circularia* Walcott, pp. 234–235, pl. 27, figs. 12, 13.

1932 *Neobolus minima* Chapman, p. 29 (nom. nud.).

1933 *Obolella jonesi* Chapman, p. 20 (nom. nud.).

1933 *Fermoria minima* (Chapman), p. 20 (nom. nud.).

- 1933 *Fermoria granulosa* Chapman, p. 20 (nom. nud.).
- 1933 *Fermoria tripartita* Chapman, p. 20 (nom. nud.).
- 1935 *Fermoria minima* Chapman, pp. 114–116, pl. 1, figs. 1, 3.
- 1935 *Fermoria granulosa* Chapman, p. 116, pl. 1, figs. 2, 4; pl. 2, fig. 5.
- 1935 *Fermoria capsella* Chapman, p. 117, pl. 2, figs. 3, 4.
- 1935 *Protobolella jonesi* Chapman, pp. 117–118, pl. 1, figs. 5, 6; pl. 2, fig. 1.
- 1936 *Vindhyanella jonesi* (Sahni), p. 467.
- 1941 *Chuararia wimani* Brotzen, p. 260.
- 1954 *Krishnanella acuminata* Sahni and Shrivastava, p. 40, fig. 4.
- 1963 Problematica Assereto, pp. 502–503, fig. 2.
- 1969 minute unidentifiable organisms, Wade, p. 356, pl. 69, fig. 7.
- 1969 *Kildinella magna* Timofeev, p. 14, pl. 6, figs. 4, 5.
- 1970 *Kildinella magna* Timofeev, pl. 1, figs. A, B, D.
- 1971 *Chuararia* sp. Hofmann, p. 24, pl. 11, figs. 5–7.

Nomenclatorial notes. The name *C. circularis* was published by Walcott in 1899 and thus has Linnean priority. All remaining names have been placed in synonymy as the present writers do not feel that the known fossils show sufficient features for consistent diagnosis of separate species, let alone genera. Furthermore, there has been an element of doubt in that most writers have compared their material with *C. circularis* and have distinguished it only on the basis of either size or on features which are mostly diagenetic. Rowell (1971, pp. 72–73) has discussed the confused nomenclatorial history of *Fermoria*, and it need not be repeated except to note that he overlooked the fact that Chapman had introduced the names without diagnoses in 1933, two years before the formal descriptions (Chapman 1935).

Species diagnosis. As for genus.

Type specimens. Walcott's (1899) type material was catalogued under U.S. National Museum no. 33800 and consists of six flakes of shale, each with one or more specimens. One flake is unfossiliferous, and there is also one small bottle that contains indeterminate fragments, again without any observable fossil. The original of Walcott's figure 13 cannot be identified in the collection. The original of his figure 12 is probably the specimen illustrated here as Pl. 61, fig. 1; this specimen is now designated lectotype and is still catalogued under USNM 33800. A number of specimens have been selected from the collections made by Ford and Breed (1969, 1972) and these have been added to the U.S. National Museum reference collection and are catalogued under USNM catalogue 36, no. 181859.

Type locality. See under Stratigraphic Occurrence below.

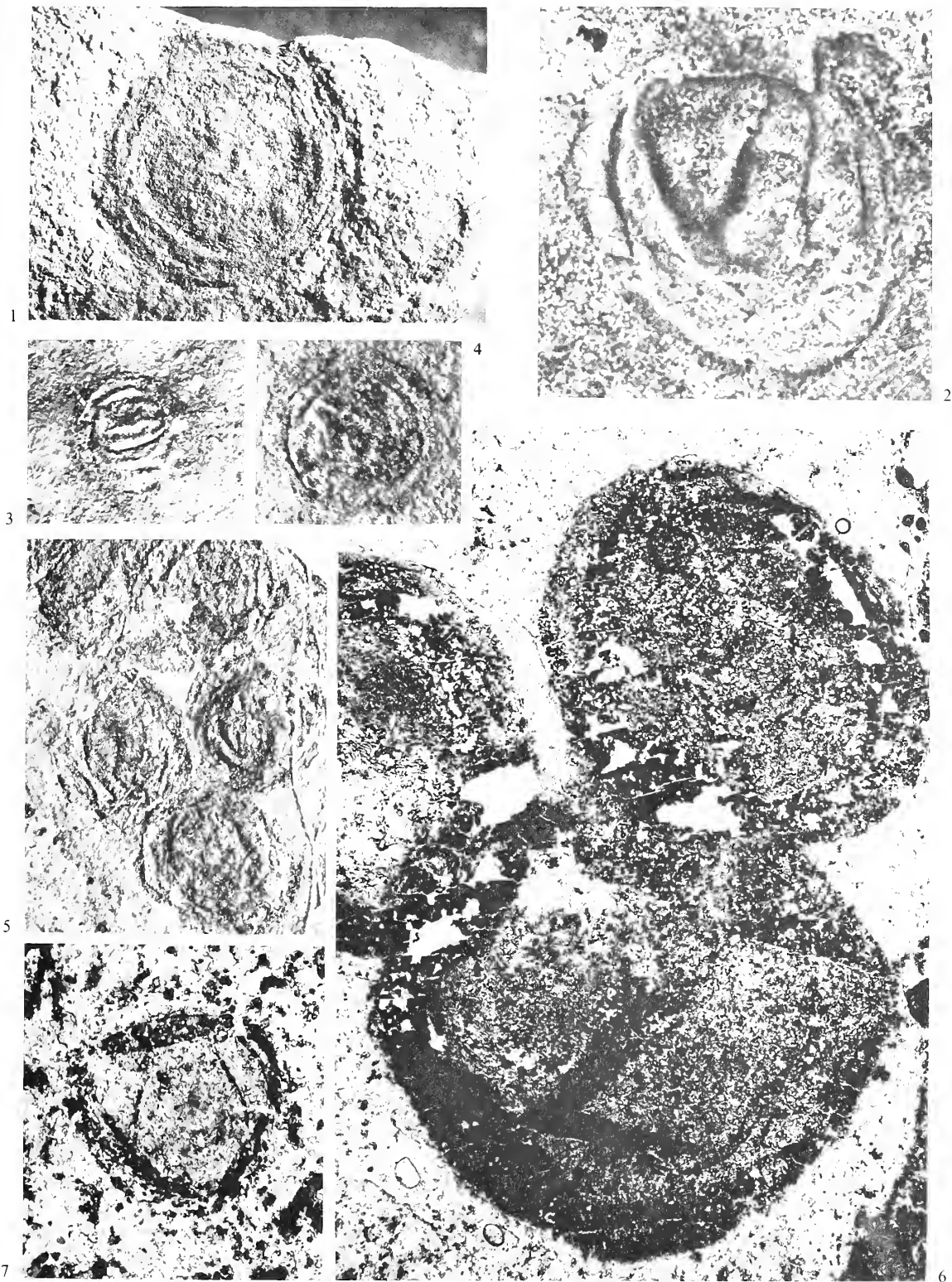
Dimensions. Individuals are commonly 2 to 2.5 mm in diameter. Walcott (1899, p. 234) recorded specimens ranging from 2 to 5 mm diameter though the largest illustrated (pl. 27, fig. 12) is barely 3 mm.

The Indian specimens of '*Fermoria*' seen by the authors range between 2 and 3 mm though Chapman (1935, p. 115) noted the largest as 4.5 mm diameter.

The Iranian specimens of '?*Fermoria*' according to Stöcklin *et al.* (1964) ranged from 1 mm to 'several mm', but the specimens seen by the authors range only between 2 and 3 mm. Assereto's unpublished photographs indicate specimens up to 6 mm being common though the scale on the photos raises some doubts. Wade's specimens from Central Australia range up to 8 mm whilst those from the Hector Formation only reach 4 mm. Brotzen (1941), Eisenack (1966), and Timofeev (1969) noted a size range from 0.5 mm upwards to about 2.5 mm and the last two have indicated that there is a continuous range downwards to much smaller sizes. Eisenack noted his smallest specimens as being only 62 μ m but expressed the feeling that there should be still smaller juveniles. This extreme range down into the sizes normally

EXPLANATION OF PLATE 61

Figs. 1–7. *Chuararia circularis* from Awatubi Member, Kwagunt Formation, Chuar Group, late Precambrian, of Nankoweap Butte, Grand Canyon, Arizona. 1, Lectotype, $\times 10$, U.S. Nat. Museum, 33800. 2, $\times 25$, Univ. Leic. 49398b. 3, $\times 25$, Univ. Leic. 49375. 4, $\times 25$, Univ. Leic. 49495. 5, Small cluster, $\times 25$, Univ. Leic. 49392. 6, Peel of small cluster, $\times 40$, Univ. Leic. 56744. 7, Peel showing infolded margins, $\times 25$, Univ. Leic. 56743a.



expected for nanno-plankton raises considerable difficulties both of nomenclature and definition, since nanno-plankton of this general nature have been placed in a number of genera and species by palynologists, chiefly in Russia (see Downie 1967; Timofeev 1965, 1969, 1970). Surface ornament and textures present in juveniles are not necessarily present in the mature forms, so that *Chuarina* may include adults of several smaller species. The definition of *Chuarina* is thus arbitrarily restricted to forms larger than 0.5 mm. Roblot (1964) figured a 'sporomorph' 256 μm in diameter from the Brioverian of Normandy which could well be a small *Chuarina*.

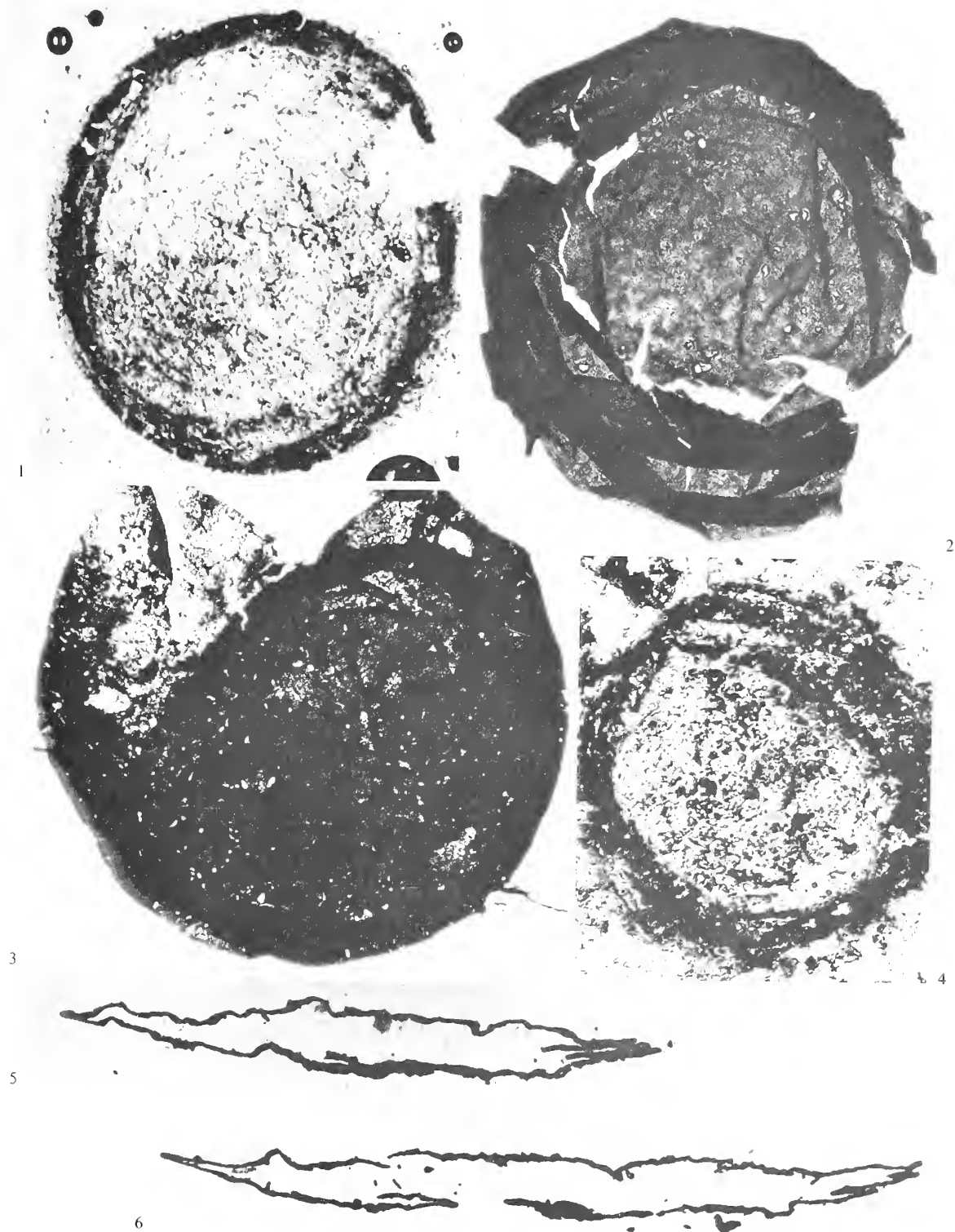
Remarks. Topotype specimens of *C. circularis* occur as black carbonaceous discs on the bedding laminae of dark blue-black shale. The discs may be solitary or in clusters, of which the largest so far seen numbered twenty-three. Individuals in the clusters never show overlap, though some lateral crushing may be seen. This is taken to indicate that the individuals were spheroidal, or at least inflated discoidal, when deposited, since spheroids do not normally pile up on top of one another. The clusters do not suggest that there was any direct connection between individuals but rather that they came to rest washed together in random fashion. The same observation can be made regarding the specimens from Iran, where clusters of fifty or more have been seen.

Chuarina shows no surface ornament, except wrinkles and cracks due to crushing. Examination with the scanning electron microscope simply shows the grain size of the enclosing sediments impressed on the fossil. Frequent mud-cracked and ripple-marked surfaces indicate intermittent desiccation, and the wrinkles are thus probably due to shrinkage on drying. They show no regular behaviour except for the concentric wrinkle or wrinkles near the margin of many specimens. This is particularly well seen in the Iranian specimens. Serial sections of *C. 'wimani'* show, as Eisenack (1966) noted, two simple walls with a thickness of 50 to 70 μm . The preservation of *C. circularis* from the Grand Canyon has not permitted successful serial sections as yet. The walls of *C. 'wimani'* meet about 0.25 mm from the margin, giving the false impression of a narrow marginal flange.

A number of diagenetic effects have been observed on both *C. circularis* and *C. 'wimani'*, and they appear to have counterparts in some descriptions and photographs of '*Fermoria*'. Most obvious is the effect of minute cubes of pyrite in the shale, which give a granulose effect, presumably the cause of Chapman distinguishing *F. granulosa* as a separate species. A solitary cube can be seen in some photographs of *C. 'wimani'*. Otherwise cracking and distortion seem to be the main effects. Many *C. circularis* show radial cracks in the margin, commonly three or four but sometimes many more. This may be the reason why Chapman distinguished *F. tripartita*. Some specimens show openings in the young stages according to Eisenack,

EXPLANATION OF PLATE 62

Figs. 1-6. *Chuarina circularis* from the late Precambrian of the Grand Canyon and Sweden. 1, Peel with marginal crushing simulating a flange, $\times 25$, from Grand Canyon, Univ. Leic. 56745. 2, *C. 'wimani'*, separated and mounted, showing wrinkling of flanks, $\times 30$, Visingsö Series, Sweden. Univ. Uppsala Visingsö Colln. 3, *C. 'wimani'*, separated and mounted, showing burst open appearance, $\times 30$, Visingsö Series, Sweden (= Wiman 1894, pl. 5, fig. 2). Univ. Uppsala Visingsö Colln. 1-9. 4, Peel, $\times 25$, from the Grand Canyon. Univ. Leic. 56743b. 5, 6, *C. 'wimani'*, two serial sections, showing thickened or duplicated flange on one side, $\times 35$, Visingsö Series, Sweden. Univ. Uppsala Visingsö Colln. 1-9.



FORD and BREED, *Chuaridictyon*

but the only one observed in the 'mature' specimens is quite clearly where the spheroid burst open, either on initial crushing or perhaps during life (Pl. 62, fig. 3).

The specimens from the Hector Formation show more relief than any of the others, but this is also thought to be a diagenetic effect in the rather more indurated argillite matrix. Small round slickensided marks are probably crushed gas bubbles and indicate considerable compaction. Some *Chuarina* from the Hector are convex and others concave on the same lamina and both show wrinkles due to shrinkage or compaction. The impressions in the Australian material are sufficiently strongly developed in fine-grained sandstone to indicate that the globular bodies were not fully compressed when the sandstone was indurated.

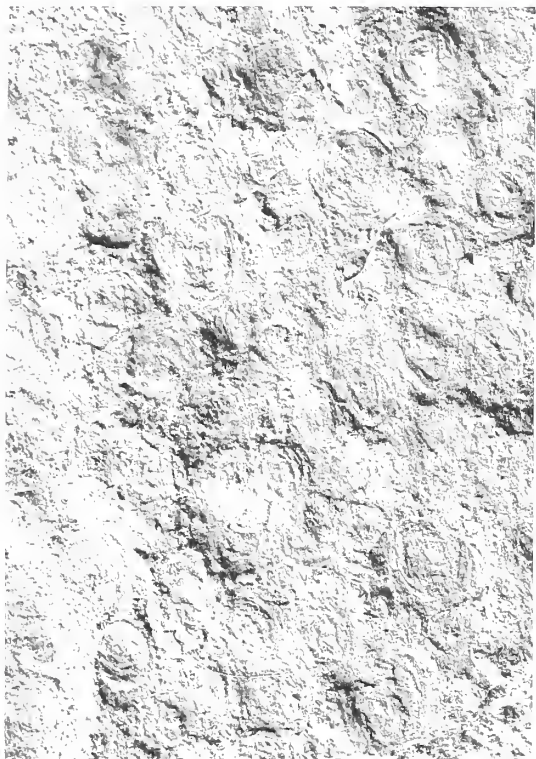
Chemical composition. As Eisenack (1966) observed, the fossils are easily incinerated and leave a white ash. Eisenack found this was silica in his specimens, but some clay minerals and pyrite appear to be present in others. He regarded the silica, clay, and pyrite as of diagenetic origin. The substance is insoluble in KOH, concentrated HCl, HF, and H₂SO₄ even after heating. Cold concentrated HNO₃ has no effect, but boiling HNO₃ bleaches the substance. Schülze solution bleaches the substance more quickly, but can be completely destructive. Eisenack examined some specimens of *C. 'wimani'* for phosphate by chemical means, with negative results. Examination of *C. circularis* from the Grand Canyon by electron microprobe by Mr. Jarosewich in the Smithsonian Institution also failed to reveal phosphorus. The last test indicates that *Chuarina* is not of brachiopod nature, whilst the remainder suggest only that it is organic, largely carbon. Eisenack also noted pronounced shrinkage on treatment with KOCl which, he claimed, distinguished *Chuarina* from pollen, spores, and hystrichospheres (and acritarchs presumably), as it was a characteristic reaction of fossil chitinous foraminiferids. However, this test is not considered valid by all palynologists. Further tests by electron microprobe are thought to be pointless as they would only determine elements that were likely to be present in the enclosing shale.

Biological affinities. As Eisenack (1966) and Timofeev (1970) have noted, there is a size range from nanno-plankton up to 2 mm. Timofeev has applied the name *Kildinella* (a sphaeromorphid acritarch) with a new trivial name *magna* (1969, 1970) to a specimen previously named *C. 'wimani'* by Brotzen, without discussion of reasons for so doing. He has further placed this genus in two separate 'groups' of acritarchs, Sphaeromorphida and Megasphaeromorphida, without making it clear what status his 'groups' have in relation to the Group Acritarcha of Evitt (1963) and the Subgroup Sphaeromorphitae of Downie, Evitt, and Sarjeant (1963).

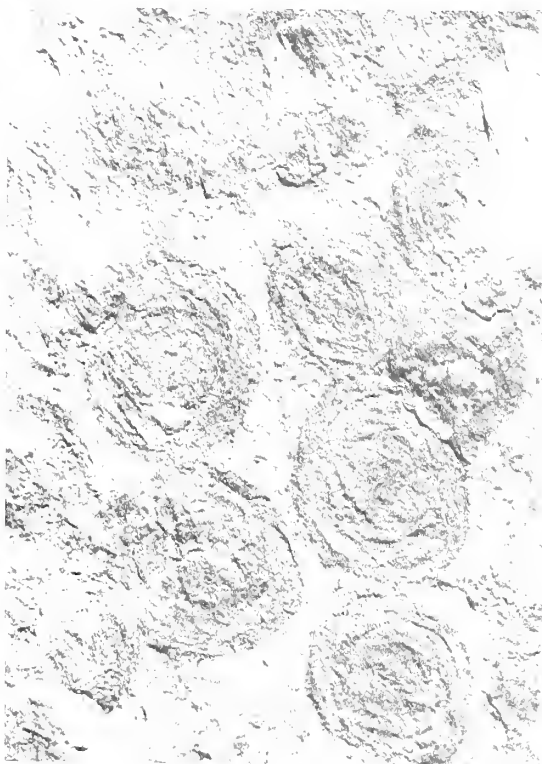
Assignment to higher taxa also presents problems. The 'group' Megasphaeromorphida erected by Timofeev (1969) is little more than a convenient grouping for large planktonic organisms, and seems to be broadly equivalent to superfamily status. Alternatively the present authors feel that there is some merit in placing

EXPLANATION OF PLATE 63

Figs. 1-4. *Chuarina circularis* from the late Precambrian of Iran, Australia, and Grand Canyon. 1, 2, From the Chapoghlu Shale, W. Elburz, Iran, $\times 10$, Univ. Leic. 58123. 3, From Central Australia, $\times 10$, latex cast of University of Adelaide, Geology Department spec. F16472. 4, Cluster from the Grand Canyon, $\times 10$, Univ. Leic. 49398a.



1



2



3



4

Chuar with *Leiosphaeridia* in the family Leiosphaeridae. Comparison with the descriptions of *Leiosphaeridia* and *Tasmanites* provided by Wall (1962) and by Schopf (in Tschudy and Scott 1969) shows that *Chuar* is similar to both but much larger. *Tasmanites*, however, has a punctate wall and has been compared with the modern *Pachysphaera pelagica* and *Halosphaera minor* of the Class Prasinophyceae, Phylum Chlorophyta. *Chuar* has no visible punctation, so that it is more appropriately referred to the family Leiosphaeridae of the Acritarcha.

All current writers (e.g. Glaessner 1966; Cloud 1969; Timofeev 1970) have noted *Chuar* as a fossil alga. The writers support this assignment and, following Glaessner (1966) and Timofeev (1970), regard *Chuar* as an unusually large acritarch-like organism, or organisms, comparable with *Leiosphaeridia*.

It may be noted that many late Precambrian and Cambrian micro-plankton with diameters from 0.1 to 0.25 mm have been recorded (e.g. Roblot 1964; Timofeev 1965, 1969, 1970). Perhaps only a few of these forms grew to the size of *Chuar*. Obviously more palaeopalynological research needs to be done on these rocks to extract the full range of nanno-plankton as well as the larger forms. Downie (in Ford and Breed 1969) provided preliminary notes on the nanno-plankton. In spite of *Chuar* being placed in a group separate from *Pachysphaera*, the observation by Parke (in Wall 1962, p. 359) that the latter releases a flagellated stage raises the possibility that *Chuar* may have done so. Few specimens show any sign of an opening but they may either have split equatorially and so show no opening whilst lying in this plane, or they may have been immature when fossilized. One specimen of *C. 'wimani'* (Pl. 62, fig. 3) has obviously split open but this may have been during burial or extraction.

STRATIGRAPHIC OCCURRENCE

Walcott (1899, p. 234) noted that his specimens were collected 730 ft (219 m) beneath the summit of the Chuar terrane in the Kwagunt Valley of Grand Canyon. On referring to his measured section of the Chuar (1894, pp. 508–512) this appears to be close to the Cherty Pisolite in the Walcott Member of the Kwagunt Formation as defined by Ford and Breed (1972a, 1973), but Walcott was ambiguous in that the measurement of 730 ft (219 m) could have been either by altitude or by stratigraphic thickness. However, Ford and Breed (1969, 1972a, 1973) found *Chuar* in shales over a thickness of about 100 ft (30 m) on Nankoweap Butte, overlooking Kwagunt Canyon, with the greatest abundance in two beds about 30 and 80 ft (9 and 24 m) below the Flaky Dolomite, a horizon at the base of the Walcott Member and the top of the Awatubi Member. Rare specimens were also found some 5000 ft (1500 m) lower in the Chuar Group, in shales about 100 ft (30 m) below the top of the Tanner Member. The cherty pisolite near the base of the Walcott Member has recently yielded a flora of microscopic filamentous and spheroidal algae (Schopf, Ford, and Breed 1973).

The age of the Chuar Group has been discussed by Ford *et al.* (1972) and by Ford and Breed (1972a, 1973) and appears to be less than 1000 m.y., but definitely Precambrian, i.e. Upper Riphean.

The Swedish Visingsö Formation containing *C. 'wimani'* is now regarded as

belonging to the Varegian Formation, which is the younger part of the Eocambrian, deposited less than 950 m.y. ago (Magnusson 1965).

The Iranian specimens come from the Chapoghlu Shale regarded by Stöcklin *et al.* (1964) as in the lower part of a series of Upper Precambrian to ?Lower Cambrian age.

The Hector Formation of Canada is unconformably covered by Cambrian and rests unconformably on Beltian, and is thus part of the Windermere Series, recently dated by Harrison and Peterman (1971) as between 570 and 850 m.y. Licari and Cloud (1968) reported the discovery of nanno-plankton resembling the modern green algal family Oocystaceae in these beds.

Timofeev (1970) noted that Megasphaeromorphida occurred in the Upper Riphean of Eastern Siberia, and Shatsky (1952) also recorded *Chuarina* in the Upper Riphean, though he gave no details.

The occurrences of *Fermoria* are more difficult to place owing to the confusion of records of truly organic remains with those of inorganic substances. It must suffice to say that the Vindhyan rocks are regarded by most writers on India as being of late Precambrian age (Howell 1956; Pascoe 1959).

The Central Australian occurrence is in beds assigned to the topmost division of the Upper Precambrian. The presence of numerous medusoids suggests a correlation with the Ediacaran of South Australia, but none of the medusoids is common to both localities and the Ediacaran fauna has not been found in association with *Chuarina* elsewhere.

Sporomorphs up to 256 μm diameter have been recorded from the Brioverian of Normandy by Roblot (1964, pl. 11, fig. 12) which could well be a small *Chuarina*. The Brioverian is generally regarded as late Precambrian.

Thus all known occurrences of *Chuarina* and fossils here regarded as synonymous, are in late Precambrian rocks, broadly falling within the Upper Riphean division of Precambrian time, though the lack of radiometric age data on most of the sediments concerned allows no placing more accurate than between 1000 and 570 m.y. ago.

CONCLUSIONS

It is concluded that *Chuarina* is of plant origin, most probably being a large leiosphaerid acritarch. An arbitrary lower size limit is adopted of forms larger than 0.5 mm. They are generally preserved as flattened hollow spheroids, with cracks and wrinkles owing to crushing and diagenesis. Forms previously named *C. wimani*, *Kildinella magna*, and *Fermoria minima* are thought to be at present indistinguishable from *C. circularis*. The stratigraphic range seems to be limited to the Upper Riphean, roughly from 1000 m.y. ago to the beginning of the Cambrian. Occurrences are now known in Arizona, Canada, Sweden, France, Siberia, Iran, India, and Australia, and it seems clear that these carbonaceous spheroids provide a stratigraphic index fossil for late Precambrian rocks.

Acknowledgements. Thanks are due to the Grand Canyon National Park authorities for their assistance in many ways, and to Hatch River Expeditions and Arizona Helicopters Inc. for assistance in reaching the field area. A grant from the Grand Canyon Natural History Association facilitated field work, and one of us (T. D. F.) received a Fulbright Travel Grant and help from the University of Leicester Research Board.

Thanks are also due to the following for their assistance in procuring specimens and photographs: Dr. Ellis Yochelson (U.S. Geological Survey) for loan of specimens and supplying notes and photos of type specimens; Professor Preston Cloud (University of California) for the gift of specimens from the Hector Formation and for copies of Assereto's photographs of Iranian material; Professor Martinsson (University of Uppsala) for loan of Wiman's specimens; the Director-General of the Geological Survey of India in Calcutta for the gift of specimens of *Fermoria*; Dr. Khadem, Managing Director of the Geological Survey of Iran, for the gift of Iranian *Fermoria*; to Professor Glaessner (University of Adelaide) for supplying latex casts of Dr. M. Wade's Australian material; and to Dr. W. S. Gussow for assistance with details of the Hector Formation locality.

Mr. Michael Hayles (University of Leicester) has taken most of the photographs.

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Addendum. Since writing the above, the authors have heard that Dr. W. C. Gusow has prepared a note on *Chuarina* from the Hector Formation, of Banff National Park, Canada. This will be published in *Journal of Palaeontology*, 1973, 47, no. 6.

VISÉAN TRILOBITES FROM HOLWELL, SOMERSET

by GERHARD and RENATE HAHN

ABSTRACT. Three species of trilobites from the Clifton Down Limestone (Viséan) at Holwell Quarry in the Mendip Hills (Somerset) are described: *Linguaphillipsia matthewsi* sp. nov., *Phillipsia (Phillipsia) holwellensis* sp. nov., and *Cummingella jonesi jonesi* (Portlock 1843). This is the first record of the genus *Linguaphillipsia* Stubblefield 1948 from the Carboniferous Limestone of western Europe.

THE stratigraphical relationships and age of trilobites from the Carboniferous Limestone facies of the Lower Carboniferous are still poorly known, certainly so when compared with what is known about trilobites in the Culm facies (G. and R. Hahn 1971).

A recently discovered fauna from low in the Clifton Down Limestone (Viséan) at Holwell Quarry, Somerset (ST 727 452), includes three species of trilobite, the subject of this paper. Dr. S. C. Matthews (University of Bristol) is working on other aspects of the rich fauna. The thirty trilobite specimens are well preserved and partly silicified. They belong to three species: *Linguaphillipsia matthewsi* sp. nov., *Phillipsia (Phillipsia) holwellensis* sp. nov., and *Cummingella jonesi jonesi* (Portlock 1843). The majority of the specimens belong to *L. matthewsi*, five (pygidia only) to *P. (P.) holwellensis*, one (a pygidium) to *P. (P.)* cf. *holwellensis*, and two (one pygidium, one fragment of a free cheek) to *C. jonesi jonesi*.

The specific composition of the trilobite fauna is surprising as only one of the three species, *C. jonesi jonesi*, belongs to a characteristic western European genus. *L. matthewsi* is the first record of this genus in western Europe and specifically is closest to *L. ohmorensis* (Ohkubo 1951) from Japan. Although *Phillipsia (Phillipsia)* is a common subgenus in the Lower Carboniferous of western Europe *P. (P.) holwellensis* is closest to *P. (P.) conserrata* Weber 1937 from the ?Viséan of the southern Urals.

Acknowledgements. We are grateful to Dr. S. C. Matthews (University of Bristol) for making available to us material originally discovered by Dr. N. H. Trewin (University of Aberdeen) and to Mr. R. G. Godwin for the excellent photographs.

Repository. The material is deposited in the Geology Museum, University of Bristol, and bears the numbers BU 21000-21030. Indeterminable fragments are unnumbered.

DESCRIPTIONS

Family PROETIDAE Hawle and Corda 1847
Subfamily LINGUAPHILLIPSINAE G. and R. Hahn 1972
Genus LINGUAPHILLIPSIA Stubblefield 1948

Type species. *Linguaphillipsia terapaiensis* Stubblefield 1948.

Diagnosis. Treatise, p. 401, and G. and R. Hahn 1972, p. 360 ('Beziehungen').

[Palaeontology, Vol. 16, Part 3, 1973, pp. 551-561, pl. 64.]

Linguaphillipsia matthewsi sp. nov.

Plate 64, figs. 1-6; text-figs. 1-2

Derivation of name. After Dr. S. C. Matthews.*Holotype.* Cephalon BU 21000; Pl. 64, fig. 1; text-fig. 1.*Type locality.* Holwell Quarry, Somerset, England (National Grid Reference ST 727 452).*Type horizon.* Clifton Down Limestone, Viséan.*Distribution.* Known only from type locality and type horizon.*Paratypes.* Four fragments of cranidia (BU 21001-21004), four free cheeks (BU 21005-21008), 2 fragmentary free cheeks (BU 21009-21010), 4 pygidia (BU 21019-21022), 7 thoracic segments, complete or broken (BU 21011-21018).*Diagnosis.* A species of *Linguaphillipsia* with the following characteristics. Glabella long, partially overhanging the anterior border, markedly constricted between γ - γ , between δ - δ only slightly broader than between β - β . Palpebral lobes situated posteriorly, long facial suture without a straight portion between ϵ - ζ . Eyes large, genal spines medium in length. Pygidium slightly triangular in outline, with 17-18 rings and 10-12 ribs on each pleura. Border of medium breadth, separated by a well-impressed border furrow. Relief and sculpture (nodes) on the cephalon and pygidium well marked.*Description.* *Cephalon* (holotype, external mould, BU 21000). Lateral view (text-fig. 1b). Glabella rising above anterior border, continuously curved to a point near occipital furrow; occipital furrow well incised. Occipital ring somewhat higher than glabella, reaching highest point in occipital node, situated near posterior margin. Border vertical on cranidium, overlapped by glabella, ornamented along its total length by 7-8 parallel lines which extend on to genal spine. Free cheek strongly vaulted, eye large, rising somewhat posteriorly.Dorsal view (Pl. 64, fig. 1; text-fig. 1a). Outline oval, only slightly broader than long (without genal spines). Glabella long, tongue-like in shape, extending forward almost to anterior margin, markedly constricted at γ . Anterior part well rounded and arched, posterior part flatter and broader than anterior part, greatest breadth between δ - δ . Glabellar furrows (1p-3p) deeply incised. 1p strongly curved backward, cutting preoccipital lobes (L1) out of glabella, and extending to occipital furrow. 2p-3p short; 2p directed slightly backward, but 3p directed slightly forward. Occipital furrow nearly straight (tr.), with only slight backward curvature behind L1 on each side. Occipital ring heavily arched in its centre, but immersed on each side behind L1. Dorsal furrows deeply incised. Fixed cheek with very long, moderately diverging anterior

EXPLANATION OF PLATE 64

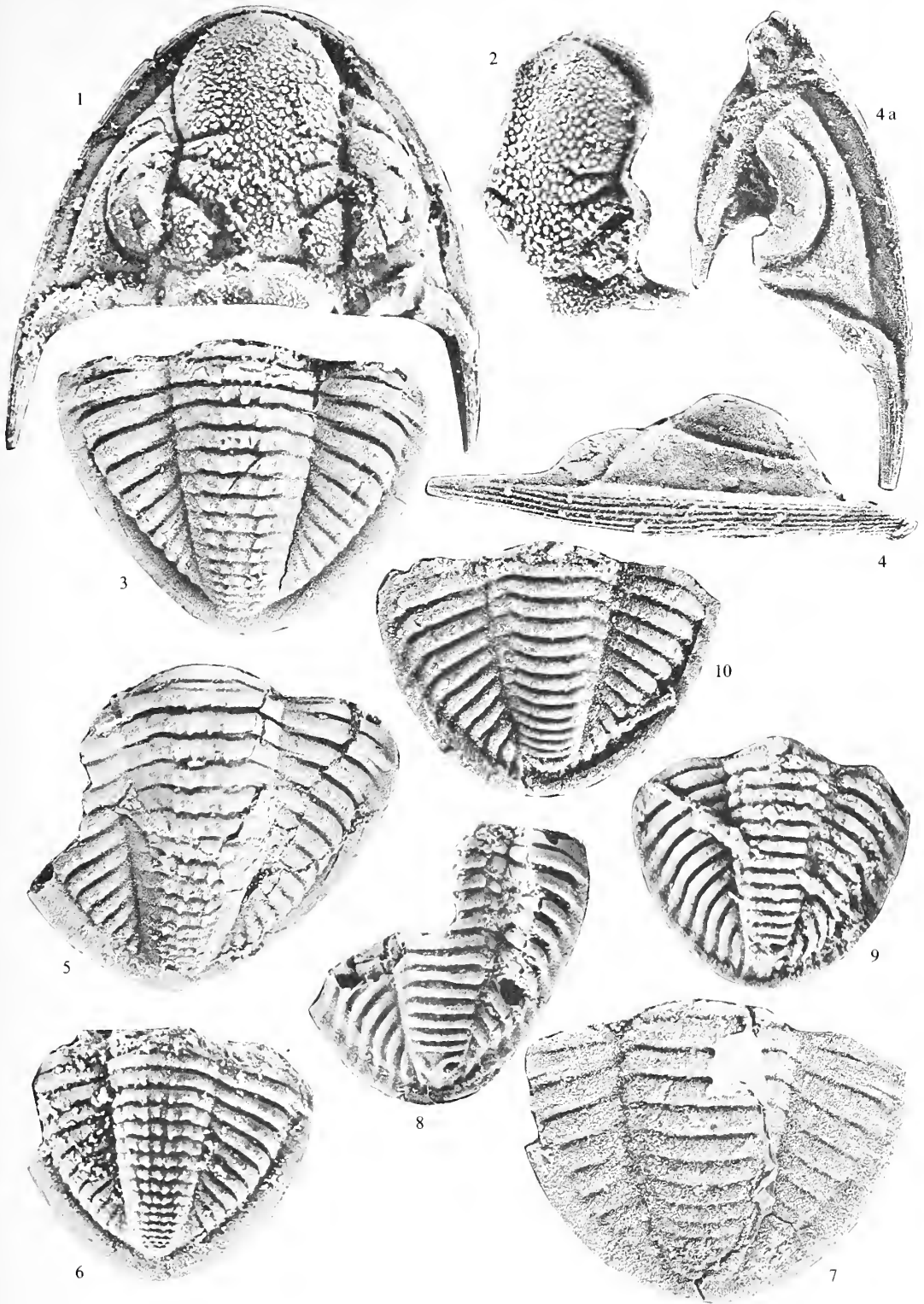
Figs. 1-6. *Linguaphillipsia matthewsi* sp. nov. 1, Cephalon, holotype, $\times 5.9$ (BU 21000). 2, Cranidium, (broken during transport after photographing, therefore without number and scale). 3, Large pygidium, $\times 7.7$ (BU 21020). 4, Free cheek, $\times 6.0$ (BU 21005). 4a, Dorsal view; 4b, Lateral view. 5, Large pygidium, $\times 5.5$ (BU 21021). 6, Medium sized pygidium, $\times 4.8$ (BU 21019).

Fig. 7. *Cummingella jonesi jonesi* (Portlock 1843). Pygidium, right pleural lobe (broken during transport after photographing), $\times 5.2$ (BU 21029).

Figs. 8-9. *Phillipsia* (*Phillipsia*) *holwellensis* sp. nov. 8, Pygidium, $\times 2.9$ (BU 21024). 9, Pygidium, right pleural lobe (broken during transport after photographing), $\times 3.2$ (BU 21025).

Fig. 10. *Phillipsia* (*Phillipsia*) cf. *holwellensis* sp. nov. Pygidium, left pleural lobe (broken during transport after photographing), $\times 6.8$ (BU 21028).

All specimens from Viséan at Holwell, Somerset.



G. and R. HAHN, trilobites from Holwell

part (γ - β), long palpebral lobe, and short posterior part. β situated anteriorly, rounded; γ , δ , and ϵ also gently rounded, no straight portion ϵ - ζ evolved. Posterior part of fixed cheek short (exsag.), medium in length (tr.). β situated slightly inward of δ . Border of the free cheek relatively broad, limited by a distinct border furrow. Striations of the border only partly visible. Free cheek ascending rapidly from inner side of border to eye; eye socket separated by a well-marked eye furrow. Eye large, strongly curved, lenses not preserved. Posterior border of free cheek separated by deeply incised border furrow, which extends laterally to meet outer border furrow, then curves backwards into shallow spinal furrow. Genal spine of medium length, sharply pointed, ornamented with some striations, divided longitudinally by spinal furrow into two portions. Internal portion rounded, larger and more elevated than external portion, which diminishes towards tip of spine. Surface of glabella covered by coarse nodes; nodes on occipital ring finer; only few nodes on cheek region. Doublure as wide as border on free cheek; narrowed on the genal spine, slightly broadened anteriorly. Front part occupied by rostral plate which lies exactly beneath the glabella. Doublure covered with striations similar to those seen on the border in lateral view and dorsal view. Doublure of occipital ring not preserved.

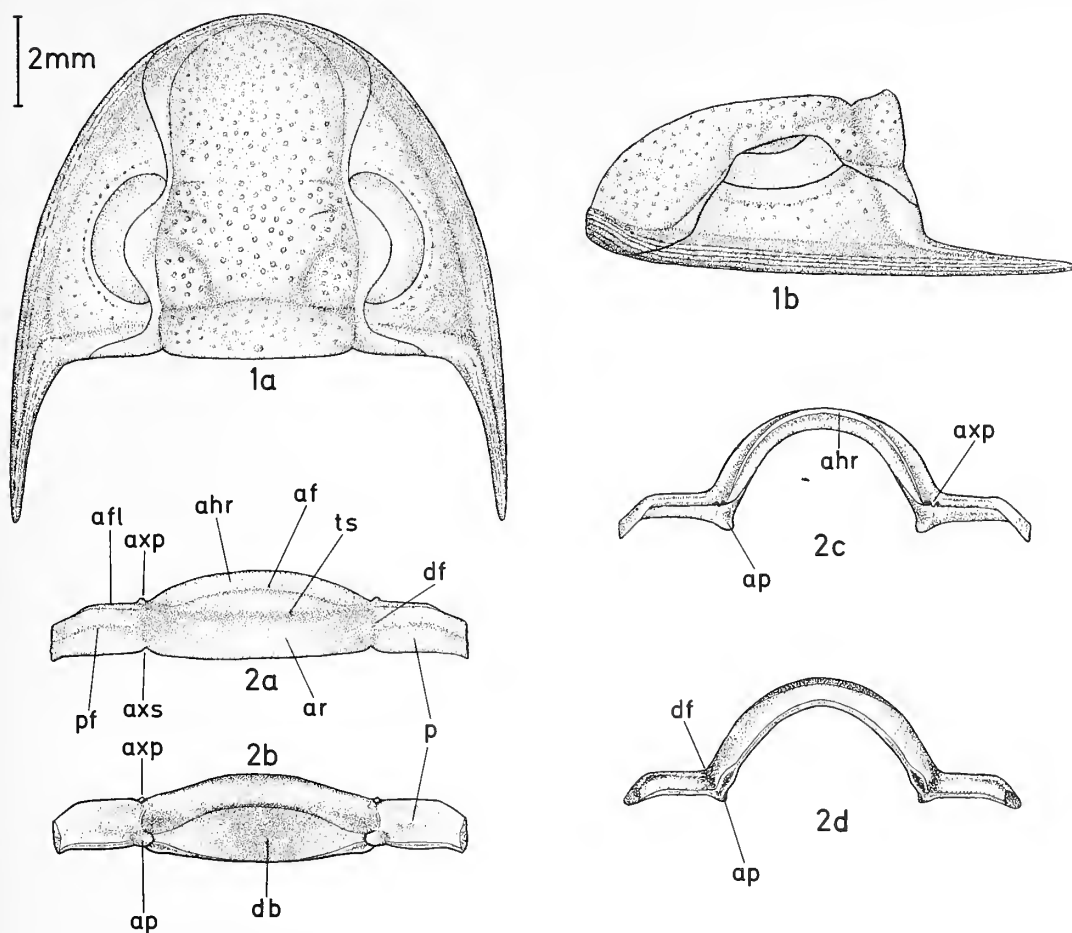
Measurements (in mm). Lengths: cephalon (without genal spine) 8.0, cephalon (with genal spines) 11.7, glabella 6.5, β - γ 2.75, palpebral lobe (γ - ϵ) 2.9, ϵ - ω 1.25, eye 3.3; breadths: cephalon (at the base of the genal spines) 11.2, cranium between β - β 5.1, cranium between δ - δ 5.8, glabella between δ - δ 4.6.

Thoracic segment (BU 21011). Dorsal view (text-fig. 2a). Axis broad (tr.) and narrow (sag.), subdivided into a short (sag.) anterior part that disappears laterally, and a longer (sag. and exsag.) posterior part, which is separated from anterior part by distinct furrow; anterior part situated somewhat lower than posterior portion. Articulating half-ring short, not as long (sag.) as anterior part of axis; axial furrow well pronounced, extending laterally to meet furrow that divides axis. Dorsal furrows slightly incised. Inner (adaxial) part of each pleuron situated horizontally, outer (abaxial) part bent downward (broken on BU 21011, but visible on BU 21012). Pleural furrow beginning at dorsal furrow, extending nearly to outer border. Anterior flange well pronounced, axial process small, fulcral process not differentiated; posterior flange not well separated from the pleura, axial socket and fulcral socket indistinct. Exact shape of lateral pleural border not preserved in any of specimens at hand. Ventral view (text-fig. 2b). Posterior doublure very prominent, covering nearly whole axis (sag.). Apodemata well evolved, node-like. No vertical rim between inner and outer part of pleura as seen in *Treatise*, figs. 49B, 50.

Anterior view (text-fig. 2c). Axis strongly arched; apodemata relatively short, situated beneath the dorsal furrow on each side. Inner part of pleuron horizontally disposed, outer part bent downward at an angle of about 45°. Axial process on each side visible as a little node. Posterior view (text-fig. 2d). Arching of axis as in anterior view. Posterior wall of the segment slightly grooved above the apodemata, grooves continuing on each side of posterior wall of pleuron, visible ventrally also (see text-fig. 2b). Dorsal furrows distinct, but nearly obsolete in anterior view. (As a whole the thoracic segments are similar to those of *Paladin* (*Paladin*) *helmsensis* (Whittington 1954, pl. 3, figs. 7-16).) Number of thoracic segments in *L. matthewsi* unknown (only isolated segments are present), but presumably totalling nine as in nearly all Carboniferous Proetidae. Affiliation of the described thoracic segments to *L. matthewsi* not proven, but probable because of rarity of all other trilobite species in the Holwell fauna in comparison with *L. matthewsi*.

Pygidium (BU 21019). Side view. Rhachis nearly as high as pleural lobe, curving gently back to last ring, then falling down vertically to short, convex postaxial portion which is part of pygidial border. Rings prominent, strongly arched, with steep posterior slopes. Pleural ribs also prominent, well separated by pleural furrows. Anterior part more nearly horizontally disposed than behind rhachis. Posterior view. Rhachis well arched, curved semicircularly. Inner half of pleura directed horizontally, outer half steeply sloping downward. Anterior part of border sloping parallel to outer half of pleura.

Dorsal view (Pl. 64, figs. 3, 5-6). Outline slightly triangular in shape, somewhat broader than long. Rhachis long, nearly as broad as a pleural lobe, gently tapering posteriorly, with termination well rounded. 17-18 rings; rings 1-10 very prominent, last rings indistinct. Each ring divided (trans.) into a spinous central portion and on each side a smooth portion (which covers the region where the nearly invisible impressions of the pygidial muscles are situated). Central part ornamented with 5-7, slightly backwards directed, short spines, one of which covers sagittal line. Axial furrows directed straight (tr.) centrally, showing slight



TEXT-FIGS. 1-2. *Linguaphillipsia matthewsi* sp. nov. Viséan, Holwell, Somerset, England.

1. Cephalon, holotype, BU 21000 (see Pl. 64, fig. 1). *a*, Dorsal view; *b*, Lateral view.

2. Thoracic segment, BU 21011. *a*, Dorsal view; *b*, Ventral view; *c*, Anterior view; *d*, Posterior view.

Abbreviations. *afl* anterior flange; *ahr* articulating half-ring; *ap* apodeme; *ar* axial ring; *axp* axial process; *axs* axial socket; *db* doublure; *df* dorsal furrow; *af* axial furrow; *p* pleura; *pf* pleural furrow; *ts* transversal furrow, dividing axial ring in an anterior and a posterior portion.

backward curvature against dorsal furrow; anterior axial furrows well incised, posterior furrows only slightly incised. Dorsal furrows distinct. Pleural lobe with 10 ribs and place for one more. Ribs well separated by narrow, deeply incised pleural furrows. Rib furrows vestigial, visible as weak line on anterior ribs only: on first rib grooved against border, separating clearly anterior and posterior branch of rib. Anterior branch of ribs distinctly broader (exsag.) than posterior branch; ribs rounded in cross-section, ornamented with small node at half-length (tr.). Ribs terminating at well-incised border furrow which separates relatively narrow, convex curved border from remaining part of pleural regions. First rib furrow continuing on to border. Terminal part of border in contact with posterior slope of rhachis. Connecting half-ring and connecting half-ribs (sag., exsag.) narrow; connecting half-ribs marked by slight process which is directed anteriorly and is situated somewhat inward of rib nodes. Doublure (visible in cross-section on left pleura) as wide as border, pressed against it, ornamented with striations.

Measurements. See Table 1.

TABLE 1. Measurements (in mm) of three pygidia of *Linguaphillipsia matthewsi* sp. nov.

	Pygidium		Rhachis		Number of rings	Number of ribs
	Length	Breadth	Length	Breadth		
BU 21019	7.9	10.0	7.0	3.5	17	10 (+1)
BU 21020	5.75	6.75	5.2	2.6	16 (+1)	9 (+1)
BU 21021	9.3	11.3	8.5	4.0	18	12

Variations. Among the free cheeks significant variation is found only in the structure of the border region. In BU 21005 the border furrow is relatively shallow and the border itself only slightly arched (Pl. 64, fig. 4), but in BU 21007 and BU 21008 the border furrow is more deeply incised and the border well arched. These two latter free cheeks are both smaller than BU 21005 (approximately half as long as BU 21005), so that these differences of the border regions may be interpreted as having arisen during postlarval ontogeny.

Among the pygidia the number of rings and ribs differs only slightly (see Table 1). The rib furrows are somewhat better expressed in BU 21020 (Pl. 64, fig. 3) and BU 21021 (Pl. 64, fig. 5) than in BU 21019 (Pl. 64, fig. 6). In all other respects the available pygidia are very similar, accentuating the specific characteristics of *L. matthewsi*.

Discussion. Among the characteristic features of *L. matthewsi* the most important one is the way in which the glabella encroaches on the anterior cephalic border. In *L. terapaiensis* Stubblefield 1948, *L. paczoltovicensis* (Jarosz 1914) and related species the glabella is separated from the anterior border by a deeply incised, prominent border furrow; in *L. silesiaca* (Scupin 1900), which is closely related to *L. terapaiensis*, the glabella is lengthened anteriorly and presses against the anterior border, but does not encroach on it. In *L. longicornuta* (Leyh 1897) and its allies the anterior border is broad (sag.) and plane, not arched, and the border furrow is vestigial. In these species the glabella also terminates at the border, and does not encroach on it. Only in *L. ohmorensis* (Ohkubo 1951) from the lowermost Carboniferous of Japan does the glabella encroach on the posterior part of the border in the manner seen in *L. matthewsi*. As both these species are similar in most of their other features, it seems probable that *L. matthewsi* might have descended from the older Japanese species. The main differences between *L. matthewsi* and *L. ohmorensis* are found in the structure of the pygidia: in *L. ohmorensis* the pygidium is more elongate and its border is broader. The number of rings and ribs is similar in the two species (17–18 rings and 10–12 ribs in *L. matthewsi*, 17 rings and 11 ribs in *L. ohmorensis*). Other differences between the two species are of minor interest; they involve the more slender glabella, the rather lesser arching of the cephalic border, the smoother surface, lacking granulation, of *L. ohmorensis*. It is possible that some of these differences are simply due to post-mortem influences, because in *L. ohmorensis* it is the inner mould that is known and in *L. matthewsi* the outer.

The geographical distribution of *L. ohmorensis* and *L. matthewsi* is perplexing, the one being found in Japan, the other in England. But *Linguaphillipsia* was a genus typical of the Tethys region during the Lower Carboniferous and has been found in nearly all parts of the Eurasiatic Tethys; in Austria, Turkey, Central Asia, SE. Asia, Japan, and Australia. From this central pool it seems that species occasionally invaded the border regions of Tethys: Germany, Poland, the Moscow Basin, and the Urals. It may be merely an accident of preservation that one of the two related species is found in the eastern part of the Tethys region, in Japan, and the other

near its western end, in England. Probably species closely related to *L. ohmorensis* and *L. matthewsi* would have spread out through most parts of the Tethys, as was the case with the *L. terapaiensis*-group, whose distribution is known from Poland to SE. Asia.

Subfamily PHILLIPSINAE Oehlert 1886
Subgenus PHILLIPSIA (PHILLIPSIA) Portlock 1843

Type species. *Phillipsia kellyi* Portlock 1843.

Diagnosis. Osmólska 1970, p. 79, and G. and R. Hahn 1972, p. 391 ('Beziehungen').

Phillipsia (Phillipsia) holwellensis sp. nov.

Plate 64, figs. 8–9; text-fig. 3

Derivation of name. After Holwell Quarry, Mendip Hills, England.

Holotype. Pygidium BU 21023₁; text-fig. 3.

Type locality. Holwell Quarry, in the Mendip Hills, Somerset, England.

Type horizon. Clifton Down Limestone, Viséan.

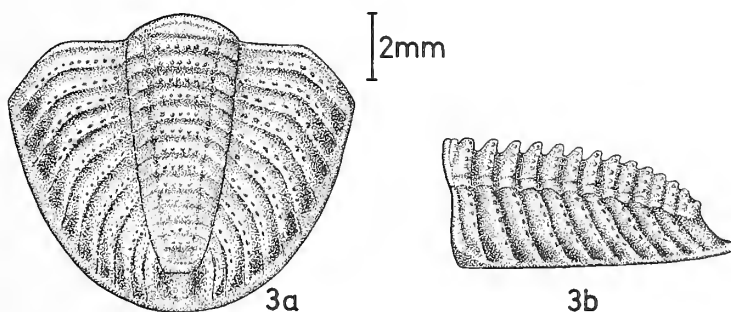
Distribution. Known only from the type locality and the type horizon.

Paratypes. 6 pygidia, partly broken, BU 21023₂₋₃, 21024–21027.

Diagnosis. A species of *Phillipsia (Phillipsia)* with the following characteristics: pygidium with 13–14 rings and 11–12 ribs. Posterior ribs sharply curving backwards. Posterior branches of the ribs suppressed, forming only the vertically directed posterior slope of each rib. Border very narrow, covered by the terminal portions of the ribs. End of rhachis peculiarly constructed (see below).

Description (holotype, BU 21023₁). Side view (text-fig. 3b). Rhachis not nearly as high as pleural lobes, curving down gently in its posterior half; postaxial portion inclined at about 45°. Rings prominent, rhachis furrows deeply incised. Pleural ribs also prominent, well separated by pleural furrows. Border horizontally disposed.

Posterior view. Rhachis well arched in a nearly semicircular curve. Dorsal furrows deeply incised. Pleural lobes transversely arranged where they first arise from dorsal furrow, then curving downwards very



TEXT-FIG. 3. *Phillipsia (Phillipsia) holwellensis* sp. nov. Viséan, Holwell, Somerset, England. Holotype pygidium, BU 21023₁. a, Dorsal view; b, Lateral view.

steeply in their outer parts but returning to horizontal disposition at border; anterior ribs sloping nearly vertically.

Dorsal view (text-fig. 3a). Outline oval, nearly as broad as long. Rhachis long, relatively narrow, clearly divided laterally into well-arched central portion and less well-arched lateral portions which cover region of impressions of pygidial muscles. Number of rings 13; rings prominent, separated by deeply incised, relatively broad (sag.) rhachis furrows; posterior rings also well differentiated. Terminal part of rhachis blunt, peculiar in its construction: behind the last ring there follows a very broad and shallow furrow that changes into a slight elevated rim at the very end of the rhachis. Postaxial portion separated from the rhachis by a distinct step. Dorsal furrows well incised. Pleural lobes sub-divided by 12 ribs on each side. Anterior ribs nearly transverse; in their direction posterior ribs directed clearly backwards. Rib furrows suppressed, visible only on the anterior ribs, rather more clearly seen on BU 21024 and BU 21025 (Pl. 64, figs. 8-9). Posterior branches of ribs confined to the vertically orientated posterior slope of each rib. Pleural furrows deeply incised, broad (exsag.). Ribs continuing on very narrow border, which is distinct from rest of pleural lobes only by its curving back into a horizontal position. Connecting half-ring (broken medially in holotype) and connecting half-ribs narrow (sag., exsag.), projecting only slightly. Surface of holotype nearly smooth, but on BU 21024 and BU 21025 with a row of very small nodules on each ring and rib (Pl. 64, figs. 8-9). Doublure (visible on BU 21023₂) narrow, with 7-8 soft striations.

Measurements (in mm). Length of pygidium 9.7, length of rhachis 8.5, breadth of pygidium 10.0, breadth of rhachis 4.0.

Variations. See under *Phillipsia* (*Phillipsia*) sp., below.

TABLE 2. Comparison of pygidia of best-known species of *Phillipsia* (*Phillipsia*) Portlock 1843

	<i>Rings</i>	<i>Ribs</i>	<i>Post. branches of ribs</i>	<i>Extension of ribs</i>
<i>Ph. (Ph.) gemmulifera</i> (Phillips 1836)	17	13	Not suppressed	Not on border
<i>Ph. (Ph.) ornata</i> Portlock 1843	19-21	16-18	"	On border
<i>Ph. (Ph.) truncatula</i> (Phillips 1836)	18	16	"	Not on border
<i>Ph. (Ph.) magnoculata</i> Osmólska 1970	16	13	"	"
<i>Ph. (Ph.) kellyi</i> Portlock 1843	17	13	Suppressed	"
<i>Ph. (Ph.) moelleri</i> Osmólska 1970	20	15	"	"
<i>Ph. (Ph.) conserrata</i> Weber 1937	16	10	"	On border
<i>Ph. (Ph.) holwellensis</i> sp. nov.	14	11-12	"	"

Discussion. As shown by Table 2, *Ph. (Ph.) holwellensis* has a peculiar combination of morphological features such as is not seen in any other species of *Phillipsia* (*Phillipsia*). These features are: 1, the low number of rings and ribs; 2, the fully posteriorly directed posterior ribs; 3, the suppression of the posterior branches of the ribs; 4, the prolongation of the ribs on the border; and 5, the very weak sculpture. A similar number of rings and ribs is seen only in certain Russian and Australian species, e.g. *Ph. (Ph.) conserrata* Weber 1937 (16 rings, 10 ribs), *Ph. ? (Ph. ?) dungenensis* Mitchell 1918 (14 rings, 12 ribs), and *Ph. (Ph. ?) rockhamptonensis* Mitchell 1918 (12 rings, 8 ribs). The latter two Australian species differ markedly from *Ph. (Ph.) holwellensis* in that the posterior branches of their ribs are not suppressed and by the lesser backward curvature of their posterior ribs (as far as can be judged from the photographs given by Mitchell). Rather more closely similar to *Ph. (Ph.) holwellensis* is *Ph. (Ph.) conserrata* from the ?Viséan of the southern Urals, which nevertheless differs in two characteristics: there are more rings, but fewer ribs, and the surface is ornamented by a coarse granulation (see Osmólska 1970 and G. and R. Hahn 1972).

Ph. (Ph.) holwellensis differs from all described species of *Phillipsia* (*Phillipsia*) so far known in western Europe not only by its lesser number of rings and ribs and its soft ornamentation, but also in its combination of suppressions of the posterior branches of the ribs and prolongation of the ribs on to the border. Suppression of the posterior branches of the ribs occurs in *Ph. (Ph.) kellyi* Portlock 1843 and *Ph. (Ph.) moelleri* Osmólska 1970, but in neither of these species do the ribs invade the border. On the other hand, *Ph. (Ph.) ornata* Portlock 1843, the ribs continue on to the border, but the posterior branches of the ribs are not suppressed. Finally, in *Ph. (Ph.) gemmulifera* (Phillips 1836), *Ph. (Ph.) truncatula* (Phillips 1836), and *Ph. (Ph.) magnoculata* Osmólska 1970 the posterior branches of the ribs are not suppressed, nor do the ribs invade the border. In both these respects they differ from *Ph. (Ph.) holwellensis*.

Ph. (Ph.) holwellensis appears as an isolated occurrence in the Viséan of England, and is most nearly related to *Ph. (Ph.) conserrata* from the southern Urals.

Phillipsia (Phillipsia) cf. holwellensis sp. nov.

Plate 64, fig. 10

Among the collection from Holwell there is one pygidium (BU 21028) which is similar to *Ph. (Ph.) holwellensis* in many features, especially in its low number of rings (13) and ribs (11) and in the peculiar structure of the terminal part of its rhachis, but which differs in three respects: its outline is more rounded, its last ribs have a lesser backward inclination, and (the most important) its border is somewhat elevated and is not invaded by the ribs (see Pl. 64, figs. 8–10).

Although this pygidium looks rather different from that of *Ph. (Ph.) holwellensis*, it is probable that it belongs to this species. The elevation of the border may have been due to post-mortem factors; it has developed to a relatively high degree on the right pleural lobe but is not seen in the anterior part of the left pleural lobe. The other differences may be interpreted as due to biological variation.

Subfamily CUMMINGELLINAE G. and R. Hahn 1967

Genus CUMMINGELLA Reed 1942

Type species. Phillipsia jonesii Portlock 1843.

Diagnosis. Treatise, p. 401, and G. and R. Hahn 1972, pp. 341–342 ('Beziehungen').

Cummingella jonesi jonesi (Portlock 1843)

Plate 64, fig. 7

*1843 *Phillipsia jonesii* Portlock, 308, pl. 11, figs. 3a–d.

1970 *Cummingella jonesi jonesi*, Osmólska, 55–56, pl. 5, figs. 3–4, text-figs. 5A, G, P, S.

1972 *Cummingella jonesi jonesi*, G. and R. Hahn, 348–351, 351 (with full synonymy).

Type, type locality, type horizon, distribution. See G. and R. Hahn 1972, pp. 350, 351.

Remarks. Among the Holwell trilobites are two specimens which can be referred to *Cummingella jonesi jonesi*. One is a pygidium (BU 21029, Pl. 64, fig. 7), originally complete, now broken along the fracture visible on the rhachis in the photograph, the other is the posterior part of a left free cheek, BU 21030.

Specimen BU 21029 compares very well with the pygidium of the lectotype figured by Stubblefield (1952, pl. 1, figs. 1a-c) in the shape of the pygidium, the shape of the rhachis, the number of rings (12+) and ribs (9), the breadth of the border and its arching. As in *C. jonesi jonesi* only the four anterior rib furrows continue distinctly on the border, whereas in *C. jonesi laticaudata* (Woodward 1884) (see Osmólska 1970, pl. 5, figs. 8-9) and in *C. jonesi orleiensis* Osmólska 1970 (see Osmólska 1970, pl. 5, fig. 1) the posterior rib furrows also encroach on the border. This feature determines the subspecific identity of the pygidium found at Holwell.

BU 21030 shows the posterior part of a free cheek, with an elevated lateral and posterior border, both of which are separated from the rest of the cheek by well-incised furrows. A genal spine is not present. The character of the free cheek is therefore as is found in *C. jonesi jonesi*.

These specimens of *C. jonesi jonesi*, although they add no new morphological information, do nevertheless contribute something to our stratigraphical knowledge of the subspecies. In all earlier recorded occurrences (including the type specimens) the exact stratigraphical location has been unclear. Stubblefield (1952) cites only 'Carboniferous Limestone', and Osmólska (1970, p. 55) states '(?Middle) Viséan' without more precise information. The first indication of a more exact stratigraphical attribution was given in G. and R. Hahn (1968), where specimens from Heiligenhaus (Germany) were reported to be confined to cuII δ , Lower Viséan. The Holwell specimens seem to occur at a comparable stratigraphical horizon. It is possible that *C. jonesi jonesi* was already extant in cuII β - γ (see the discussion in G. and R. Hahn 1968, pp. 441-442), but this is not yet confirmed, neither morphologically nor stratigraphically. Occurrences younger than the cuII/cuIII boundary and genuinely referring to *C. jonesi jonesi* are not known to us.

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SYMBIOTIC RELATIONSHIPS BETWEEN ECTOPROCTS AND GASTROPODS, AND ECTOPROCTS AND HERMIT CRABS IN THE FRENCH JURASSIC

by T. J. PALMER and C. D. HANCOCK

ABSTRACT. Certain gastropods from the Pierre Blanche de Langrune (Upper Bathonian) at Lion-sur-Mer, Calvados, France, have been encrusted by a succession of ectoproct zoaria. After the death of the gastropods, the vacated shells, with their encrustations, have been occupied by hermit crabs. Abrasion of the shell during locomotion of the crabs produces flat areas near the shell aperture, and discontinuities in the ectoproct colony growth. The relationship between the ectoproct and the inhabitant of the shell is considered to be one of true symbiosis.

IN the course of work by one of us (T.J.P.) on the palaeoecology of Upper Bathonian faunas in England and northern France, collections were made from the upper caillasse (= shell bed) within the Pierre Blanche de Langrune (*Clydoniceras discus* Zone), exposed on the foreshore at Lion-sur-Mer, Calvados. The caillasse rests on a hardground 9 m beneath the top of the Pierre Blanche. Among the more striking objects to be found in this bed are colonies of encrusting ectoprocta, whose over-all shapes approximate to that of a trochiform gastropod. These colonies are relatively common, and it is a feature of all of them that part of the colony, usually next to the aperture, is worn flat (Pl. 65, fig. 1). A section through the colony confirms the opinion that it has been built up by successive layers of ectoproct, of the genus *Berenicea*, growing on a gastropod shell (probably *Ataphrus* sp.) (Pl. 65, figs. 2, 3).

We postulate that the following sequence of events has given rise to the objects as we find them in the caillasse:

1. In certain, but not all, of the colonies, colonization by the ectoproct has started before the completion of growth of the gastropod. In these cases, the outer whorl of the shell may be seen to enclose a layer or two of the ectoproct zoaria between itself and the adjacent inner whorl (Pl. 65, fig. 4). Whilst the gastropod is alive, the shell is supported by the foot during locomotion. In this event, the whole of the upper surface of the shell is available for colonization by the ectoproct, and none of the shell is being dragged along the substrate and abraded. The first few layers of zoaria thus cover the shell uniformly (Pl. 65, fig. 3).

2. After the death of the gastropod, the shell is occupied by a hermit crab. No longer being supported by a fleshy foot, it is dragged along the substrate. Any zoaria covering the area of contact with the substrate are worn off, whilst growing zoaria are prevented from expanding to cover this area. Therefore the subsequent layers grow asymmetrically around the shell, and the area in contact with the substrate remains flat (Pl. 65, figs. 3, 5). Even when the crab retracts into the shell, the shell rests on the flat area, and is therefore not available as substrate to the spreading ectoproct.

3. The layers of zoaria continue to accrue whilst the shell is inhabited by the hermit crab, or, more likely, a succession of hermit crabs. The crabs have therefore to main-

tain for themselves an opening from the shell to the outside. The genetic programme for the shell aperture to be laid down in a trochospiral arrangement has been lost with the death of the gastropod. Therefore the aperture maintained by the pagurid leads straight to the outside (Pl. 65, fig. 5), rather than spirally, as when the gastropod was alive.

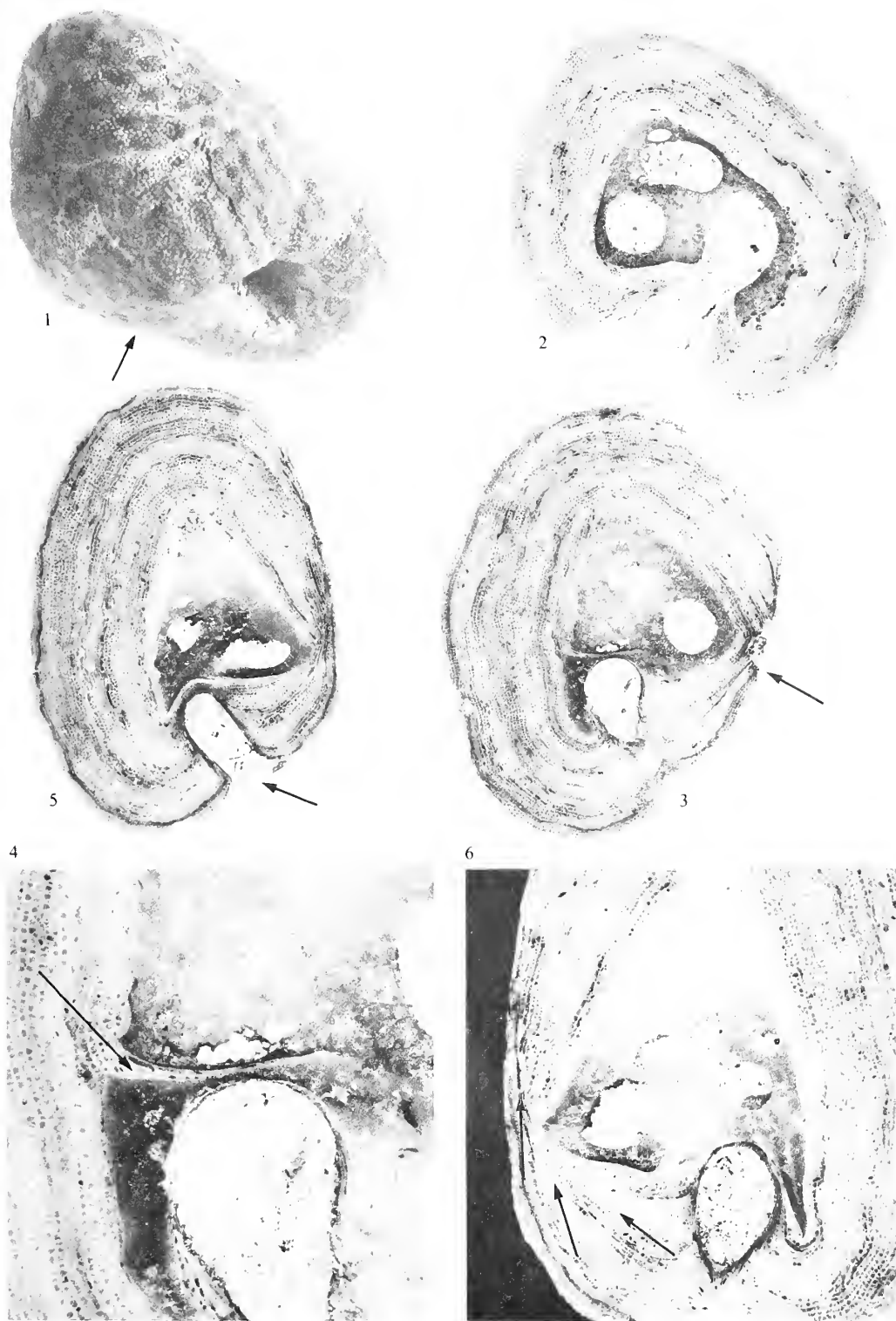
4. The colony now grows only by addition of successive layers of ectoproct zoaria over the surface, and not according to a trochospiral pattern as when the gastropod was alive. These zoaria tend to round off the angulations of the trochiform shell, and the shape of the colony changes from being dominantly conical to dominantly ovoid. This effect is enhanced by the continued abrasion on one side (compare the over-all shape of the colony in Pl. 65, fig. 5 with that of the original gastropod). This change in shape results in a change in the location of the area which is dragged along the substrate, and consequently in the stable resting position of the colony when the crab is withdrawn into the shell, from the base of the trochospire to the long side of the ovoid, where the convexity is least. A section through the colony shows how the flattened area migrates with successive layers of zoaria as the over-all shape of the colony changes from coniform to ovoid (Pl. 65, fig. 6).

DISCUSSION AND CONCLUSIONS

Of the twenty-six examples of the encrusted gastropods collected by the authors from this bed (Oxford University Museum catalogue numbers J. 40001-40026), all but one show the pagurid wear marks, and in none is the hole which allowed emergence of the crab overgrown by ectoprocts. It would seem, then, that demand for housing by pagurids was high, and that only very seldom did a dwelling remain vacant for any significant period of time. Such a conclusion is in keeping with observations made independently by the two authors, in the Canary Islands (C.D.H.), and off the Florida Keys (T.J.P.), that empty gastropod shells are virtually never found on the sea bottom. Either they contain a gastropod, or they contain a hermit crab. Considering that the crabs rely on being able to change their shells each time that

EXPLANATION OF PLATE 65

- Fig. 1. Colony of ectoproct zoaria encrusting a trochiform gastropod. The lower left corner of the colony has been worn away (arrowed) due to abrasion against the substrate during locomotion of the hermit crab which occupied the shell, OUM, J. 40001, $\times 2.2$.
- Fig. 2. Section through colony along plane sub-parallel to worn area, showing successive layers of ectoproct zoaria, OUM, J. 40002a, $\times 3.0$.
- Fig. 3. Section through colony cutting across worn area (arrowed). Encrustation of this specimen started before death of the gastropod (see fig. 4). Consequently, the first few layers of zoaria at the point of wear, are unabraded, OUM, J. 40003a, $\times 2.8$.
- Fig. 4. Part of fig. 3 showing four layers of zoaria (arrowed) enclosed between the last whorl of the gastropod and the preceding whorl. This indicates that colonization by the ectoproct started whilst the gastropod was still alive, $\times 8.0$.
- Fig. 5. Section through colony showing the aperture (arrowed) maintained by the hermit crab. It leads to the outside in a straight line, OUM, J. 40004a, $\times 3.0$.
- Fig. 6. Details of the change in location of the area of abrasion: the arrows point along the planes of contact with the substratum, for successive growth stages of the colony. These planes of contact, where abrasion occurred, change location as the over-all shape of the colony becomes less trochospiral, and more ovoid, OUM, J. 40004b, $\times 4.6$.



PALMER and HANCOCK, symbiotic relationships

they outgrow their previous one, it seems not unlikely that any change by a larger individual is rapidly followed by the reoccupation of the recently vacated shell by a slightly smaller individual, and so on until one very small shell is vacated and left vacant.

Associations between gastropods, encrusting organisms, and hermit crabs are known from periods other than the Jurassic. Wear marks ascribed to hermit crabs have been described on Recent gastropods encrusted by hydractinians (Schäfer 1962). Similarly worn, but unencrusted, gastropods have been described from the Pliocene of Belgium by Boekschoten (1967), and an unworn example encrusted by the ectoproct *Cellepora* sp., from the Pliocene of Britain, has been figured by Pinna (1972, p. 33).

Busk (1857, pl. 9, fig. 6c) also figures *Cellepora edax* Busk encrusting a gastropod, and Wood (1872, p. 55) discusses the encrustation of *Turritella crassicosata* by *Edax*. The Oxford University Museum Pleistocene collection contains five specimens showing wear marks on gastropod shells encrusted by hydractinians (OUM, Q. 1512–1516); there is also a *Natica* sp. from the Coralline Crag (Pliocene), which is encrusted by *Cellepora edax* and similarly worn.

Busk (loc. cit.) considers that *Cellepora* was parasitic upon the gastropod shell, since it frequently appears, both in Pliocene and Recent examples, to have effected the solution of the underlying shell. However, in these examples there is no evidence that there was any occupant of the shell at the time during which the solution occurred, and the inference of a parasitic relationship is not justified. In the Bathonian specimens, the ectoproct colony was both active and growing during the life of the gastropod, as well as during the subsequent occupation of the shell by the hermit crab. In this case, there was no destruction of the shell by the ectoproct, and the relationship between gastropod and ectoproct would appear to have been one of true symbiosis. The shell provides a stable substrate, and the behaviour of the gastropod prevents it constantly being rolled around and abraded by current activity. In turn, the ectoproct offers the gastropod protection by disguise, and it also strengthens the shell against attack by mollusc-eating vertebrates and predatory decapods. This reasoning applies equally if the shell is occupied by a hermit crab; in this case, however, the ectoproct probably gains further by gathering food particles released by the scavenging behaviour of the crab, as well as those suspended in the crab's respiratory currents.

Acknowledgements. The authors would like to thank W. J. Kennedy, A. Hallam, and F. Fürsich for their useful comments, and J. R. McAvoy, S. M. Baker, and Miss Helen Birch for technical assistance.

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Note added in press. Further discussion, particularly on the identity of the ectoproct, may be found in: Fischer, J.-C. and Buge, E. 1970. *Atractosoeicia incrustans* (d'Orbigny) (Bryozoa Cyclostomata) espèce bathonienne symbiotique d'un Pagure. *Bull. Soc. géol. France*, **12**, 126–133.

PALYNOLOGIC CORRELATION OF THE DORSET 'WEALDEN'

by N. F. HUGHES and C. A. CROXTON

ABSTRACT. Using the *Cicatricosisporites* group of palynomorphs, events raised from ten selected samples from the 'Wealden' of Worbarrow Bay, Dorset, are bracket-correlated with events of similar nature from the Warlingham Borehole, Surrey. Although sedimentation rates appear to have differed, deposition at Worbarrow seems to have continued throughout much of Berriasian to Aptian time as at Warlingham. The constituent data of the events comprised graded comparison records with the use of twelve new biorecords and some of those published by Hughes and Moody-Stuart (1969).

IN this paper we attempt to correlate by means of a selection of palynologic data, a section of about 1400 ft (425 m) of 'Wealden' strata exposed in the cliffs of Worbarrow Bay, Dorset. These beds overlie conformably some slightly dubious 'Upper Purbeck' beds north of Worbarrow Tout (Arkell 1947, and earlier authors) presumably of Berriasian age; they are overlain more or less conformably by 'Lower Greensand', with marine bivalves, which is presumably of Aptian age. These 'Wealden' strata may therefore be of any age from Early Berriasian to Late Aptian.

The attempted correlations are with the Wealden section of the Warlingham Borehole, Surrey, which is itself not yet firmly correlated with an international scale. The correlations are therefore not scale-dated as it would be premature to do this; it should, however, be possible to date Worbarrow automatically as soon as dates for parts of the Warlingham reference are agreed.

The appropriate rock samples and preparations have been deposited in the Sedgwick Museum, Cambridge.

Method. The method is explained in Hughes and Moody-Stuart (1969, pp. 86-87) and correlation is based on palynologic events raised from rock samples, in this case restricted to palynomorphs of the *Cicatricosisporites* group. The events are composed of graded comparison records (Hughes and Moody-Stuart 1967), based on taxa described as biorecords which in this case all come from Warlingham or Worbarrow rocks. Some previously described events and biorecords are taken from Hughes and Moody-Stuart (1969); the numerous new events and their constituent comparison records, plus twelve new biorecords, are presented systematically in a condensed tabular form. All these taxa are fully employed in the stratigraphic correlation; those not so required are omitted from the paper.

The handling of taxa is as described in Hughes (1971). No comparison is made with published Linnéan taxa as there is no stratigraphic purpose in doing so. Comparison records and biorecords may be reassembled subsequently into taxa under the Rules of Botanical Nomenclature (Stafleu *et al.* 1972) if required for some gross palaeoecologic synthesis.

Notation. Each biorecord bears a unique number which may be quoted with author initials and date if referred to outside the paper. The accompanying letter and number in italics is the observer's working identifier but is subsequently a non-search item.

Each event is numbered in a similar way with the working sample (field) number in italics as a non-search item; several events of different taxal origin may be raised from one sample. Comparison records may be uniquely referred to either as 105 event *W128* cf. 6 *B5*, or as 105 event cf. 6 *CICATR*.

SYSTEMATIC DESCRIPTIONS OF BIORECORDS

Description common to all biorecords below. All trilete miospores; amb shape, equatorial shape, general distribution of muri, and mural profile may be taken from photographs. Measurements and other data are given on Tables 1 and 2, diagrammatic mural profiles to scale on text-fig. 1. Lips are simple, low, membranous unless otherwise stated. The ratio of radial to interradian exine thickness is given on Table 2, and no further reference is made to it in descriptions. On Table 2 measurements of exine include the murus in spores of negative sculpture, and exclude it in those of positive sculpture unless otherwise stated.

No comment is made under preservation concerning the frequent folding of thin-walled spores.

For preparation details see the appropriate event preparation Table 5, and for sample sediment details see Appendix.

17 *CICATR B20*

Plate 66; text-fig. 1

Description. Laesura may be sinuous. Proximal face sometimes shows a small smooth triangle or reduced muri (figs. 1, 3, 5). Proximal muri: three interradian sets of approximately 4. Polar view: 0–4 muri (in profile) cross radial margin (figs. 1, 4). Distally three sets of 4–12 muri form an asymmetrical pattern (fig. 9).

Preservation. 21% torn, often radially (figs. 6, 7).

Local distinction. 25 *CICATR B21* is larger and has more and narrower muri which are more closely spaced and have the characteristic 'swirling' pattern. 28 *CICATR DG* is larger with a thicker exine and negative sculpture.

EXPLANATION OF PLATE 66

Magnification, $\times 1000$.

Figs. 1–12. Biorecord 17 *CICATR B20*, Slide KO18/7. 1, Proximal aspect; OR 28.7 117.8. 2, Distal aspect, low focus; OR 29.1 117.9. 3, Proximal aspect; OR 35.0 125.3. 4, Proximal aspect; OR 49.7 110.0. 5, Proximal aspect; OR 54.4 118.0. 6, Distal aspect, low focus; OR 37.4 110.6. 7, Distal aspect, low focus; OR 53.4 123.6. 8, Oblique aspect; OR 30.0 121.3. 9, Proximal aspect, low focus; OR 41.1 127.3. 10, Equatorial aspect; OR 35.0 119.0. 11, Equatorial aspect; OR 38.3 116.4. 12, Oblique aspect; OR 39.6 126.4.

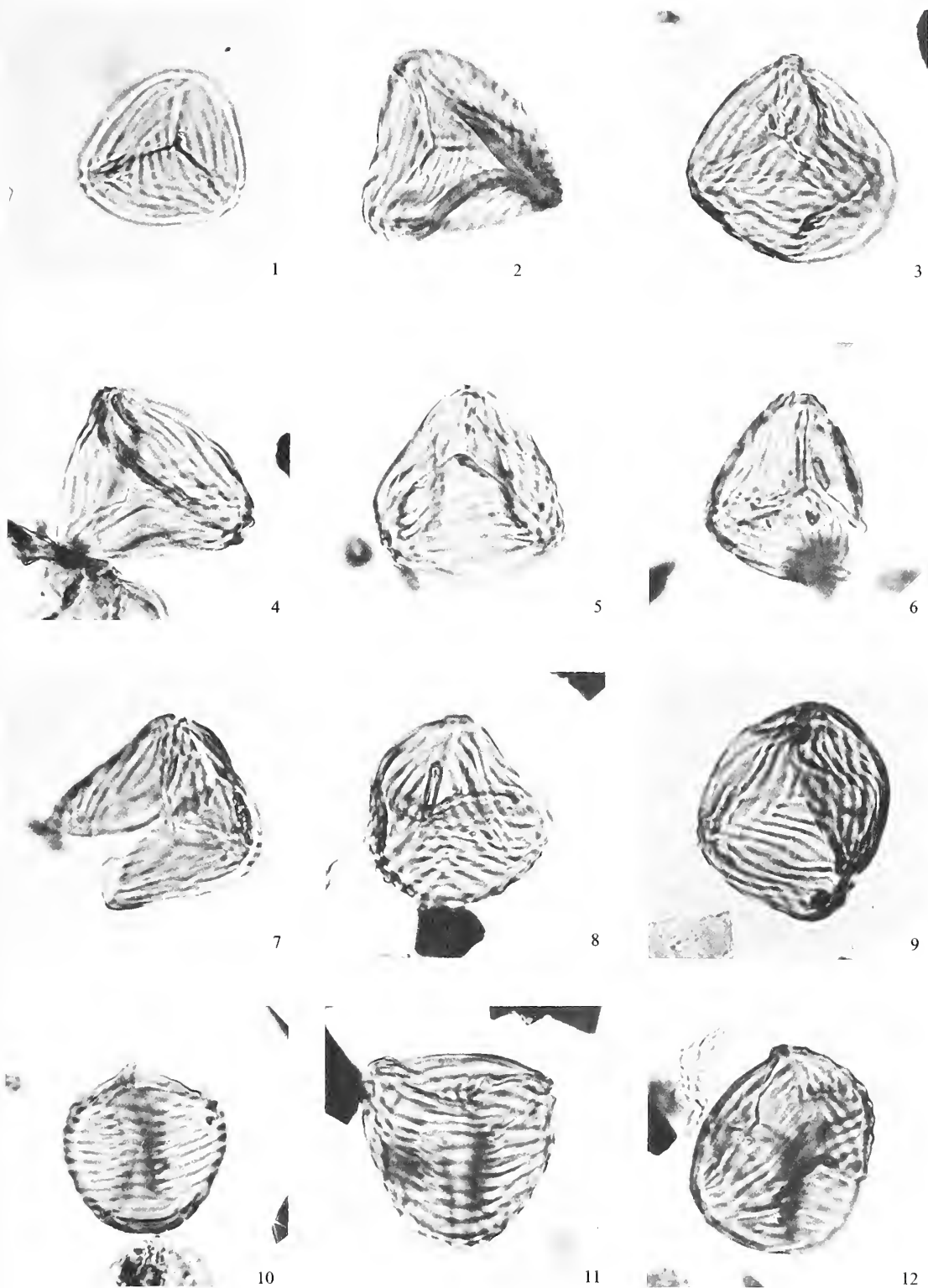


TABLE 1. Sample, preparation, and diameter information for twelve biorecords.

CICATR Biorecord	Record Sample	Preparations	Diameter 100 specs. μm		Factors possibly influencing measurem'ts				
					Aspect %			Fern spore size index	
			Limits	Mean	Pol.	Equ.	Obl.	<30	30-50 μm
17. B20	WM 1655	K018/2,3,5,6,7	(22)	31.4 (44)	4.5	54	22	24	13 67 20
18. C3	WM 1749/8	V411/6,7,8,9	(30)	43.0 (61)	5.8	84	10	6	26 47 27
19. A6	WM 1681/6	V500/4,5,6,7	(27)	43.9 (63)	6.6	45	30	25	10 61 29
20. DD	WM 1415/3	V963/4	(39)	60.8 (92)	10.6	58	23	19	18 51 31
21. C4	WM 1415/3	V963/2-4. W103/1-3	(32)	45.9 (58)	5.3	77	18	5	18 51 31
22. DB	WM 1415/3	V963/1-4. W103/1-3 J035/3	(36)	59.0 (80)	10.5	72	19	9	18 51 31
23. DCE	WM 1415/3	V963/2-4. W103/1-3	(47)	70.1 (95)	10.4	75	13	12	18 51 31
24. C5	W III	W190/1,2,3,4,5,6,7	(28)	43.1 (58)	6.3	73	21	6	29 61 10
25. B21	W III	W190/1,2,3,4,5,6	(25)	38.4 (55)	7.1	49	34	17	29 61 10
26. A5T	W 9	W197/4,5,6	(31)	40.5 (55)	5.3	56	26	18	16 63 21
27. C6	W 14	V198/1-4. W262/1,3	(28)	42.1 (63)	6.2	54	39	7	19 43 38
28. DG	WM 1217/6	W058/1,2,3,8,7	(28)	37.2 (50)	4.6	66	22	12	23 51 26

18 CICATR C3

Plate 67; text-fig. 1

Description. Width of one lumen (0.8) 1.7 μm (4.5) (86). Proximal muri: three inter-radial sets of 1 or 2. Distal mural pattern either three sets of 2 (occasionally 3) muri forming a central tri-radial lumen (figs. 4, 6) or a set of sub-parallel muri (fig. 7). Radial equatorial features are extensions of the coalesced outer muri from adjacent interradial sets; ratio length/width at half-length: (0.6) 1.2 (2.7) (82); some are parallel-sided and others cone-shaped. These features may not extend beyond the periphery of the amb (fig. 6).

Preservation. Characteristically split immediately adjacent to the radial equatorial feature. Corrosion of muri takes the form of cross striations (fig. 9).

Local distinction. 7 CICATR C1 has narrower and more numerous muri, a thinner exine, and positive sculpture. 20 CICATR DD is larger and has a radial lumen. 27 CICATR C6 has narrower muri with a different mural profile and variable radial equatorial extensions.

EXPLANATION OF PLATE 67

Magnification of figs. 1-9, $\times 1000$; fig. 10, $\times 2000$.

Figs. 1-10. Biorecord 18 CICATR C3. 1, Proximal aspect; V411/6, OR 56.5 117.0. 2, Proximal aspect; V411/6, OR 50.0 119.5. 3, 4, Distal aspect, low and high focus; V411/6, OR 35.0 121.0. 5, Proximal aspect; V411/7, OR 28.8 123.5. 6, Distal aspect, low focus; V411/6, OR 25.0 124.0. 7, Distal aspect; V411/8, OR 26.5 126.0. 8, Equatorial aspect; V411/7, OR 43.1 109.9. 9, Distal aspect; V411/8, OR 24.7 119.9. 10, Part of oblique aspect, showing mural profile; V411/7, OR 25.3 129.4.



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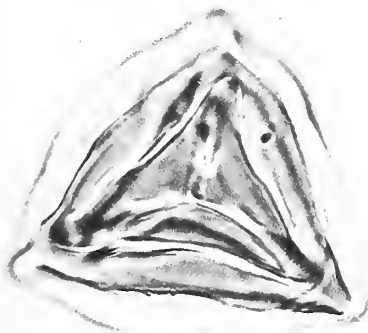
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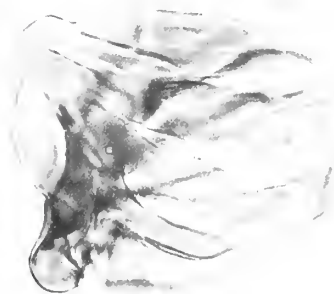
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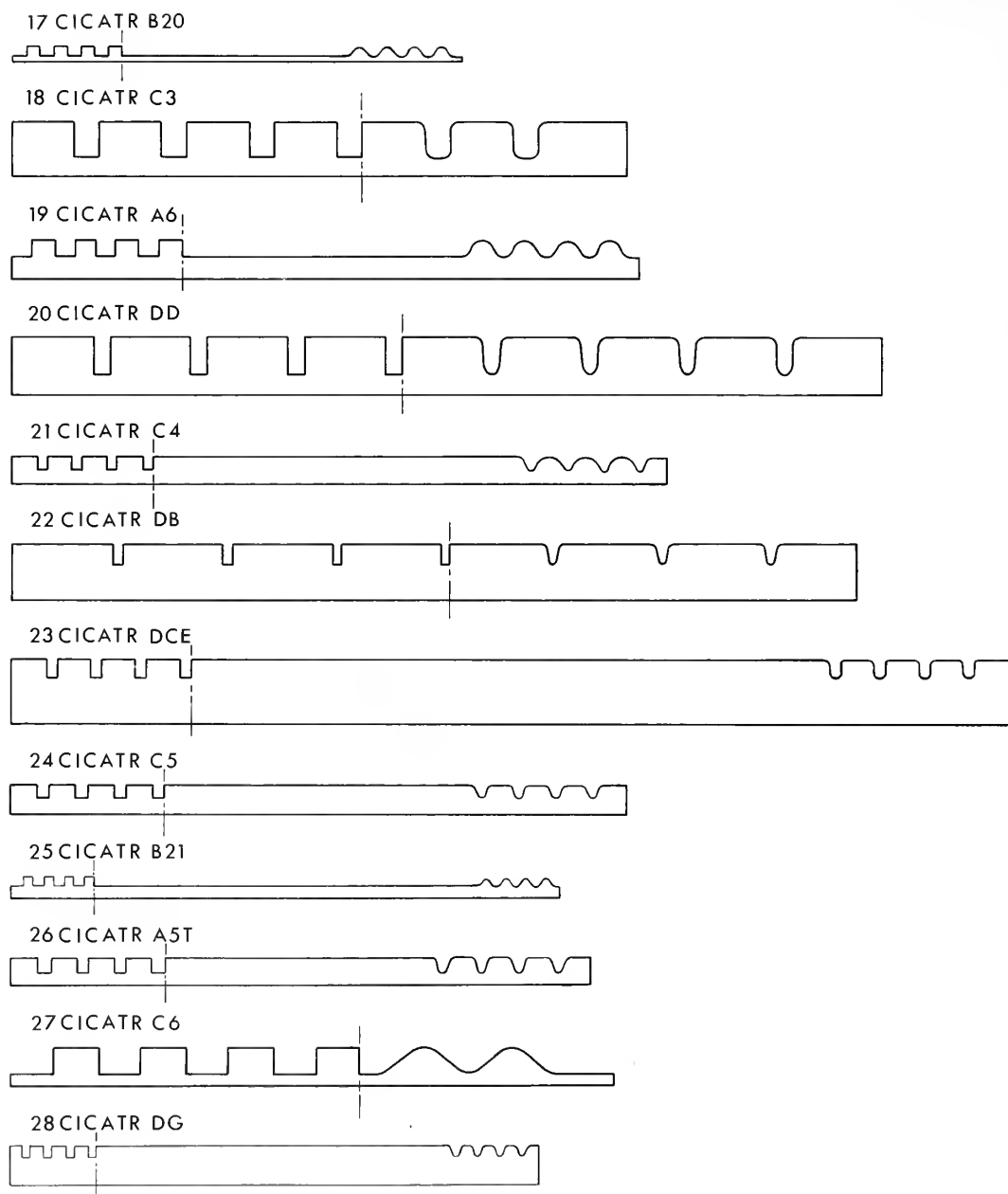
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9



TEXT-FIG. 1. Mural profile diagrams of twelve biorecords, all to same scale. Left, four muri and lumina constructed from measurements made on spores, $\times 2000$. Right, some sketched profiles.

TABLE 2. Exine and sculpture measurements for twelve biorecords. Certain measurements are omitted from the table when they are believed to lack significance, e.g. for four adjacent muri when the mean would exceed the spore radius; other comments in text.

CICATR Biorecord	Exine μm				Laesura	Sculpture μm								
	Interradial		Radial or Equatorial Extens.			Ratio Radial/ Interradial		+ve or -ve	Width of muri		4 adjacent muri and lumina		Height of muri	
	Limits & Mean	No.	Limits & Mean	No.		Limits & Mean	No.		Limits & Mean	No.	Limits & Mean	No.	Limits & Mean	No.
17. B20	(0.6) 1.0 (2.0) incM	58	(0.6) 1.5 (2.5) incM	49	(1.0) 1.9 (2.0)	48	Long	+	(0.5) 0.9 (1.5)	95	(4.8) 7.6 (10.0)	1.0 93	(0.4) 0.7 (1.3)	62
18. C3	(1.5) 3.9 (5.5)	82	(2.5) 5.6 (8.0)	82	- - -	-	Long	-	(2.0) 4.4 (6.5)	97	- - -	-	- 2.5 -	1
19. A6	(1.0) 1.5 (2.0) exM	41	(1.5) 2.3 (3.5) exM	41	(1.0) 1.5 (2.2)	41	Long	+/-	(1.0) 1.6 (2.7)	100	(7.0) 11.9 (20.0)	21 98	(0.7) 1.2 (2.0)	50
20. DD	(2.0) 4.1 (6.0)	68	(3.0) 5.6 (9.0)	54	(1.0) 1.4 (2.7)	51	Long	-	(3.0) 5.6 (9.0)	100	(16.0) 27.1 (40.0)	5.0 58	(1.5) 2.6 (3.5)	19
21. C4	(1.0) 1.9 (3.0)	71	(2.0) 4.3 (6.5)	77	(1.3) 2.3 (4.3)	71	Long	-	(1.0) 1.8 (3.0)	100	(7.0) 9.9 (13.0)	1.1 79	- 1.0 -	2
22. DB	(2.0) 4.0 (8.0)	71	(3.0) 6.0 (12.0)	71	(1.0) 1.5 (3.3)	71	Short	-	(4.0) 7.0 (11.0)	100	(20.0) 30.5 (43.0)	5.6 55	(1.0) 1.5 (2.0)	9
23. DCE	(3.0) 4.6 (8.0)	96	(3.0) 6.4 (13.0)	72	(1.0) 1.3 (2.3)	72	Short	-	(1.5) 2.4 (4.0)	100	(9.0) 12.5 (20.0)	21 100	(1.0) 1.3 (2.0)	21
24. C5	(1.0) 2.1 (4.0)	72	(3.5) 7.4 (15.0)	90	- - -	-	Long	-	(1.3) 1.9 (3.0)	93	(8.0) 10.7 (15.0)	1.5 58	- 1.0 -	3
25. B21	(1.0) 1.6 (2.0) incM	96	(1.0) 1.7 (2.0) incM	33	(1.0) 1.1 (1.5)	33	Long	+	(0.3) 0.6 (1.0)	99	(4.0) 5.7 (9.0)	1.1 99	(0.4) 0.7 (1.0)	28
26. A5T	(1.0) 2.0 (3.0)	87	- - -	-	- 1.0 -	31	Short	-	(1.3) 1.9 (2.5)	100	(8.0) 10.8 (15.0)	1.3 96	(0.5) 1.1 (1.5)	35
27. C6	(1.5) 2.8 (5.5) incM	77	2.5 (4.4) 8.0	56	- - -	-	Long	+/-	(1.0) 3.2 (7.0)	98	- - -	-	(1.5) 2.4 (3.5)	7
28. DG	(2.0) 2.8 (4.5)	97	2.0 (3.6) 5.5	75	(1.0) 1.3 (2.2)	75	Long	-	(0.5) 1.0 (1.7)	100	(4.0) 6.2 (9.0)	1.0 88	(0.7) 0.9 (1.0)	4

19 CICATR A6

Plate 68; text-fig. 1

Description. Prominent lips (figs. 1, 2, 3). Proximal face: some specimens have a small smooth contact area. Proximal muri: three interrarial sets of 3–5. Polar view: (0) 3 (5) muri (in profile) cross the radial margin (figs. 1, 3). Distal muri form an asymmetrical pattern of three sets of 1–15 muri (figs. 6, 7). Sub-parallel distal muri rare. Muri are sinuous and often bifurcate (fig. 7).

Local distinction. 1 CICATR AT has more muri which are straight not sinuous and a thicker exine.

20 CICATR DD

Plate 69; text-fig. 1

Description. Contact area smooth and often encompasses all of the laesura (figs. 1, 2). Lips thick (fig. 2). Proximal muri: three interrarial sets of (1) 2 (3). The distal mural pattern, of three sets of 1–5 (fig. 6) or a sub-parallel set of 4–9 muri (fig. 8), is distinguished by radial lumina each flanked by two muri which project beyond the radial margin (figs. 1, 2, 3, 5, 6, 9).

Local distinction. 18 CICATR C3 is smaller with no radial lumen. 5 CICATR A2 is smaller with thicker positive muri. 22 CICATR DB has no radial lumen.

21 CICATR C4

Plate 70; text-fig. 1

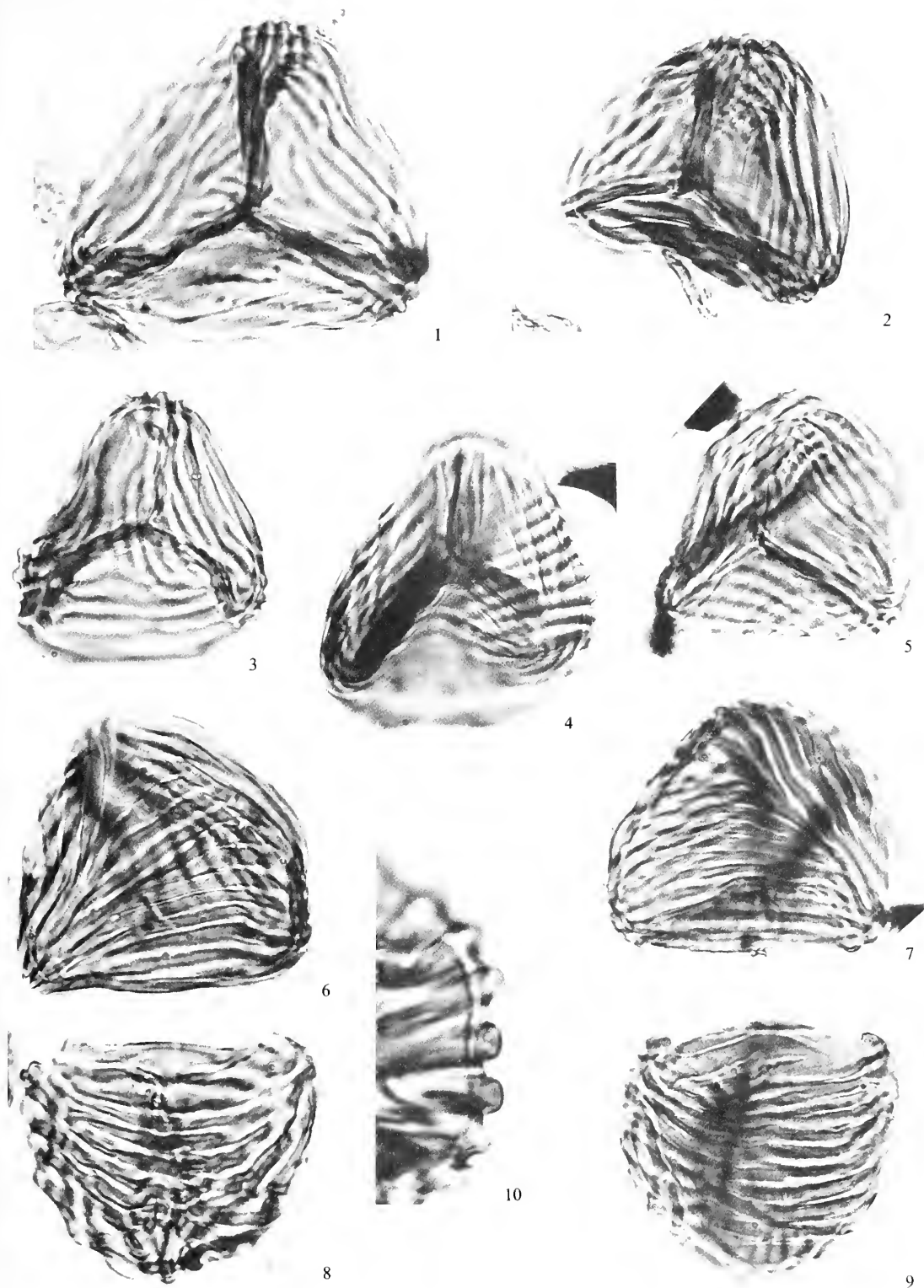
Description. Convexity of amb shape distinctive. Small smooth contact area (figs. 3, 5). Proximal muri: three interrarial sets of commonly 3–4. Distal mural pattern normally 12–20 sub-parallel muri (fig. 9), rarely three sets. Radial equatorial extensions conical in shape, ratio length/width at half-length: (0.5) 0.9 (1.7) (74). Proximally the extensions are unsculptured but on the distal side the muri extend across the extensions (figs. 1, 7).

Local distinction. 24 CICATR C5 has denser and more elongate extensions. The amb has straighter sides and there are a lower number of muri.

EXPLANATION OF PLATE 68

Magnification of figs. 1–9, $\times 1000$; fig. 10, $\times 2000$.

Figs. 1–10. Biorecord 19 CICATR A6. 1, Proximal aspect; V500/6, OR 33.7 113.5. 2, Proximal aspect; V500/6, OR 34.5 124.5. 3, Proximal aspect; V500/5, OR 63.6 127.2. 4, Proximal aspect; V500/6, OR 24.4 120.4. 5, Distal aspect, low focus; V500/6, OR 41.9 112.3. 6, Distal aspect; V500/5, OR 36.0 115.0. 7, Distal aspect; V500/5, OR 49.8 113.3. 8, Equatorial aspect; V500/5, OR 53.5 117.8. 9, Equatorial aspect; V500/5, OR 52.5 114.0. 10, Part of oblique aspect, showing mural profile; V500/6, OR 35.4 110.7.



EXPLANATION OF PLATE 69

Magnification of figs. 1-9, $\times 1000$; fig. 10, $\times 2000$.

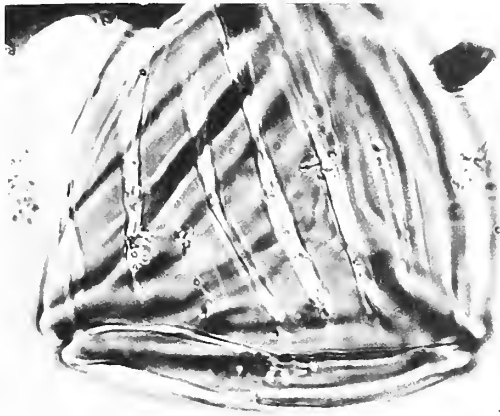
Figs. 1-10. Biorecord 20 C1CATR DD, Slide V963/4. 1, Proximal aspect; OR 40.3 121.0. 2, Distal aspect, low focus; OR 27.5 108.5. 3, Distal aspect; OR 37.6 110.3. 4, Equatorial aspect; OR 30.2 120.1. 5, Proximal aspect; OR 38.7 127.8. 6, Distal aspect; OR 39.6 124.0. 7, 8, Proximal aspect, high and low focus; OR 38.8 119.3. 9, Distal aspect; OR 37.6 110.1. 10, Part of equatorial view, showing mural profile; OR 38.0 112.0.



1



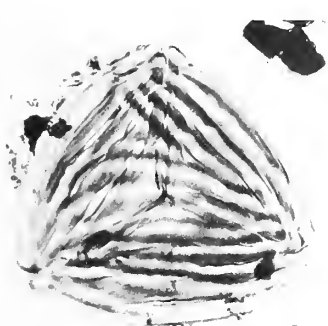
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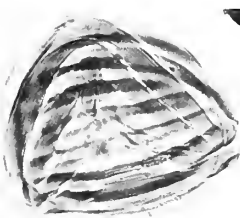
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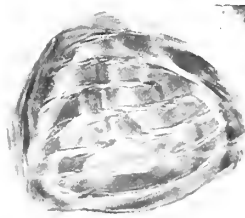
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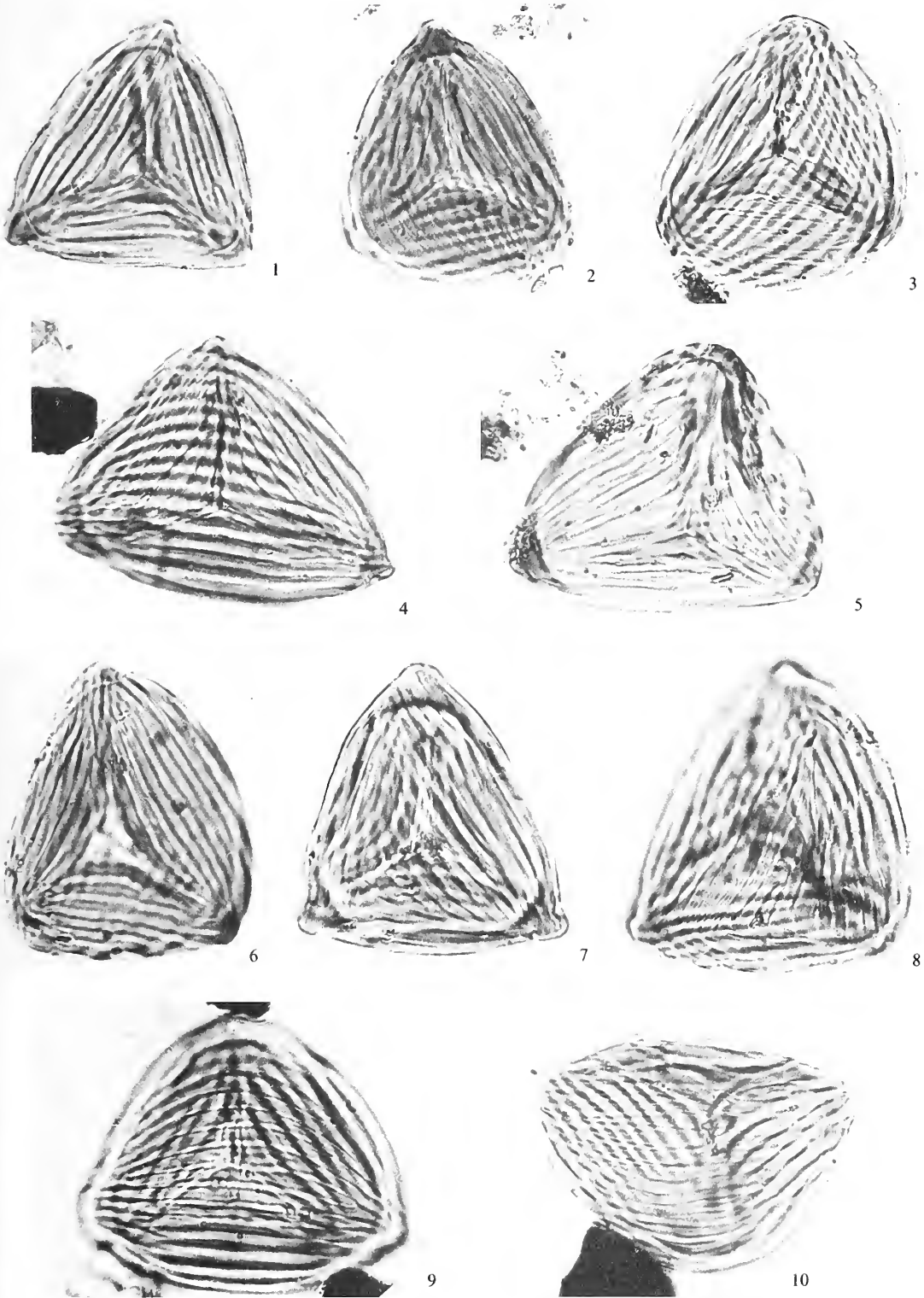


9

EXPLANATION OF PLATE 70

Magnification, $\times 1000$.

Figs. 1-10. Biorecord 21 CICATR *C4*. 1, Distal aspect, low focus; V963/2, OR 24.0 108.4. 2, Distal aspect, low focus; V963/3, OR 42.2 117.5. 3, Proximal aspect; V963/4, OR 52.7 123.2. 4, Proximal aspect; V963/2, OR 33.6 129.2. 5, Distal aspect, low focus; V963/4, OR 50.8 122.7. 6, Distal aspect, low focus; V103/1, OR 38.4 113.3. 7, Proximal aspect, low focus; V963/4, OR 51.5 115.5. 8, Distal aspect; V963/4, OR 28.6 111.0. 9, Distal aspect; V963/4, OR 53.0 124.1. 10, Equatorial aspect; V963/4, OR 34.6 127.4.



HUGHES and CROXTON, biorecord 21 CICATR C4

22 CICATR DB

Plate 71; text-fig. 1

Description. Proximal muri: three interradial sets of 2–4. Distal muri: 4–8 sub-parallel muri or three sets of muri in an asymmetrical pattern (figs. 4, 7). This taxon includes specimens with conical radial equatorial extensions grading into those with no extension (figs. 2, 7). All specimens in this case have drillings in the muri and they are therefore thought to be primary.

Local distinction. 9 CICATR AP is a similar size but the muri are narrower and more numerous. 20 CICATR DD differs in mural profile and the distinctive radial lumen.

23 CICATR DCE

Plate 72; text-fig. 1

Description. No lips have been distinguished. No unsculptured area. Proximal muri: three interradial sets of 3–15. In the radial equatorial area the lumina are discontinuous forming an interlocking pattern beyond the laesura (fig. 7). Distal face strongly convex and (13) 20 (30) muri bifurcate to accommodate this (figs. 3, 8, 9).

Local distinction. 10 CICATR AS is smaller with fewer muri and a different radial equatorial and distal mural pattern.

24 CICATR C5

Plate 73; text-fig. 1

Description. Prominent lips (fig. 2). Proximal muri: three interradial sets of approximately 3. Distal mural pattern normally three sets of up to 14 muri (fig. 7). Radial equatorial extensions are unsculptured and are long, narrow, and tapering. Ratio length/width at half-length: (1.1) 1.8 (4.0) (78).

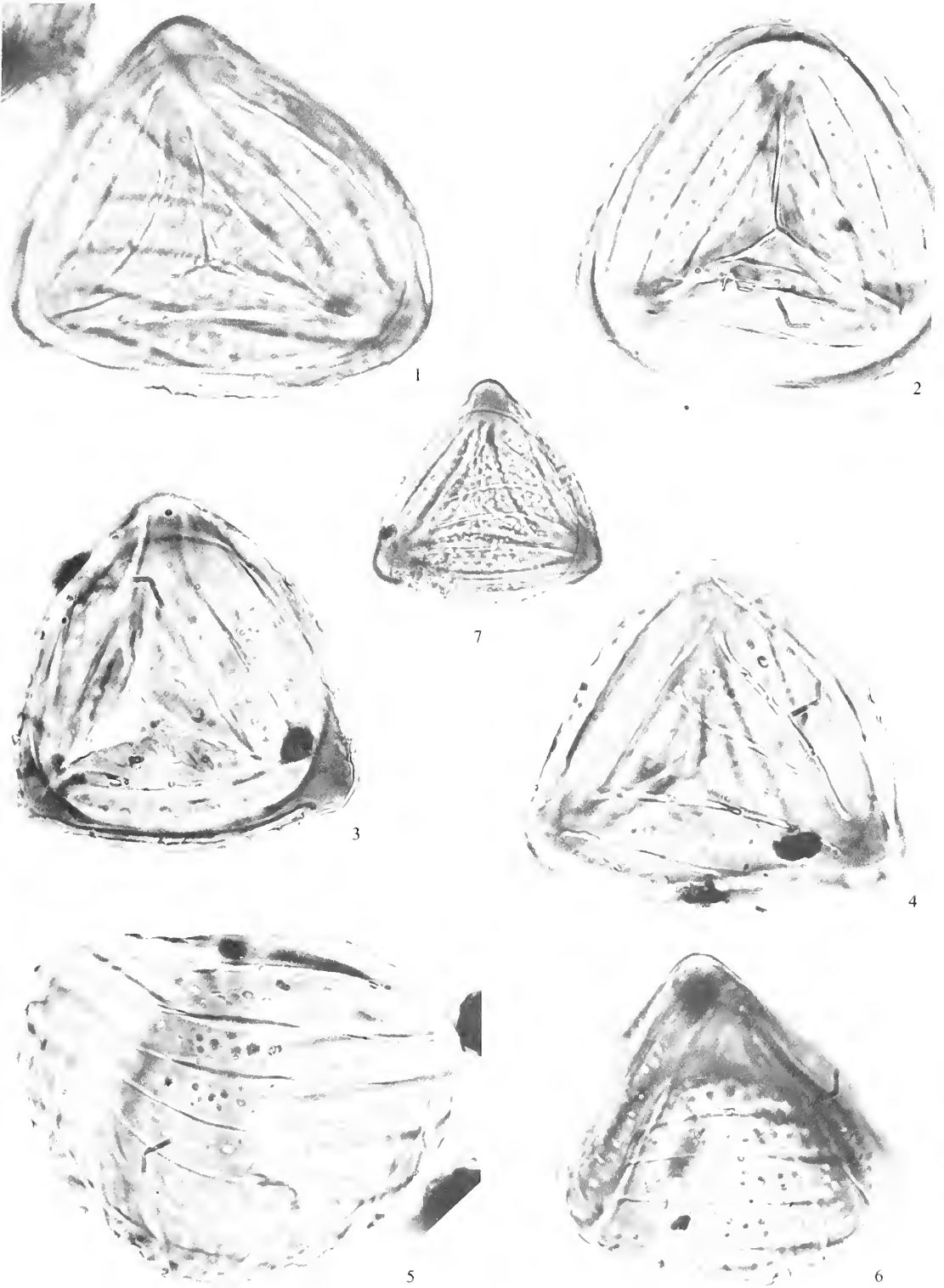
Preservation. Some specimens have 'drillings' that appear to be corrosion (fig. 9).

Local distinction. 8 CICATR C2 has 'knob-like' rather than tapering extensions and is smaller. 21 CICATR C4 has shorter, more conical extensions which are sculptured distally; the amb is more convex-sided and there are more muri.

EXPLANATION OF PLATE 71

Magnification of figs. 1–6, $\times 1000$; fig. 7, $\times 500$.

Figs. 1–7. Biorecord 22 CICATR DB. 1, Proximal aspect; JO35/3, OR 49.6 115.0. 2, Proximal aspect; V963/1, OR 40.1 116.8. 3, Distal aspect, low focus; V103/1, OR 40.5 112.2. 4, Distal aspect; V103/3, OR 36.7 113.8. 5, Equatorial aspect; V963/3, OR 55.8 110.6. 6, Oblique aspect; V963/2, OR 33.3 117.1. 7, Distal aspect; V963/2, OR 37.4 117.7.

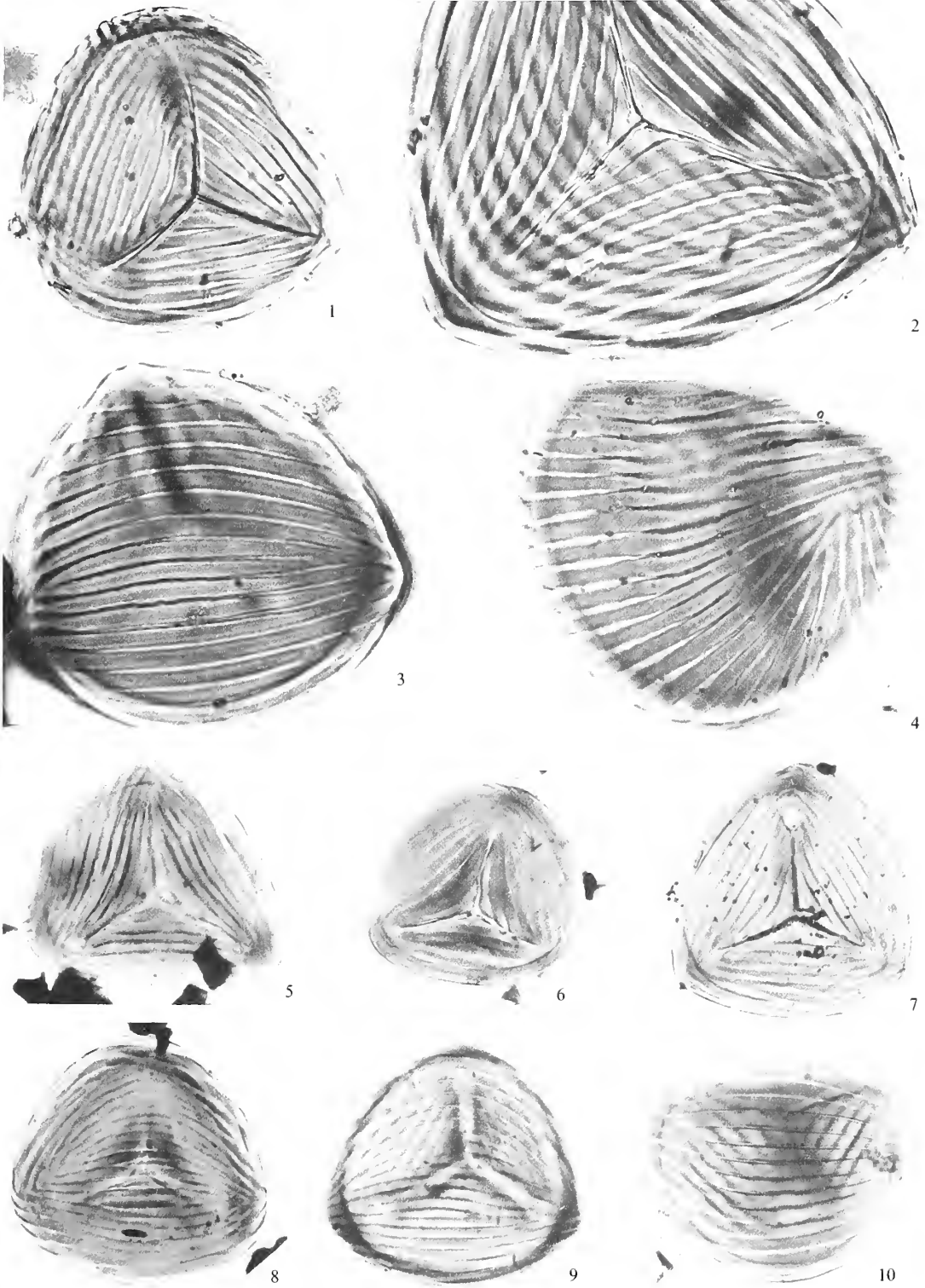


HUGHES and CROXTON, biorecord 22 CICATR DB

EXPLANATION OF PLATE 72

Magnification of figs. 1-4, $\times 1000$; figs. 5-10, $\times 500$.

Figs. 1-10. Biorecord 23 CICATR DCE. 1, Proximal aspect; W103/2, OR 32.5 106.8. 2, Proximal aspect; V963/2, OR 26.6 125.7. 3, Distal aspect; V963/3, OR 47.9 124.9. 4, Equatorial aspect; V963/3, OR 55.0 124.8. 5, Proximal aspect; V963/4, OR 49.8 118.9. 6, Proximal aspect; V963/4, OR 43.7 120.3. 7, Proximal aspect; W103/1, OR 31.7 111.6. 8, Distal aspect; V963/3, OR 40.3 129.0. 9, Distal aspect; V963/3, OR 47.4 121.2. 10, Oblique aspect; V963/3, OR 30.2 129.2.



HUGHES and CROXTON, biorecord 23 CICATR DCE

EXPLANATION OF PLATE 73

Magnification, $\times 1000$.

Figs. 1-11. Biorecord 24 CICATR C5. 1, Proximal aspect; W190/3, OR 35.2 123.6. 2, Proximal aspect; W190/4, OR 48.2 116.0. 3, Distal aspect, low focus; W190/2, OR 52.2 104.5. 4, Distal aspect, low focus; W190/5, OR 38.7 119.6. 5, Distal aspect, low focus; W190/6, OR 44.6 122.6. 6, Distal aspect, low focus; W190/2, OR 25.1 116.9. 7, Distal aspect; W190/5, OR 38.7 119.6. 8, Distal aspect; W190/5, OR 40.0 111.8. 9, Distal aspect; W190/5, OR 42.1 122.5. 10, Distal aspect; W190/6, OR 29.4 122.7. 11, Equatorial aspect; W190/6, OR 30.7 109.4.



1



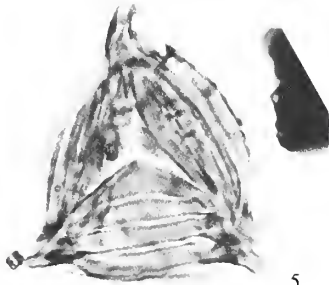
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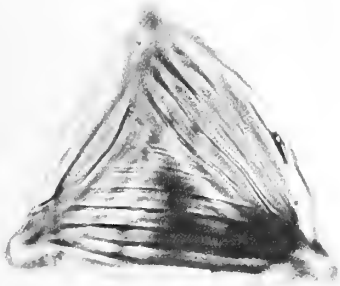
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25 CICATR B21

Plate 74; text-fig. 1

Description. Proximal face has a small smooth apical area (figs. 2, 3). Proximal muri (12–16) are in three sets oblique to the edge of the amb and meet the laesura at an angle (anticlockwise swirl) (figs. 1, 3, 6). Distal mural pattern is three asymmetrical sets of 8–12 muri or 20–25 sub-parallel bifurcating muri. Distal muri may also show clockwise swirl.

Local distinction. 17 CICATR B20 is smaller, has larger and fewer muri. 28 CICATR DG has wider negative muri and a thicker exine. In neither of the above have 'swirling' proximal muri been observed.

26 CICATR A5T

Plate 75; text-fig. 1

Description. Some specimens have a smooth contact area (figs. 2, 3). Proximal muri: three interrarial sets of 3–7. Outer proximal muri continuous round ends of laesura (figs. 1, 2, 3, 4). Distal muri: 12–20 in a sweeping 'parabolic' pattern (figs. 8, 9).

Local distinction. 10 CICATR A5S is smaller, has narrower lumina, rectangular mural profile, thicker exine, and circular lumina occur in the distal mural pattern.

27 CICATR C6

Plate 76; text-fig. 1

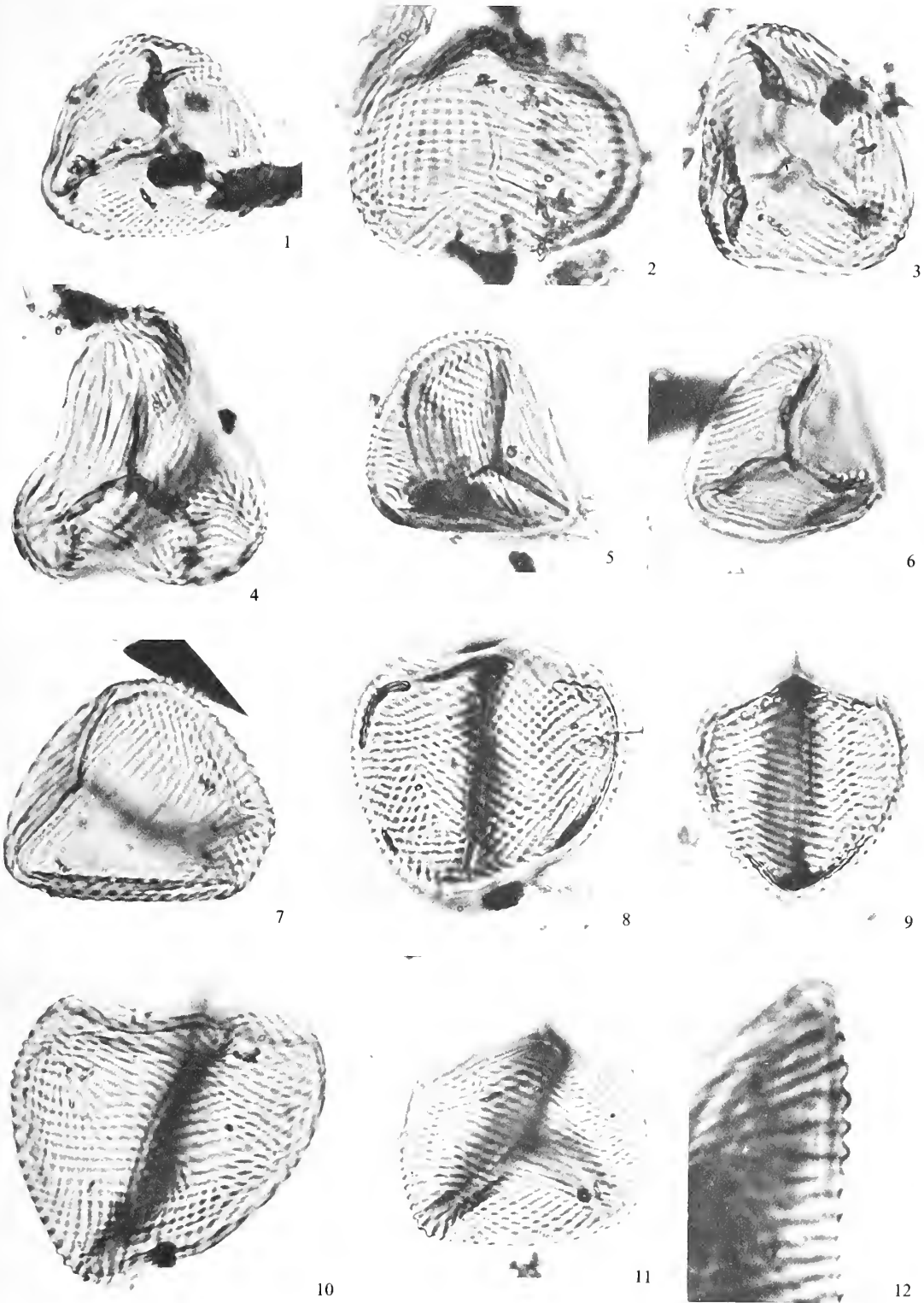
Description. Interrarial exine thickness may vary in the same specimen (fig. 6). Smooth contact area covering most of the proximal face (fig. 3). Sculpture may be positive or negative, width of one lumen: (1.0) 2.9 μm (8.0) (92). Distal muri: three asymmetrical sets of 1–7. Radial equatorial extensions variable: conical, tapering, or 'flattened'; in some specimens they are not very prominent. Ratio length/width at half-length: (0.6) 1.0 (1.7) (48).

Local distinction. 18 CICATR C3 has wider negative muri with a rectangular mural profile and more prominent and uniform radial extensions. 7 CICATR C1 has more numerous narrower muri.

EXPLANATION OF PLATE 74

Magnification of figs. 1–11, $\times 1000$; fig. 12, $\times 2000$.

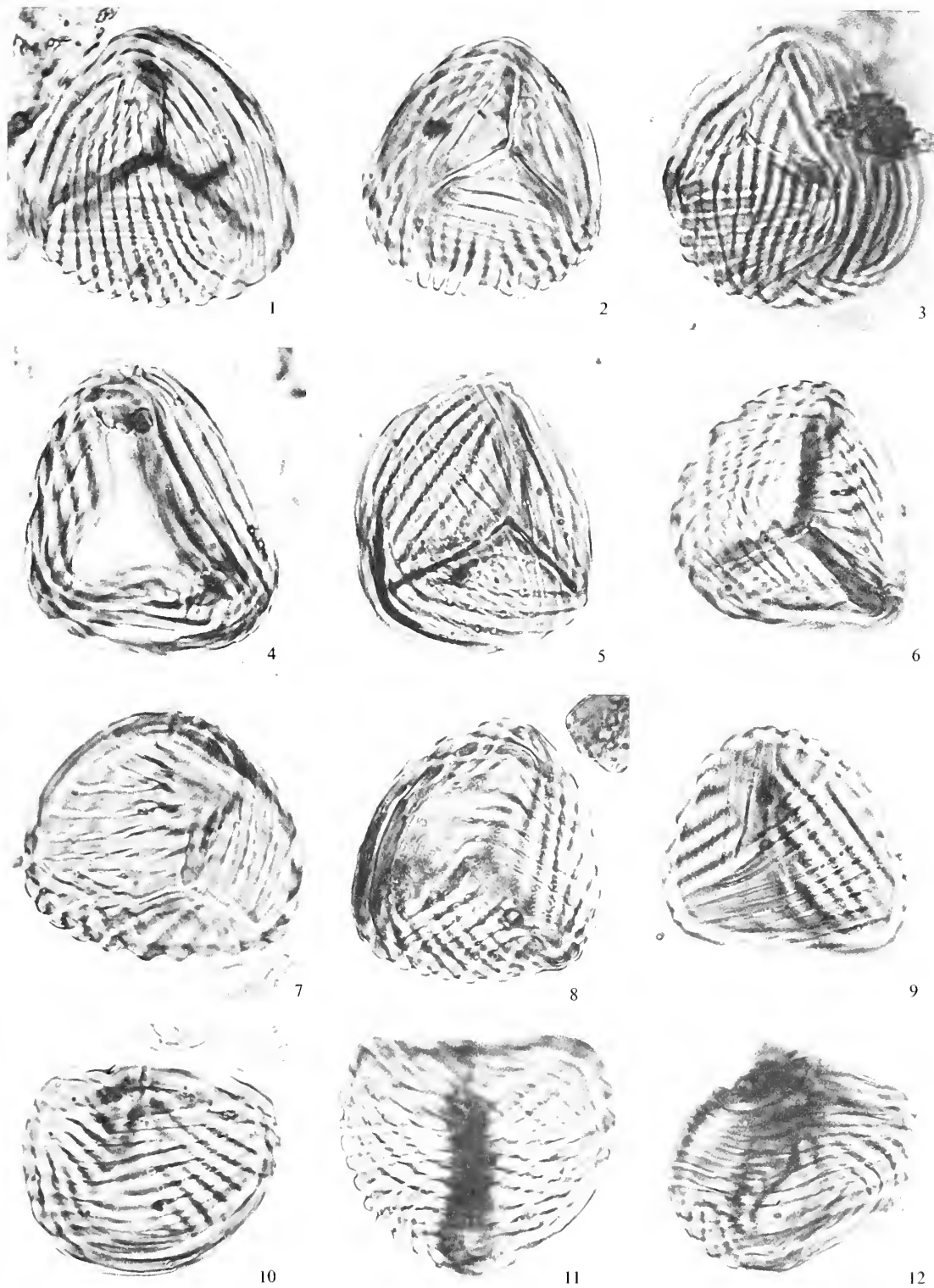
Figs. 1–12. Biorecord 25 CICATR B21. 1, Proximal aspect; W190/4, OR 26.2 116.3. 2, Distal aspect, low focus; W190/4, OR 35.5 116.7. 3, Proximal aspect; W190/2, OR 53.1 115.2. 4, Proximal aspect; W190/6, OR 30.3 109.3. 5, Proximal aspect; W190/1, OR 59.6 124.4. 6, Proximal aspect; W190/5, OR 33.5 123.9. 7, Distal aspect; W190/6, OR 53.9 118.0. 8, Equatorial aspect; W190/2, OR 27.1 123.3. 9, Equatorial aspect; W190/4, OR 36.6 125.3. 10, Equatorial aspect; W190/4, OR 51.6 123.1. 11, Oblique aspect; W190/4, OR 29.0 125.1. 12, Part of oblique aspect, showing mural profile; W190/4, OR 33.2 121.8.



EXPLANATION OF PLATE 75

Magnification, $\times 1000$.

Figs. 1–12. Biorecord 26 C1CATR A5T. 1, Proximal aspect; V197/5, OR 29·1 121·0. 2, Distal aspect, low focus; V197/5, OR 41·9 125·3. 3, Proximal aspect; V197/4, OR 32·6 117·7. 4, Proximal aspect; V197/6, OR 55·0 113·2. 5, Distal aspect; V197/7, OR 37·9 117·0. 6, Proximal aspect, low focus; V197/4, OR 58·4 104·5. 7, Distal aspect; V197/4, OR 33·1 112·6. 8, Distal aspect; V197/4, OR 26·8 122·3. 9, Distal aspect; V197/4, OR 54·7 112·3. 10, Equatorial aspect; V197/6, OR 26·0 123·0. 11, Equatorial aspect; V197/6, OR 28·2 105·7. 12, Oblique aspect; V197/4, OR 57·3 127·0.



HUGHES and CROXTON, biorecord 26 CICATR A5T

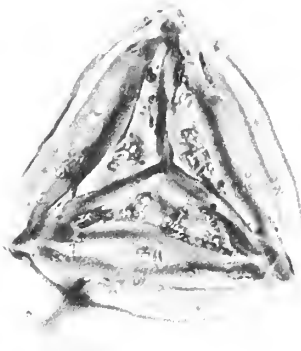
EXPLANATION OF PLATE 76

Magnification of figs. 1-11, $\times 1000$; fig. 12, $\times 2000$.

Figs. 1-12. Biorecord 27 CICATR C6. 1, Proximal aspect; V198/3, OR 30.2 109.8. 2, Proximal aspect; V198/2, OR 42.1 117.4. 3, Proximal aspect; V198/2, OR 37.1 121.0. 4, Distal aspect; W262/1, OR 28.6 110.8. 5, Proximal aspect, low focus; V198/2, OR 14.8 110.5. 6, Distal aspect; V198/3, OR 57.1 108.9. 7, Distal aspect; V198/4, OR 51.3 126.6. 8, Distal aspect; V198/2, OR 37.5 112.3. 9, Oblique aspect; W262/3, OR 60.7 125.7. 10, Distal aspect; V198/1, OR 43.3 125.3. 11, Equatorial aspect; V198/1, OR 33.1 122.0. 12, Part of oblique aspect, showing mural profile; V198/4, OR 48.0 115.1.



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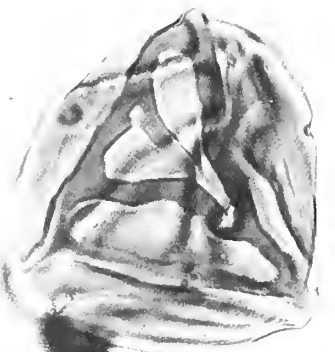
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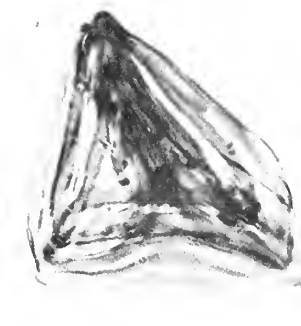
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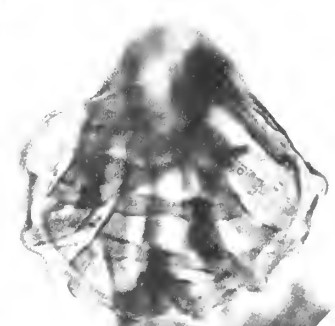
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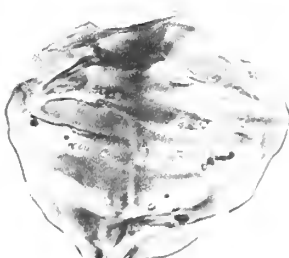
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EXPLANATION OF PLATE 77

Magnification, $\times 1000$.

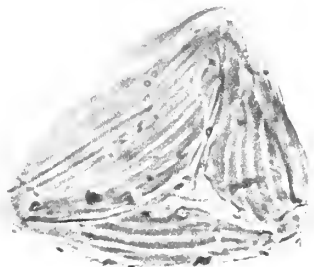
Figs. 1-12. Biorecord 28 CICATR DG. 1, Proximal aspect; WO58/2, OR 56.6 119.1. 2, Proximal aspect; WO58/7, OR 45.5 113.0. 3, Proximal aspect; WO58/1, OR 31.4 115.2. 4, Distal aspect, low focus; WO58/2, OR 46.9 114.5. 5, Distal aspect, low focus; WO58/1, OR 35.8 102.4. 6, Distal aspect, low focus; WO58/1, OR 51.6 106.9. 7, Distal aspect; WO58/3, OR 54.3 107.2. 8, Distal aspect; WO58/7, OR 51.6 123.9. 9, Equatorial aspect; WO58/8, OR 34.7 112.2. 10, Equatorial aspect; WO58/7, OR 41.6 117.3. 11, Equatorial aspect; WO58/8, OR 39.3 121.9. 12, Oblique aspect; WO58/2, OR 40.6 110.6.



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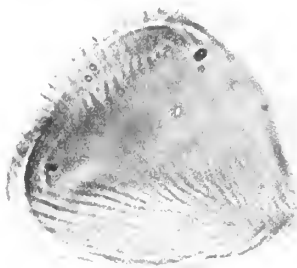
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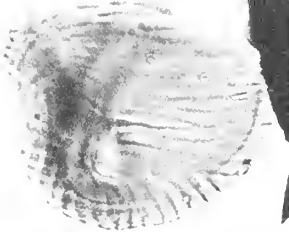
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28 CICATR DG

Plate 77; text-fig. 1

Description. Laesura may be sinuous (fig. 1). No smooth contact area distinguished. Proximal muri: three interradian sets of 15–16. Distal mural pattern: 18–25 sub-parallel muri.

Local distinction. 17 CICATR B20 is smaller with a thinner exine and positive sculpture. 25 CICATR B21 has narrower positive muri and a thinner exine, also 'swirling' proximal muri.

SYSTEMATIC DESCRIPTION OF THE EVENTS

The palynologic events are composed of comparison records graded A and B, or ungraded either if the number of specimens used was below twenty-five or if preservation was imperfect. The details are given in Tables 3–5.

Revised event. In the case of sample WM1740/6 from which Event 53 was raised (Hughes and Moody-Stuart 1969), further preparations have been studied and the constituent taxa reviewed; a new event number (81), which in effect bears the date 1972, has therefore been allotted for the new information although it has been taken from the same rock sample. In contrast the Events 43 (WM1819/5) and 36 (WM1843) have been used again; the details of these two have been presented in Table 3 for convenience of use with new events.

Unworked taxa. The column headed 'others' on the right of Tables 3 and 4 contains records, in addition to those of rare unplaceable specimens, of spores which we would previously have placed in comparison cfC. to an existing biorecord. Such records implied presumed new taxa which were not, however, made into biorecords as they were not needed for comparison in the present project, thus saving considerable time. Percentages in this category are occasionally high as in Event 100 (Table 3) or 112 (Table 4) in which in each case there were high numbers of forms not subsequently seen elsewhere. Unpublished details are filed. We feel that this principle could be applied with saving elsewhere in palynologic publication.

EVENT CORRELATION

The selected Worbarrow events are correlated individually with the reference scale section at Warlingham (text-fig. 2) by means of a bracket in each case; the bracket consists of the two statements 'After reference event X' and 'Before reference event Y'. In theory such a statement may be refined subsequently up to the limits of rock sampling. No attempt is made to *equate* a Worbarrow event with a reference event as this is logically impossible.

The points considered to be critical in each correlation are set out below but the list should be read in conjunction with Tables 3–5.

105 EVENT W128: between events 36 WM1843 and 72 WM1795; occurrence of both cf. 6 B5 and cf. 8 C2 (suggesting proximity to event 43 WM1819/5); high percentages cfA. 1 AT, cfA. 4 AW, and cfA. 7 C1; absence of cf. 10 A5S and cf. 17 B20.

TABLE 5. Preparation data for events.

Sample	Event	Biorecords	Preparation	Preparation Details	
				Oxidation Cold con.HNO ₃	Min Short Sep.Cent.
W111	115	24.C5,25.B21	W190	10mins	✓
W9	114	26.A5T	W197	10mins	✓
W12B	112		V206	30mins	✓
W14	111	27.C6	V198	30mins	✓
			W262	10mins	✓
W2	110		V192	30mins	✓
W15	109		W131	10mins	✓
W121	108		W172	10mins	✓
W18	107		V200	25mins	✓
W124	106		W180	10mins	✓
W128	105		W184	10mins	✓
WM1060/9	103		W235	10mins	✓
WM1153/2-8	101		W065	30mins	✓
WM1217/6	100	28.DG	W058	30mins	✓
WM1275/6	99		W070	30mins	✓
WM1319/2	98		W107	20mins	✓

Sample	Event	Biorecords	Preparation	Preparation Details	
				Oxidation Cold con.HNO ₃	Min Short Sep.Cent.
WM1394/1	97		W055	30mins	✓
WM1415/3	96	20.DD,21.C4	V963	20mins	✓
		22.D8,23.DCE	W103	30 mins	✓
			J035	30 mins	✓
WM1456/5	94		V958	25 mins	✓
WM1537	90		V947	20 mins	✓
WM1569	89		V513	20 mins	✓
WM1610/6	88		V913	30 mins	✓
WM1645	87		V501	25 mins	✓
WM1655	86	17.820	K018	20 mins	✓
WM1681/6	83	19.A6	V500	25 mins	✓
WM1740/6	81		V416	25 mins	✓
WM1749/8	79	18.C3	V411	15 mins	✓
WM1757	77		Y380	60 mins(S)	✓
WM1795	72		V535	25 mins	✓
WM1819/5	43		V533	25 mins	✓
WM1843	36		V016	10 mins	✓

(S)=Schulze's solution

- 106 EVENT *W124* and 107 EVENT *W18*: technically also between events 36 *WM1843* and 72 *WM1795*, but probably after event 43 *WM1819/5* on superposition and on absence of cf. 6 *B5* in spite of comparable 'fern spore size index' with event 105 *W128* (see above).
- 108 EVENT *W121*: between events 72 *WM1795* and 83 *WM1681/6*; occurrence of cf. 18 *C3*, but not of cf. 19 *A6*; high percentages of cfA. 10 *A5S* and cfA. 4 *AW*.
- 109 EVENT *W15*: between events 81 *WM1740/6* and 87 *WM1645*; occurrence of cfA. 19 *A6*, but not cf. 24 *C5*, cf. 25 *B21*, or cf. 26 *A5T*; high percentages of cfA. 10 *A5S*, and cfA. 17 *B20*.
- 110 EVENT *W2*: between events 86 *WM1655* and 90 *WM1537*; occurrence of cf. 24 *C5*, cf. 25 *B21*, and cf. 26 *A5T*, but not of cf. 20 *DD* and cf. 23 *DCE*; last occurrence of cf. 5 *A2*.
- 111 EVENT *W14*: between events 89 *WM1569* and 97 *WM1394/1*; occurrence of cf. 22 *DB*, cf. 23 *DCE*, and cf. 27 *C6*.
- 112 EVENT *W12B*: between events 89 *WM1569* and 97 *WM1394/1*; occurrence of cf. 20 *DD*, cf. 22 *DB*, cf. 23 *DCE*, and cf. 27 *C6*; last occurrence of cf. 9 *AP*.
- 114 EVENT *W9*: between events 96 *WM1415/3* and 99 *WM1215/6*; high percentage of cfA. 26 *A5T*; occurrence of cf. 24 *C5* and cf. 27 *C6*; no record of cf. 20 *DD*, cf. 22 *DB*, or cfA. 28 *DG*.
- 115 EVENT *W111*: between events 98 *WM1319/2* and 103 *WM1060/9*; occurrence of cf. 28 *DG*, cfA. 26 *A5T*; relatively high percentage of biorecord 24 *C5*.

In several cases above, we could guess at a narrower bracket but the proof could not be satisfactorily expressed at this stage, e.g. 105 Event correlation 42/44, 108 Event correlation 77/81, 109 Event correlation 83/86, 112 Event correlation 96/97, 114 Event correlation 97/98, and 115 Event correlation 99/101. It is to be expected that the application of further data from other spores would supply proof, and this process would comprise the progressive refinement or narrowing of the brackets for which we intend to provide.

As will be seen from the event numbering system there are many intermediate events in the reference scale but they are not quoted because they are not rich enough in *Cicatricosisporites* group spores to bear on the current problem; in most of these cases the fern spore size index shows low percentages of spores over 50 μm diameter.

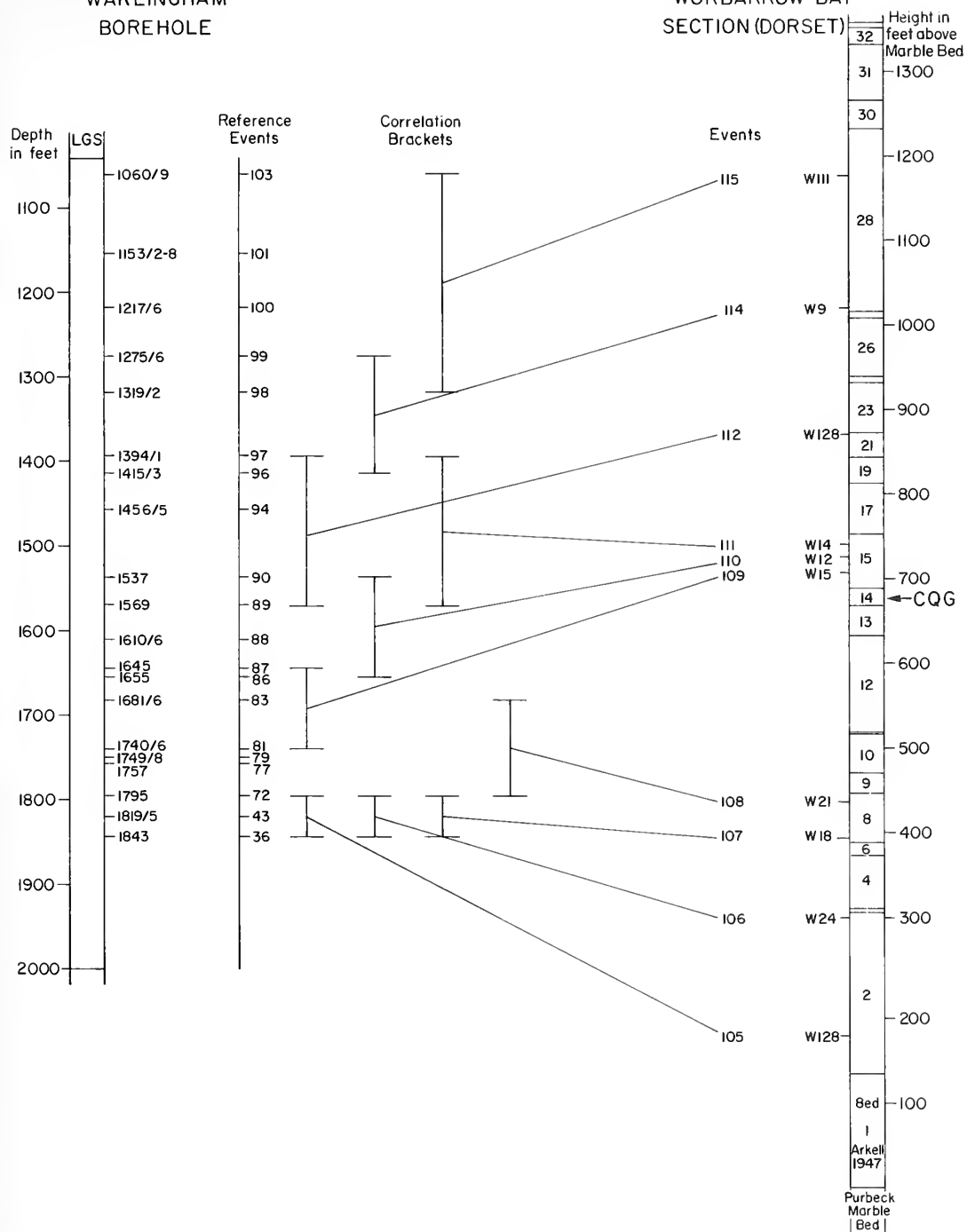
STRATIGRAPHIC CONCLUSIONS

The 'Coarse Quartz Grit' of Worbarrow Bay (Arkell 1947, Bed 14) appears to fall between events 81 and 83 on the Warlingham scale approximately around 1700 ft depth in the borehole. Worssam and Ivimey-Cook (1971) of the Institute of Geological Sciences consider this depth to lie in the Upper Tunbridge Wells Sandstone, based on general lithologic grounds and partly on ostracod correlations. Hughes and Moody-Stuart (1969) made palynologic correlations that suggested that the 1700 ft depth correlated with rocks rather lower in the outcrop succession of the Hastings Beds. Further work will be necessary to reconcile these views, but we suggest that it may not be entirely valid to identify outcrop formations such as the Wadhurst Clay at such a distance from the Central Weald, and near to the basin margin.

The age of the 'Coarse Quartz Grit' is still not better known than late Valanginian/

WARLINGHAM BOREHOLE

WORBARROW BAY SECTION (DORSET)



TEXT-FIG. 2. Diagram to show correlation brackets of ten Worbarrow Bay *Cicatricosisporites* events, on a reference scale of events of similar origin from Warlingham Borehole. CQG = the prominent 'Coarse Quartz Grit'.

early Hauterivian (Hughes 1958). Although this bed is only 20 ft (6 m) thick, it presumably represents some distinct tectonic event in south-west England or perhaps in the then adjacent Iberia (Allen 1972).

COMMENTS ON METHOD

Starting work in a new section. We found it advisable to make provisional biorecords of twenty-five specimens and brief comparison records in the first place, so that the considerable time and effort necessary to make 100 specimen biorecords, etc., could be saved when these were not required for any specific correlation. Observer-time is the only real bottleneck in the procedure.

Assemblage-types (Batten 1973). Samples have not yet been fully analysed in this way, and no mathematical expression has been devised to allow for the effect of the 'Fern Spore Size Index', both on biorecords and on events.

Future work. Supplementation of the present work by use of several other promising groups of palynomorphs in the same way will strengthen and refine these correlation brackets.

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APPENDIX OF SAMPLE DESCRIPTIONS

WARLINGHAM BOREHOLE

Unregistered samples, by courtesy of the Geological Survey in 1956.

WM1060/9	Mudstone, light olive grey (5 Y 6/1); mica. Plant fragments present.
WM1153/2-8	Mudstone, light olive grey (5 Y 6/1), laminated; mica. Plant fragments abundant.
WM1217/6	Siltstone, mottled light olive grey (5 Y 6/1) and yellowish grey (5 Y 7/2), unsorted; mica. Plant fragments common.
WM1275/6	Mudstone, greenish grey (5 GY 6/1), laminated; mica. Plant fragments present.
WM1319/2	Mudstone, light olive grey (5 Y 6/1); mica. Plant fragments present.
WM1394/1	Siltstone, yellowish grey (5 Y 7/2), wavy laminations. Plant fragments common. Pyritized plant fragments.
WM1415/3	Siltstone, light olive grey (5 Y 6/1) and pale yellowish brown (10 YR 6/2), laminated; carbonate; mica. Plant fragments present.
WM1456/5	Banded medium grey (N5) mudstone and yellowish grey (5 Y 7/2) siltstone; mica.
WM1537	Siltstone, greenish grey (5 GY 6/1), wavy laminations; mica.
WM1569	Mudstone, yellowish grey (5 Y 8/1); mica.
WM1610/6	Mudstone, light olive grey (5 Y 6/1); mica. Plant fragments common.
WM1645	Mudstone, light olive grey (5 Y 6/1); mica. Plant fragments common.
WM1655	Siltstone, banded very light grey (N8) and light grey (N7), wavy laminations; mica.
WM1681/6	Siltstone, pinkish grey (5 YR 8/1), laminated; mica. Plant fragments present.
WM1740/6	Siltstone, banded yellowish grey (5 Y 8/1) and medium light grey (N6); mica. Plant fragments present.
WM1749/8	Mudstone, banded light olive grey (5 Y 6/1) and very light grey (N7); mica. Plant fragments present. Ostracods abundant.
WM1757	Siltstone, yellowish grey (5 Y 8/1), wavy laminations; mica. Ferruginous staining, greyish orange (10 YR 7/4).
WM1795	Mudstone, medium light grey (N6), laminated; calcareous; mica. Plant fragments present. Ostracods abundant.
WM1819/5	Shale, banded light grey (N7) and medium grey (N5); mica.
WM1843	Siltstone, light olive grey (5 Y 6/1), wavy laminations; mica. Plant fragments common.

WORBARROW BAY

W111	Fine sandstone, light olive grey (5 Y 5/2), unsorted; semi-consolidated. Abundant plant fragments.
W9	Unsorted siltstone with larger pebbles, light brownish grey (5 YR 6/1). Abundant plant fragments.
W12B	Banded fine sandstone and siltstone, pale yellowish brown (10 YR 6/2); semi-consolidated. Plant fragments present.
W14	Mudstone, medium light grey (N6). Plant fragments abundant. Ostracods.
W2	Medium sandstone, light brownish grey (5 YR 6/1), unsorted. Plant fragments common.
W15	Medium sandstone, pale yellowish brown (10 YR 6/2), unsorted. Plant fragments common.
W121	Siltstone, dark yellowish brown (10 YR 4/2), unsorted. Large plant fragments abundant. Ferruginous stains, light brown (5 YR 5/6).
W18	Mudstone, medium light grey (N6). Plant fragments present.
W124	Banded siltstone, greyish olive (10 Y 4/2) and greyish yellow (5 Y 7/2), unsorted. Small plant fragments present. Ferruginous staining, dark yellowish orange (10 YR 6/6).
W128	Fine sandstone, dark greenish grey (5 GY 4/1), unsorted. Large plant fragments. Ferruginous stains.

[Owing to Authors' revision there are no pages 602-606]

ISOTOPIC RATIOS AND WEALDEN ENVIRONMENTS

by P. ALLEN, M. L. KEITH, F. C. TAN, and P. DEINES

ABSTRACT. Isotopic methods of assessing Wealden palaeoenvironments are reviewed. Emphasis is placed on the importance of using only primary, skeletal, untransported carbonates. Recrystallization and cementation generally reduce the $^{13}\text{C}/^{12}\text{C}$ and $^{18}\text{O}/^{16}\text{O}$ ratios of Wealden carbonates. Hence, while those with high $^{13}\text{C}/^{12}\text{C}$ are likely to be marine, those with low $^{13}\text{C}/^{12}\text{C}$ cannot be assigned to a depositional environment unless known to be primary.

Ratios from aragonitic shells of one species each of *Cassiope*, *Neomiodon*, and *Filosina*? indicate 'marine' conditions. Less certainly, marine conditions may be indicated by calcitic shells of pelecypods (one species each of *Lio-strea* and *Neomiodon*), gastropods (one species of *Paraglauconia*), and ostracods (two species of *Cypridea* and one of *Mantelliana*). Forms not assignable to 'marine' or 'fresh' water are three species of *Cypridea*, one species each of *Theriosynoecum*, *Damonella*, *Filosina*, *Unio*, *Viviparus*, and a corbulid, and two species of *Equisetites*. The new data support the transgressive models for the major Wealden clay formations.

Interpretation of transitional water temperatures from $^{18}\text{O}/^{16}\text{O}$ ratios is unreliable. Nevertheless, values from primary aragonites in the Hastings Beds (*Neomiodon*) and Weald Clay (*Filosina*, *Cassiope*) lie in the range of modern marine molluscs from warm temperate waters. This is consistent with current opinion based on other palaeontological evidence.

AN earlier reconnaissance (Allen and Keith 1965) suggested that, in the Wealden clay formations, $\delta^{13}\text{C}$ broadly reflects the variable depositional salinities inferred from palaeontological evidence. Subsequent work on body-fossils and trace-fossils confirms the fluctuating salinities, particularly for the Weald Clay, and the marginal environments postulated (Shephard-Thorn *et al.* 1966; Smart *et al.* 1966; Anderson 1967; Anderson *et al.* 1967; Worssam and Thurrell 1967; Thurrell *et al.* 1968; Kilenyi and N. W. Allen 1968; Dines *et al.* 1969; Kennedy and MacDougall 1969; Batten 1969; Watson 1969).

Such environments yield isotopic ratios that are so far impossible to interpret in detail (Keith and Parker 1965). This, combined with problems of Wealden diagenesis and our previous use of whole-rock samples, led us to investigate the limitations of the isotopic method more fully. In particular *Neomiodon*, with its widely ranging $\delta^{13}\text{C}$ and varying degrees of recrystallization (Allen and Keith 1965, table 1), merited further examination.

LIMITATIONS OF ISOTOPIC METHODS

General. The isotopic basis for interpreting ancient depositional environments and for distinguishing marine carbonates from ^{13}C -deficient freshwater carbonates was discussed in an earlier paper (Allen and Keith 1965) and will not be repeated here, except for caveats regarding limitations on palaeosalinity estimates derived from $\delta^{13}\text{C}$. Measurements of isotopic compositions are reported in the standard δ -notation, i.e. as differences of $^{13}\text{C}/^{12}\text{C}$ (and $^{18}\text{O}/^{16}\text{O}$) ratios in parts per thousand relative to those of the Chicago PDB standard, a Cretaceous belemnite:

$$\delta^{13}\text{C} = \left(\frac{^{13}\text{C}/^{12}\text{C}_{\text{sample}} - ^{13}\text{C}/^{12}\text{C}_{\text{standard}}}{^{13}\text{C}/^{12}\text{C}_{\text{standard}}} \right) 1000.$$

Interpretation of past salinities can be based on isotopic comparisons of 'ideal' ancient carbonates with the $\delta^{13}\text{C}$ ranges of modern carbonates (Keith *et al.* 1964). Two categories appear meaningful: 'marine' ($\delta^{13}\text{C} > -2\text{‰}$) and 'freshwater' ($\delta^{13}\text{C} < -2\text{‰}$), with some overlap across the arbitrary boundary. An 'ideal' sample (not easily obtained or recognized in practice) would consist of unrecrystallized carbonate formed in isotopic equilibrium with the environment to be determined and still retaining the original population of carbon (and oxygen) atoms. Complications arise mainly because other kinds of carbonate may be associated, including (a) clastic carbonates from limestones, (b) biogenic carbonates with variable or non-equilibrium carbon isotopic compositions due to vital effects (e.g. of corals, echinoids) or to localized concentrations of decomposing organic matter, (c) carbonates formed in other environments and transported to the site of deposition, or intermixed following environmental change at the depositional site, (d) carbonates formed by diagenetic recrystallization or cementation in pore-waters of variable salinity.

Any of these complications can be troublesome in samples from marginal variable-salinity environments (Keith and Parker 1965; Lloyd 1969). The present investigation relates particularly to (c) and (d). We emphasize, as did Tan and Hudson (1971), the importance of using well-preserved skeletal carbonates wherever possible, rather than whole-rock samples.

Extraneous CaCO_3 . In so far as the Weald Basin was bordered by Jurassic and Lower Carboniferous limestones (Allen 1961, 1967a), complication (a) is always possible, though no actual clasts of limestone have been confirmed in the Wealden of the Weald. The misleading influence of biogenic carbonates (allochems) transported from other environments in the same basin is illustrated by sample S8126 of Allen and Keith (1965, fig. 1 and table 1). This sample contains, among the presumably indigenous oysters, reworked bioclastic materials, both marine and non-marine (echinoid plates and spines, *Viviparus* shells, ostracod carapaces). Any salinity estimate based on the $^{13}\text{C}/^{12}\text{C}$ ratio of the whole rock (-4.3‰) is clearly invalid. Sediments deposited during marine transgressions across less saline environments must generally be suspect for this reason.

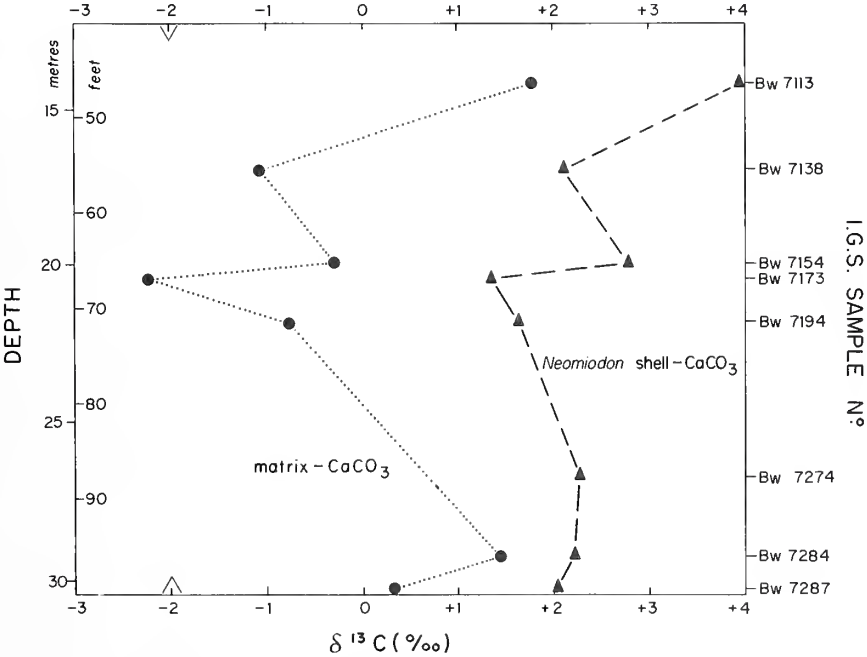
The complicating effects of interstitial materials and recrystallization were investigated by analysing materials from the I.G.S. borehole No. 1 at Wadhurst Park, Sussex (Anderson *et al.* 1967). Eight *Neomiodon medius* beds in the Wadhurst Clay, with shells preserved wholly or partly as aragonite, were sampled from 14.20 m to 30.25 m depth. All the shell samples gave carbon isotopic compositions in the marine range $\delta^{13}\text{C} > -2\text{‰}$ (Table 1). All the matrices, substantially calcite, gave lower $\delta^{13}\text{C}$ values than the shells (text-fig. 1). ^{18}O varied in the same way. Thus the matrix carbonates may have originated or recrystallized in less saline environments than those of *Neomiodon*, or possibly came from organisms whose calcification processes involved different degrees of isotopic fractionation (see below). Nevertheless the matrix samples, as well as the embedded shells, seem to be marine rather than freshwater. There is only one borderline analysis (Bw 7173 matrix) with $\delta^{13}\text{C}$ less than -2‰ .

Indigenous CaCO_3 . Even carbonates demonstrably formed in the same environment

TABLE 1. Wadhurst Clay of Wadhurst Park: isotopic comparisons between aragonitic *Neomiodon medius* shells and their more calcitic matrices (I.G.S. borehole No. 1, Grid reference TQ 6325 2911).

Specimen Nos.		Depth (m) in borehole	Components	Mineral (X-ray)	Isotopic analysis	
I.G.S.	Reading Univ./ Penn. St. Univ.				$\delta^{13}\text{C}(\text{‰})$	$\delta^{18}\text{O}(\text{‰})$
Bw 7113	S8129	14.20*	Shells	Aragonite	+3.95	-1.79
	68-426		Matrix	Calcite	+1.78	-3.26
Bw 7138	S8131	17.04	Shells	Aragonite	+2.10 { +2.11†	-2.35 { -2.30†
	68-428		Matrix	Calc. and arag.	-1.05 { +2.09†	-3.30 { -2.39†
Bw 7154	S8132	19.91	Shells	Arag. > calc. (tr.)	+2.78	-2.72
	68-429		Matrix	Calcite	-0.27	-5.50
Bw 7173	S8133	20.42	Shells	Arag. = calc.	+1.35	-3.00
	68-430		Matrix	Calcite	-2.19	-5.37
Bw 7194	S8134	21.79	Shells	Aragonite	+1.61	-2.24
	68-431		Matrix	Calcite	-0.78 { -0.65† -0.90†	-5.80 { -5.50† -6.09†
Bw 7274	S8135 68-432	26.77	Shells	Aragonite	+2.28	-3.53
Bw 7284	S8136	29.26	Shells	Arag. = calc.	+2.21	-2.65
	68-433		Matrix	Calcite	+1.46	-5.98
Bw 7287	S8137	30.25‡	Shells	Calc. + arag.	+2.05	-3.87
	68-434		Matrix	Calcite	+0.31	-4.76

The total thickness of Wadhurst Clay is about 67 m. † Duplicate analyses.
* Horizon c. 47 m below Lower Tunbridge Wells Sand. ‡ Horizon c. 4 m above Top Ashdown Pebble Bed.



TEXT-FIG. 1. Wadhurst Clay of Wadhurst Park. Carbon isotopic ratios ($\delta^{13}\text{C}$) from Table 1 of separated *Neomiodon medius* (▲) and matrix CaCO₃ (●). I.G.S. borehole No. 1.

are not necessarily straightforward to interpret isotopically. Some organisms, though living under similar conditions of salinity, temperature, etc., show different abilities to fractionate carbon and oxygen isotopes when depositing CaCO_3 (Keith and Weber 1965). Decomposing organic matter adds another complication, generating CO_2 with variable $\delta^{13}\text{C}$ depending partly upon the origin of the organic matter. A further source of variation, in some cases, is isotopic fractionation between CO_2 and CH_4 .

Nevertheless, we show below that the ^{13}C -palaeosalinities derived from Wealden carbonates are significant when considered in terms of the broad categories of 'marine' and 'freshwater' as defined on p. 608. But the transitional environments of the Wealden, with waters of highly variable ^{18}O -content and salinity, offer little hope of yielding useful ^{18}O palaeotemperatures: the temperature effect is small compared with those of mixing and evaporation.

CaCO₃ recrystallization and cementation. Diagenetic crystallization of aragonite and calcite can modify pre-existing isotopic ratios (Gross 1964; Hodgson 1966; Stahl and Jordan 1969; Tan and Hudson 1971, and their refs.). The necessary conditions include interstitial waters with different compositions from those of the depositional environment. Recrystallization may occur soon after deposition, for example during evaporation from closed basins (Keith and Parker 1965), or on tidal flats such as sabkhas, where diagenesis occurs in the presence of supersaline porewaters. At the other extreme, transitional carbonate sediments may undergo diagenesis in the presence of low-salinity groundwater. This was apparently important in several of the samples described here.

Diagenesis affected the matrices of most of the samples from Wadhurst Park No. 1. It certainly changed all three from borehole No. 2, 200 m away (Table 2). The *Neomiodon medius* shells from this core are almost entirely calcite and there is either a little or no matrix carbonate. They give lower values of $\delta^{13}\text{C}$ than any in borehole No. 1. This is a good example of analyses yielding no useful information

TABLE 2. Wadhurst Clay of Wadhurst Park: isotopic ratios of dominantly calcitic *Neomiodon medius* shells and matrices (I.G.S. borehole No. 2, Grid reference TQ 6308 2920 about 200 m from No. 1; horizon of top about 18.64 m above top of No. 1).

Specimen Nos.		Depth (m) in borehole	Components	Mineral (X-ray)	Isotopic analysis	
I.G.S.	Reading Univ./ Penn. St. Univ.				$\delta^{13}\text{C}(\text{‰})$	$\delta^{18}\text{O}(\text{‰})$
Bw 7353	S8138 68-435	16.15	Shells	Calc. > arag.	-5.17	-7.87
Bw 7377	S8139 68-436	16.36	Shells	Calcite	-2.29	-3.46
			Matrix	Calcite	-0.39	-4.68
Bw 7385	S8140 68-437	16.43*	Shells	Calc. > arag.	-3.37 { -3.42† -3.25†	-5.79 { -5.89† -5.70†
			Matrix	Calcite	-0.81 { -0.91† -0.72†	-2.78 { -2.79† -2.77†

* Horizon c. 30.6 m below Lower Tunbridge Wells Sand and c. 36.4 m above Top Ashdown Pebble Bed.

† Duplicate analyses.

about an original depositional environment. The shells are recrystallized, they give lower $\delta^{13}\text{C}$ ratios than their matrices (cf. borehole No. 1) and they straddle the arbitrary division ($-20_{\text{‰}}$) between marine and freshwater shells.

Four analyses of *Neomiodon*-rock previously published (Allen and Keith 1965, table 1) probably reflect the combined influences of calcite cementation and the diagenetic change of aragonite to calcite. The rocks are shelly calcareous sandstones ('Tilgate stone'), comprising quartz clasts and calcite valves cemented with clear calcite (S8112, S8113, S8115, S8118). All give low $\delta^{13}\text{C}$ (-8.3 to $-4.70_{\text{‰}}$). Three other samples (S8109-S8111) are quartz-free, virtually uncemented, and their *Neomiodon medius* shells retain some aragonite. All yield substantially higher $\delta^{13}\text{C}$ values (-1.3 to $+0.20_{\text{‰}}$). Apparently some of the $\delta^{13}\text{C}$ variation previously attributed to a wide salinity tolerance in *Neomiodon* arises from the postdepositional production of calcite through the action of groundwater.

In general, therefore, cementation or recrystallization reduced the $^{13}\text{C}/^{12}\text{C}$ and $^{18}\text{O}/^{16}\text{O}$ ratios of the Wadhurst sediments. The same is true of the Weald Clay. Prentice (1969, pp. 3-4) describes Weald Clay cycles and concludes that they record upward-decreasing salinities which are parts of a general salinity series *Cassiope* \rightarrow 'Cyrena' [presumably *Filosina*] \rightarrow 'Paludina' [presumably *Viviparus*] \rightarrow ostracods \rightarrow *Equisetites*. This series has been largely confirmed. During the course of our work a small cycle at Ewhurst, high in the Weald Clay (Table 3), showed how effectively recrystallization of shell aragonite could destroy original isotopic evidence.

Shells of Wealden age from Germany show the same kind of variation. Marine *Cucullaea*, collected (with the ammonite *Platylenticeras*) from the basal Valanginian of Sachsenhagen (1 m above the Wealden), are entirely calcite, though originally aragonite (Hall and Kennedy 1967). Their $\delta^{13}\text{C}$ - and $\delta^{18}\text{O}$ -values are low (-2.3 and $-8.50_{\text{‰}}$), i.e. spuriously 'freshwater' (samples S8128/68-444). On the other hand *Neomiodon* (S8161) and *Paraglauconia* (S8162) from the underlying Wealden, though similarly recrystallized to calcite, have carbon ratios ($\delta^{13}\text{C} = -1.32$ and $-1.66_{\text{‰}}$ respectively) in the arbitrary marine range.

HASTINGS BEDS

Salinity. Palaeontological evidence suggests that, of the two major Wealden subdivisions, the lower (or Hastings Beds) records a generally narrower range of salinities. Prior to our isotopic work, no macrofossils of near-marine aspect were known, nor any microfossils, though foraminifera had been alluded to in general terms (Anderson *et al.* 1967, p. 175). Salinity variations had, however, long been suspected and sought (e.g. Allen 1962, p. 226). The basis was the observed antipathy, on single lamination surfaces, between swarms of *Neomiodon* (Casey 1955b) and the other fossil assemblages. The latter, hinting at rather fresher water, include stoneworts (one species of *Circonitella*: Watson 1969), liverworts (two species of *Hepaticites*: op. cit.), probable liverworts preserved *in situ* (op. cit., fig. 13), horsetails *in situ* (two or three species of *Equisetites*), and dominant *Viviparus*, *Physa*, *Unio*, or *Cypridea* spp. (Anderson *et al.* 1967). *Neomiodon* was thought to have lived in more brackish conditions. Its German contemporaries were already known to consort with unequivocally brackish fossils (Allen 1967a, p. 60). The new isotopic evidence places *Neomiodon*

TABLE 3. Small cycle in upper Weald Clay, laneside ditch, 1 km ESE. parish church, Ewhurst, Surrey (TQ 101 401).

Subsample Nos.		Stratigraphy	Thick- ness (m)	Component analysed	Palaeontological salinity	Isotopic analysis		
Reading Univ.	Penn. St. Univ.					$\delta^{13}\text{C}$ (‰)	$\delta^{18}\text{O}$ (‰)	Environmental category
S8155	71-153	Large- <i>Viviparus</i> limestone (scattered <i>Lepidotus</i> scales)* Laminated clays	0.05	<i>Viviparus</i> shells (calcite)	Freshwater	-5.22	-4.41	Indeterminate
S8154	71-152	Pebbly glauconitic calcareous <i>Filosin</i> † sandstone forming isolated runnel- casts (scattered clay pellets to 1.2 × 1.6 cm, ostracods,† large- <i>Viviparus</i> , and <i>Lepidotus</i> scales)	1.00 0.01	— <i>Filosina gregaria</i> shells (calcite)	— Brackish water	— -5.04	— -5.77	— Indeterminate

----- Erosion surface -----

* Horizon: I.G.S. Bed 8b of Thurrell *et al.* 1968.

† Disarticulated valves, many broken.

medius squarely in our 'marine' category. This recalls Tan and Hudson's work (1971) showing that well-preserved aragonitic shells of *Neomiodon* from the Hebridean Middle Jurassic have a 'marine' range of $\delta^{13}\text{C}$.

The notion that salinity exerted a major control arose from the theory that the Hastings clays were broadly transgressive and the sandstones regressive (Allen 1959). Accepting that these movements were caused by the sea and physically connected with it, the basal strata of each clay formation should record rising salinities (Allen 1959, p. 342) and the top sands of each arenaceous formation falling salinities. This could explain the marked antipathy between basal reedswamp and burrowed beds (Allen 1962) and the absence from the Wealden of strictly freshwater ostracod genera. If the lowest salinities were normally achieved during deposition of the regressive sands then such ostracods are the least likely to have been preserved (Anderson 1967, *in litt.*).

Salinities from Wadhurst Clay. Previous isotopic analyses of aragonite-bearing *Neomiodon medius* from the ?transgressive basal Wadhurst (S8109-S8111, in Allen and Keith 1965) strengthened the idea that, as the waters rose, their salinities rose too ($\delta^{13}\text{C} = -1.3$ to $+0.20\text{‰}$).

Salinity fluctuations in the type-area of Wadhurst Park (I.G.S. boreholes Nos. 1-3) were independently investigated by Anderson, using ostracods (in Anderson *et al.* 1967). Less saline and more saline episodes were recognized, assuming that the former are recorded by *Cypridea*-dominated faunas and the latter by 'non-*Cypridea*' faunas (*Theriosynoecum*, *Mantelliana*, *Rhinocypris*, Darwinulids, *Dicrorygma*). We attempted to test the distinction by analysing *C. laevigata* carapaces ('the nearest to a freshwater ostracod we have in the Purbeck-Wealden') and *T. allenii* ('strongly brackish to marine'), kindly prepared and so interpreted by Professor F. W. Anderson from the Westfield I.G.S. borehole (TQ 8204 1614, Shephard-Thorn 1971). *C. laevigata* gave a freshwater ratio ($\delta^{13}\text{C} = -4.4\text{‰}$) but its carapaces enclosed much secondary calcite. Those of *T. allenii* were too few for analysis; associated aragonitic fragments (molluscan?) gave a marine ratio ($\delta^{13}\text{C} = +0.48\text{‰}$).

Our new analyses of well-preserved *Neomiodon medius* (Table 1) support the contention that the Wadhurst waters became saline at times. Rejecting isotopic ratios based on subordinate or no aragonite, we have eight horizons scattered over 16 m of the local 67-m succession. All their $\delta^{13}\text{C}$ values range from $+1.4\text{‰}$ (shell carbonate half-aragonite) to $+4.0\text{‰}$ (carbonate wholly aragonite) and thus fall into the 'marine' category.

Salinities from Grinstead Clay. Comparison of the base (?transgressive) of this formation with that of the Wadhurst Clay raises an interesting ecological question. Strikingly similar in physical sedimentology, they differ in that the Grinstead base was not colonized widely (if at all*) by aquatic horsetails (Allen 1962, p. 236-7). Probably it also contains a richer and more abundant ostracod fauna. Perhaps more saline water explains both features.

* Rootlets (i.e. downward-branching tubules with carbonaceous linings) are found rarely and locally, but not as commonly as previously supposed, when animal burrows were mistaken for them (Allen 1959, 1960). The few true rootlets do not visibly originate at this level, but probably from rhizomes higher up, e.g. the mid-Grinstead *Equisetites* soil bed (Gallois 1963) 6-7 m above.

TABLE 4. Palaeontological and isotopic analyses of ostracod carapaces (calcite) near base of Grinstead Clay at Philpots Quarry, West Hoathly, Sussex (TQ 355 322).

Source of material		Palaeontological analysis		Isotopic analysis		
Height above TLTPWB†	Lamina	Microfauna	Salinity	$\delta^{13}\text{C}$ (‰)	$\delta^{18}\text{O}$ (‰)	Environmental category
2.90 m		<i>Mantelliana phillipsiana</i> dominant	Relatively high		Not analysed	
1.43 m to 1.32 m	C	<i>Cypridea recta tillsdenensis</i> and <i>C. bispinosa suttin-gensis</i> predominantly (S8145/71-151C)	Relatively low	+0.58* -0.13†	-2.39* -2.46†	Marine?
	B	<i>M. phillipsiana</i> , <i>Cypridea recta tillsdenensis</i> , <i>C. bispinosa suttin-gensis</i> (S8144)	Intermediate		Not analysed	
	A	<i>Mantelliana phillipsiana</i> mainly (S8143/71-151S)	Relatively high	+0.05	-2.86	Marine?
1.01 m		<i>Theriosynoecum allenii</i> dominant (S8146)	Relatively high		Not analysed	

Sample nos. given in microfauna column (Reading Univ./Penn. State Univ.)

* Treated 3 days in H_2O_2 to remove organic matter.

† Treated 3 days in sodium hypochlorite (5% solution).

‡ Top Lower Tunbridge Wells Pebble Bed.

Our new isotopic results are compared with Professor Anderson's palaeontological analyses in Table 4. Laminae A, B, and C were half-millimetre partings of closely packed ostracod carapaces, many articulated, separated by black clay (1-5 mm) with sparse carapaces. The higher salinities predicted by the transgressive model seem confirmed. However, the ^{13}C technique cannot apparently resolve all the palaeontological differences recognized by Professor Anderson and for the isotopic interpretation we assume that the ostracod calcite was primary. We have been unable to confirm the last assumption. But it appears to be strengthened, as Dr. J. D. Hudson points out, by our Hastings ostracods generally giving ^{18}O ratios that could be depositional (see below), like the aragonitic but unlike the recrystallized shells.

Shells of '*Tornatella*', *Neomiodon*, *Unio*, *Viviparus*, etc., from the succeeding clays prove to contain little or no aragonite. We therefore have no Grinstead samples of primary molluscan carbonate, and isotopic analysis does not provide reliable estimates of salinity. A new analysis of *Unio subtruncatus* shell (subsample 71-161 from Philpots Quarry, West Hoathly, Sussex) gave no aragonite, $\delta^{13}\text{C} = -7.08\text{‰}$ and $\delta^{18}\text{O} = -8.30\text{‰}$.

Temperature. No reliable temperatures can be calculated because the oxygen isotopic compositions of the marginal waters are unknown and the temperature effect is small relative to those of mixing and evaporation (Keith and Parker 1965; Lloyd 1969). Nevertheless, the $\delta^{18}\text{O}$ variation of aragonitic *Neomiodon* (-3.9 to -1.8‰)

is generally within the range of modern marine mollusc shells from warm temperature waters (Keith *et al.* 1964). This agrees well with recent opinions concerning the English Purbeck–Wealden ostracods ('water temperatures . . . suggest a Mediterranean type climate': Professor F. W. Anderson 1970, *in litt.*), molluscs ('warm temperate': late W. J. Arkell), land reptiles ('subtropical': Dr. W. E. Swinton 1970, *in litt.*), reptiles generally ('warm temperate': Dr. K. A. Kermack 1970, *in litt.*), and flora ('warm temperate . . . alternations of wet and dry periods . . . drought over some months . . . normal': Professor T. M. Harris 1970, *in litt.*). Bowen (1966), on the basis of $\delta^{18}\text{O}$ values from marine sediments, quoted temperatures of 17.4 °C to 22.1 °C for the contemporary Neocomian seas of the Hautes Alpes, 800 km SSE. of the Weald.

WEALD CLAY

Salinity. More drastic variations in environment are indicated by the Weald Clay fossils above the Horsham Stone. Palaeontologically, freshwater is suggested by numerous beds with *Chara*, *Equisetites*, *Cypridea*, *Viviparus*, and *Unio*, often as largely separate associations. Marine or near-marine conditions are recorded by at least three thin bands variously containing *Ostrea*, *Nemocardium*, *Mytilus*, *Gervillia*, *Corbula*, *Filosina*, *Melanopsis*, *Cassiope*, *Paraglauconia*, echinoids, cirripedes, foraminifera, *Ophiomorpha*, etc. (see references on p. 607). Other horizons are dominated by only one or two of these genera (Kennedy and MacDougall 1969) or by non-*Cypridea* ostracods (Anderson 1963, 1968), suggesting less stable environments. Of the ecological factors, fluctuating salinity may have been important, perhaps limiting.

Our previous isotopic reconnaissance (Allen and Keith 1965) did little more than support the broad picture. *Theriosynoecum fittoni* (identified subsequently by Professor F. W. Anderson as dominant in sample S8127) may have lived in freshwater, as deduced by Kilenyi and N. W. Allen (1968, pp. 158, 162). If confirmed, this might contrast with the Wadhurst species of the same genus, for which brackish to marine conditions are possible (cf. Tan and Hudson 1971, table 3). Unfortunately our carapaces of *T. fittoni* contained some secondary calcite; and the evidence concerning *T. allenii* is indirect, being based on associated 'marine' shell fragments.

Near the arbitrary freshwater/marine boundary our original results (1965) were suspect owing to the recrystallization of *Filosina*-aragonite to calcite (S8120) and to the choice of whole-rock analysis for the oyster bed (S8126). Subsequent determinations of $\delta^{13}\text{C}$ for the oyster-carbonate alone gave $\delta^{13}\text{C} = +1.16\text{‰}$ (Table 5).

Skeletal CaCO_3 . Like their predecessors, the Weald Clay fossil carbonates were commonly recrystallized after deposition (Table 5 and text-fig. 2).

For originally aragonitic shells, and assuming that recrystallization of aragonite generally yielded calcite, the proportion of aragonite may be used to judge whether the original isotopic ratios may have been retained. Unfortunately, we were unable to establish any independent non-isotopic criteria for identifying the primary, unrecrystallized calcite of ostracods, oysters, etc. Such criteria may eventually be developed. Thus preliminary studies show differences in the cathodoluminescence of organic and diagenetic carbonates, and most ostracod valves have a three-layered structure (formed by the calcitization of a chitinous envelope) which is frequently

TABLE 5. New isotopic and palaeontological analyses of skeletal CaCO_3 from the Weald Clay (Weald) and upper Wealden Shales (Isle of Wight), in probable stratigraphical order.

Subsample Nos.	Reading Univ./I.G.S.	Penn. St. Univ.	Locality	Palaeontological analysis		Mineral (X-ray)	Isotopic analysis	
				Identity	Salinity		$\delta^{13}\text{C}$ (‰)	$\delta^{18}\text{O}$ (‰)
			<i>Isle of Wight</i>					
S8158		71-156	Sandown	<i>Liostrea ?distorta</i>	from same bedding	Calcite	+1.16	-2.90
S8157		71-155	"	<i>Filosina gregaria</i>	surface	Calcite	-7.07	-5.32
			<i>Weald</i>					
S8155		71-153	Ewhurst, Surrey	<i>Viviparus sussexensis</i>	f	Calcite	-5.22	-4.41
S8154		71-152	"	<i>Filosina gregaria</i>	br	Calcite	-5.04	-5.77
S8151		68-352	Hambleton, Surrey	<i>Equisetites burcharthi</i> (in situ)	f	Calcite†	-23.32	-7.92
S8152		71-150A	Leigh, Surrey	<i>Cypridea rotundata</i> 56% <i>Cypridea valdensis</i> 21% <i>Damonella pygmaea</i> 23%	* f*	Calcite	-7.29	-2.90
S8156/ W1423-24 (I.G.S.)		71-154	Worthingham, Surrey	<i>Filosina ? membranacea</i>	br	Arag.	-1.01	-2.63
S8150		68-355F	Capel, Surrey	<i>Corbudit†</i>	br?	Calcite	-8.55	-9.28
S8147		68-346	Warnham, Sussex	<i>Cassiope</i>	br	Calcite > tr. arag.	-0.71	-5.82
S8149		68-348B	Capel, Surrey	<i>Cassiope</i>	br	Arag. > calc.	-1.20	-4.63
S8148		68-348A	"	<i>Cassiope</i>	br	Calc. > arag.	-2.85	-6.46

destroyed by recrystallization. Our Weald Clay ostracods, moreover, show ^{18}O ratios that could be depositional, as in the Hastings Beds (pp. 614–15).

As for the Hastings Beds, semiquantitative estimates of aragonite:calcite ratios were made from X-ray diffraction patterns. Samples in which aragonite is dominant are depicted as black rectangles in text-fig. 2. The two genera represented (*Filosina*?, *Cassiope*) deserve particular attention as potential indicators of the environment of deposition. Both appear, like *Neomiodon*, to have been 'marine'.

Shells of the freshwater mollusc *Viviparus*, presumably originally aragonite, are now calcite, and do not provide a basis for judging whether their present isotopic composition is due mainly to conditions of deposition or diagenesis. As pointed out above, calcite shells of *Filosina* (subsamples 71–152 and 71–155 belong to another species) are sometimes deficient in ^{13}C and thereby isotopically indistinguishable from recrystallized freshwater shells such as *Viviparus* (71–153).

Because of the non-preservation of aragonitic *Viviparus* shells (including those of Allen and Keith 1965) it is still not possible either to support or refute

KEY TO TABLE 5

* Identified, counted, and interpreted by Professor F. W. Anderson (some carapaces 2- or 3-layered, many infilled micrite or drusy calcite).

† Provisionally identified by Dr. R. Casey (life assemblage of articulated shells, young and old).

‡ Early post-mortem cement?

f = freshwater, *br* = brackish water, *m* = marine.

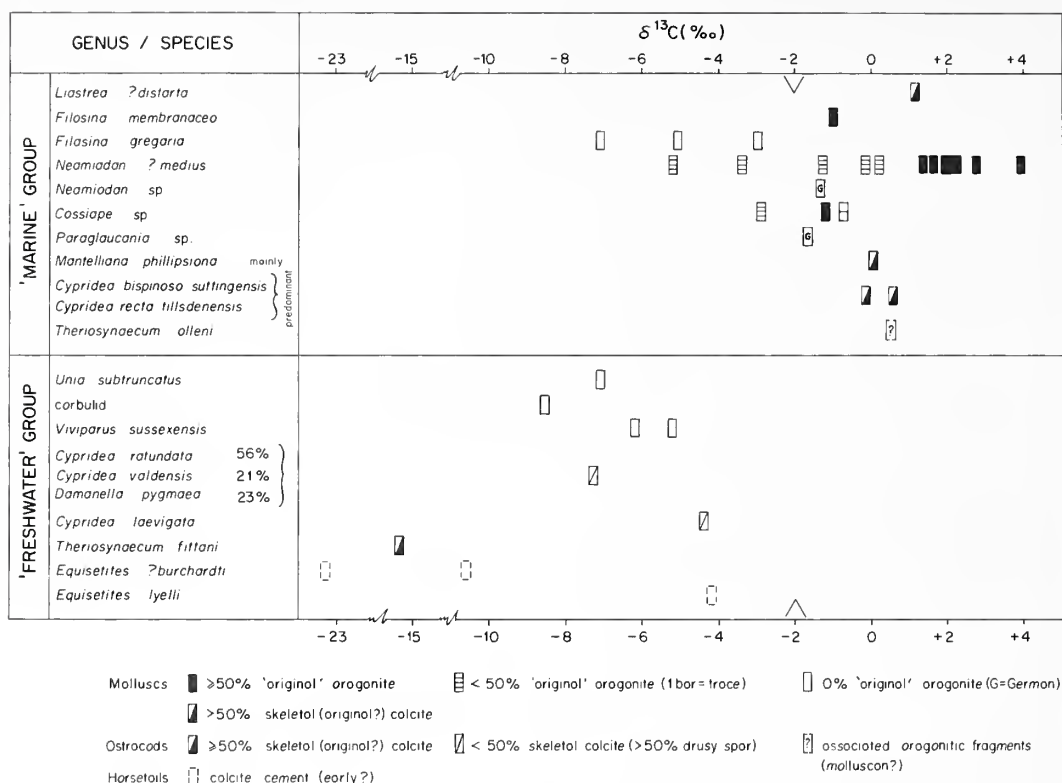
Bold type indicates samples in which the analysed carbonate was mostly aragonite (primary?).

Details of localities

- S8158 } Seacliff, Sandown, Isle of Wight (SZ 620 853).
- S8157 }
- S8155 } 1 km ESE. parish church, Ewhurst, Surrey (TQ 101 401).
- S8154 }
- S8151 Vann Lane Brickworks, Hambledon, Surrey (SU 974 374).
- S8152 Bunce Common, Leigh, Surrey (TQ 205 466).
- S8156/W1423–3 I.G.S. Warlingham boring No. 1, Surrey (TQ 349 571).
- S8150 Clock House Brickworks, Capel, Surrey (TQ 176 384).
- S8147 Graylands Brickworks, Warnham, Sussex (TQ 173 345).
- S8149 }
- S8148 } Clock House Brickworks, Capel, Surrey (TQ 176 384).

Stratigraphical horizons

- S8158 } Probably that of Bristow 1889, 15, top line.
- S8157 }
- S8155 } 1 m below I.G.S. Bed 8b, c. 90 m (300 ft) below top of Weald Clay (Thurrell *et al.* 1968).
- S8154 }
- S8151 I.G.S. Bed 7g?, c. 120 m (400 ft) below top of Weald Clay (Thurrell *et al.* 1968; Kennedy and MacDougall 1968).
- S8152 180 m (600 ft) below top of Weald Clay (Professor F. W. Anderson *in litt.*).
- S8156/W1423–4 Subjacent to I.G.S. Bed 5, c. 115 m (377 ft) below top of Weald Clay (Worssam and Ivimey-Cook 1972, pp. 22, 30, 64).
- S8150 c. 10.7 m (35 ft) above *Cassiope* Bed (S8148–9), beneath Upper Rootlet Bed (Mr. J. D. S. MacDougall).
- S8147 c. 4.9 m (16 ft) above Gossops Green Pebble Bed, c. 91 m (300 ft) above Horsham Stone (c. 150 m (500 ft) above Weald Clay base).
- S8149 } Just above Gossops Green Pebble Bed, c. 82 m (270 ft) above Horsham Stone (c. 146 m (480 ft) above
- S8148 } Weald Clay base (Mr. J. D. S. MacDougall *in litt.*)).



TEXT-FIG. 2. Wealden as a whole. Provisional environmental classification of fossils based on $\delta^{13}\text{C}$ of separated shells and carapaces. (Estimated relative frequencies of species in the ostracod faunas were supplied, with samples, by Professor F. W. Anderson. Two molluscan samples, labelled 'G', came from N. Germany.)

suggestions that some viviparids tolerated brackish or marine conditions in the Purbeck-Wealden.

Temperature. As concluded for the Hastings Beds, the $\delta^{18}\text{O}$ variation of the aragonite shells lies in the range of modern warm temperate molluscs and this is consistent with recent opinion based on other palaeontological evidence.

CONCLUSIONS

(1) Whole-rock isotopic analyses are unsatisfactory for environmental studies of marginal (transitional) sediments. Primary, skeletal, untransported carbonates only should be used. This means in practice only unfragmented articulated aragonitic material.

(2) One species each of *Filosina?* and *Cassiope* (from the Weald Clay) and of *Neomiodon* (Hastings Beds) are confirmed as 'marine'.

(3) Conversion to, and/or cementation with, calcite commonly reduces the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of Wealden molluscan shells. 'Marine' molluscs can therefore

appear as 'freshwater', isotopically indistinguishable from truly freshwater shells. This was examined closely for *Neomiodon medius*, having been misinterpreted earlier (Allen and Keith 1965) as resulting from the organisms' wide salinity tolerance.

(4) Wealden skeletal carbonates giving high $\delta^{13}\text{C}$ are therefore likely to be 'marine', even if secondary (e.g. German *Neomiodon* and *Paraglauconia*).

(5) Skeletal carbonates yielding low $\delta^{13}\text{C}$ cannot be attributed to any environment unless shown to be primary. Freshwater molluscs now recrystallized to calcite (*Unio*, *Viviparus*) are unrecognizable as such on an isotopic basis alone.

(6) Skeletal carbonate which was originally all, or nearly all, calcite (e.g. ostracod carapaces, oyster shells) should be treated with caution. Recrystallization may or may not have occurred. At present there are no certain criteria for recognizing primary calcite or for distinguishing it from secondary calcite, though there are petrological and isotopic grounds for optimism with the ostracods.

(7) Ignoring this, and assuming that any recrystallization would have reduced their ^{13}C -ratios ((3) above), one species of the ostracod *Mantelliana* and two species of *Cypridea* might be marine. Other species of *Cypridea* may be freshwater, but this cannot be confirmed isotopically until their calcite is proved to be primary.

(8) Areal distributions of horsetail-reedswamp growing in similar substrates and water-depths were possibly controlled by salinity. But the source of the ^{13}C -deficient calcite cementing the plants in their growing positions is not known, nor when it was precipitated. Where plants are absent, the ^{13}C -rich ostracod carapaces appear.

(9) New evidence supports the transgressive models for the major Hastings clay formations (Allen 1967*b*, fig. 1) in that the Wadhurst and Grinstead Clays are there seen as deposited in waters more liable to saline influxes than the intervening sands. Later, during Weald Clay times, the salty invasions became more frequent and extensive, so that not only many muds but also some sands were laid down in conditions more saline than any of the Hastings Beds.

(10) Unequivocal palaeotemperatures cannot be deduced from Wealden carbonates. Nevertheless the aragonitic shells yield ^{18}O -palaeotemperatures' broadly consistent with warm temperate-subtropical conditions, as deduced from the palaeobotanical and palaeozoological evidence.

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BUOYANCY CONTROL AND SIPHUNCLE FUNCTION IN AMMONOIDS

by H. MUTVEI and R. A. REYMENT

ABSTRACT. The question of buoyancy control of ammonoids in relation to the function of the siphuncle is analysed in the light of flotation experiments on exact models of moderately evolute and highly evolute shell types, and the structure of the siphuncle. It is demonstrated that, if the mode of life of the ammonoid animal were analogous to that of living *Nautilus*, the relatively more buoyant shell of most ammonoids would have needed considerably more liquid in its chambers than *Nautilus*, with many of the chambers completely filled. The structure of the siphuncle, and its location in the last chambers of the majority of coiled ammonoids, is such that it may have been non-functional in these chambers so that the animal did not vary the quantity of liquid in them. We believe that most ammonoids were fairly efficient at moving themselves vertically but less efficient as swimmers.

SPECULATION about the function of the chambered cephalopod shell has provided one of the more fruitful sources of research topics in palaeontology for more than a hundred years. Starting with Moseley's (1838) mathematical treatise, recently updated by Raup and Chamberlain (1967), numerous papers on the subject have appeared. A review of earlier work is given by Westermann (1971). However, as far as we are aware, the line of reasoning we use, and the data upon which it is founded, are new.

Apart from attempts at finding a purely mathematical solution for the problem (an attractive one because the shell approximates a logarithmic spiral), by determining the location of the centre of gravity and the volume of idealized and, of necessity, unornamented shells, there have been attempts to derive conclusions by a combination of deduction and direct observation on particular shell types. The most noteworthy of these trials was made by Trueman (1941). The conclusions drawn in this study have had a remarkably strong and persistent influence on workers in the field, despite the fact that some of his suppositions, such as the asserted positive correlation between the dimensions of the body chamber and those of the chambered portion of the test, are no longer possible to maintain (Reyment 1973).

Reyment (1958) made an experimental study of the post-mortal fate of chambered cephalopod shells. No attempts at reconstructing the mode of life of fossil cephalopods were made in this work, and all experiments were carried out on models of straight and coiled nautiloids, as well as the shells of two living species of *Nautilus*. In so far as the results of this work could be applied to buoyancy control interpretations of fossil chambered cephalopods, they did not suggest anything other than that the empty *Nautilus* shell can be brought into hydrostatic equilibrium with seawater by a slight increase in the load of the shell. The work of Bidder (1962) and Denton and Gilpin-Brown (1966) demonstrated that weight adjustments in the shell of *Nautilus*, for compensating for shifts in the hydrostatic conditions, are made by the secretion or transfer of relatively small quantities of liquid via the siphuncle into the final chambers. The last chamber is normally full or almost full of this liquid and earlier chambers contain progressively less and less of it. The majority of the chambers are gas-filled and empty of liquid.

Until we compared notes on our recent research on the ammonoid shell, there did not seem to be any reason to doubt that the ammonite animal functioned in the same way as the living *Nautilus*, both with respect to the operation of the siphuncular mechanism and to the approximate number of chambers containing cameral liquid. The results of our studies, Mutvei on the structure and interpretation of the ammonoid siphuncle, and Reymont on the post-mortal properties of ammonoid shells based on experiments on models, have shown that the currently accepted interpretation of the hydrostatic behaviour of the ammonoid shell cannot be sustained without modification and clarification.

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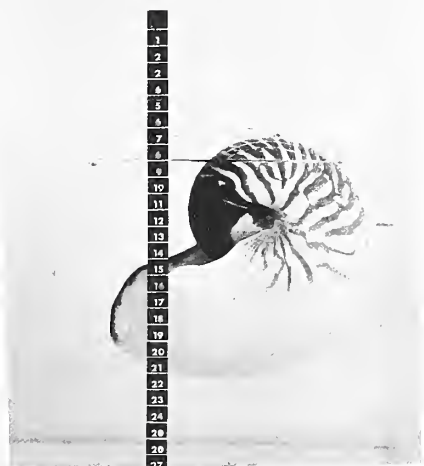
BUOYANCY OF EMPTY AMMONOID SHELLS

There are two approaches open for the study of the buoyancy of empty ammonoid shells. One is by means of accurately constructed models of shells. The other is by calculations of the buoyancy properties of various kinds of shells, the basic assumption being that the growth of the shells has taken place in accordance with the logarithmic spiral.

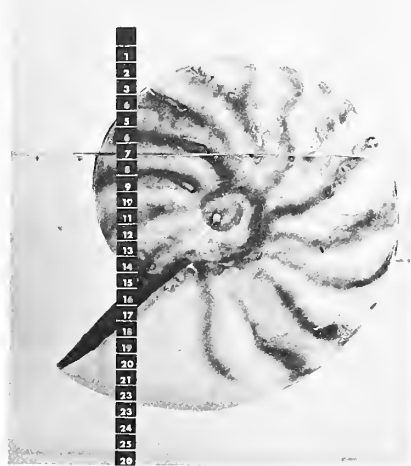
The second approach has an appeal in this day of the computer, but it has the obvious limitation that it can only give an indication of the floating orientation of a particular shell type. At the present stage of its development, it cannot be used to find the proportion of the empty shell that floats above water, nor is it suited for investigations of the critical sinking loads of particular shell types.

Study by accurately constructed models of key morphological types is the only really satisfactory means of testing hypotheses on the relative buoyancy properties of chambered shells and their application to palaeoecological reconstructions. However, such models are expensive to make, requiring the assistance of a highly skilled technician with an ability to sculpture, and suitable specimens upon which to base the models are hard to come by. A detailed account of the way in which our models were built is being presented elsewhere (Reymont 1973). They were made from plastic by the method of vacuum-moulding so as to conform exactly to the structure of the actual ammonoid shells upon which they were based. The correct specific weight (Reymont 1958) was obtained by electroplating the model, internally and externally, with a suitable metal.

The shell categories here studied by this method are of the ceratitic type, being based on *Ceratites nodosus* (von Buch), *Discoceratites intermedius* (Philippi), and *Ceratites (Acanthoceratites) spinosus* Philippi, selected from the extensive collections in the Paleontologiska Institution. All three possess the same basic shell structure, namely, high whorls, moderately evolute coiling, and moderately strong ventrolateral tuberculation: they differ from each other only in the degree of inflation of the shell. Thus, the *Discoceratites* is sub-oxynote and the *Acanthoceratites* is sub-cadicone.



TEXT-FIG. 1. Floating position of *Nautilus pompilius*. Fresh shell obtained from the Solomon Islands. Scale in cm.



TEXT-FIG. 2. Floating position for model of *Discoceratites*. Scale in cm.

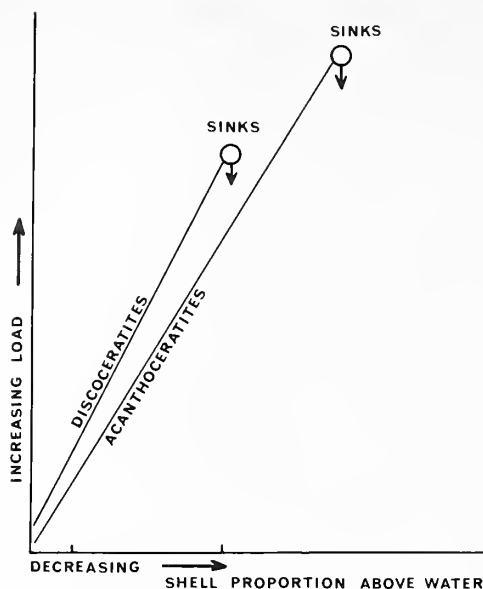
The important class of highly evolute shells was studied with models based on dactyloceratids. No particular species was used as basis for construction.

Flotational experiments. The weight increase required to cause the models of ceratitids to just attain the point of sinking was determined. This may be done in two ways: either by filling larger chambers with water, or by merely weighting the shell with lead shot in the body chamber. The former method is biologically more realistic, while the latter is more expedient and does not damage the models; it has the drawback that it is accompanied by an unrealistic displacement of the centre of gravity. Although the difference in loads yielded by the two procedures is slight (they cannot be the same because of the load to air volume ratios), the chamber-filling alternative was selected for the present work.

Firstly we draw attention to text-fig. 1, which illustrates the floating position of a fresh *Nautilus pompilius* from the Solomon Islands. This shell, which floats relatively low in the water, required no more than an increase of 13% in weight in order to sink.

Text-fig. 2 shows the floating position adopted by a model of *Discoceratites*. It floats very much higher in the water than the *Nautilus*, 27% of the shell being above water as compared with 10%. Approximate determinations of the buoyancy of the empty shells show that the ceratitids require weight increases of from 35% to 45% in order to sink. They are, therefore, when empty about three times more buoyant than the *Nautilus*. Text-fig. 3 compares, schematically, the load-to-sinking-point relationships for *Discoceratites* and *Acanthoceratites*; this is linear as to be expected. As is also to be expected, the more depressed and spacious shell requires a greater load to make it sink than does the compressed shell.

Why these substantial differences between the nautiloid and the ammonoids? There



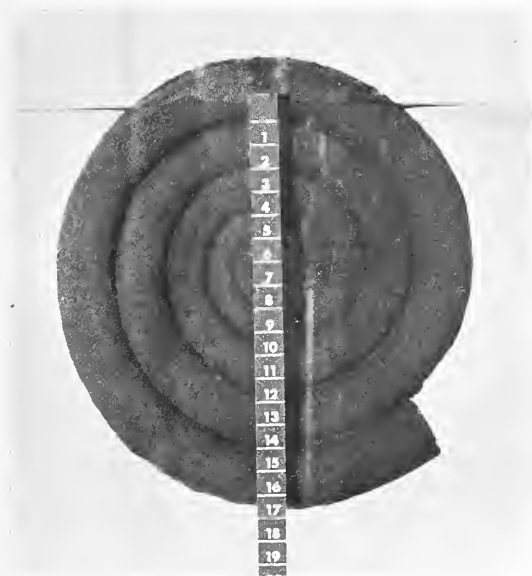
TEXT-FIG. 3. Load-to-sinking curve for the models of *Discoceratites* and *Acanthoceratites*.

are several reasons. Firstly, *N. pompilius* is highly involute and only the chambered part of the last whorl contributes to the uplift (Reyment 1958). The more evolute ceratites have a significantly greater chambered surface area available for uplift involving part of the inner whorls. Secondly, the ceratites have a greater relative cameral volume, owing to their higher whorl sections. Thirdly, ammonoids tend to contain relatively less shell substance for a given conch volume than nautiloids, owing to their mostly thinner walls: this is a well-known fact, most recently studied by Westermann (1971). Fourthly, the ammonites studied in the present connection have a smaller apical angle than the nautiloids, the body chamber does not 'flare' pronouncedly in the manner characteristic of *N. pompilius* and *N. scrobiculatus*, for example (cf. Reyment 1958, pl. 2). In consequence, the dead weight of the body chamber is less in the ammonoids studied than in the *Nautilus* species.

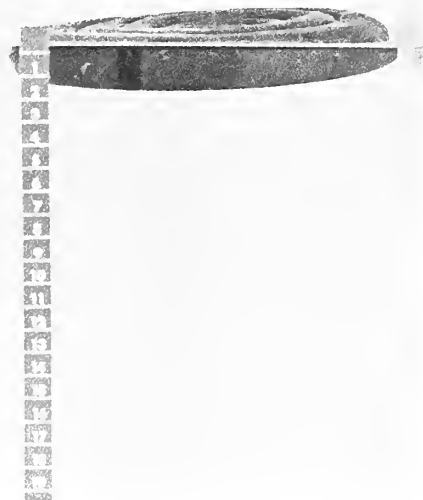
The differences between the buoyancies of the *Nautilus* shell and the ceratite models are so great that they exceed any reasonable limits of experimental error. It was ascertained experimentally that even with a construction error of 25% in the shell weight, the buoyancy differences are such as would require special explanation and interpretation.

Highly evolute shells. Two models of shells of dactylioceratid type were made. There were two categories considered in this part of the work: those with a body chamber occupying seven-eighths of a whorl, and those with a body chamber occupying one-and-a-third whorls.

The floating position taken up by the highly evolute shells was shown to be highly



TEXT-FIG. 4. Floating position for model of dactyliocerooid shell with a body chamber length of one-and-one-third whorls. Scale in cm.



TEXT-FIG. 5. Floating position for model of dactyliocerooid shell with a body chamber length of seven-eighths of a whorl. Scale in cm.

dependent on the length of the body chamber. The model shown in text-fig. 4 has the greater body chamber. It floats as low in the water as the *Nautilus* depicted in text-fig. 1. The liquid in the chambers of the living animal would not need to have occupied more than a few of the chambers. The model shown in text-fig. 5 has the smaller body chamber. In order for the ammonite to have been oriented vertically during life, numerous chambers would have had to have been permanently flooded.

IMPLICATIONS OF THE BUOYANCY EXCESS OF AMMONOID SHELLS

The relative buoyancy of the ammonoid shell becomes greater with increasingly evolute shells; this may in part be offset by an increase in the length of the body chamber. This is a logical outcome of the increase in 'effective volume' of the shell in relation to its weight. Thus, the more completely evolute the shell is, the greater is the uplift on it, and the lesser is the downward force due to the shell weight. If the ammonoid animal had the same mode of life as the living *Nautilus*, certain conclusions concerning the function of the hydrostatic mechanism of its shell are inescapable.

Empty ammonoid shells more evolute than *Nautilus*, with the same length of body chamber, must have floated considerably higher in the water. We note in passing that there is a differentiation within the species of living *Nautilus*; the slightly more evolute *N. scrobiculatus* floats higher out of the water than does *N. pompilius*, although there is a slight difference in the apical angles of the whorls of these shells (Reyment 1958).

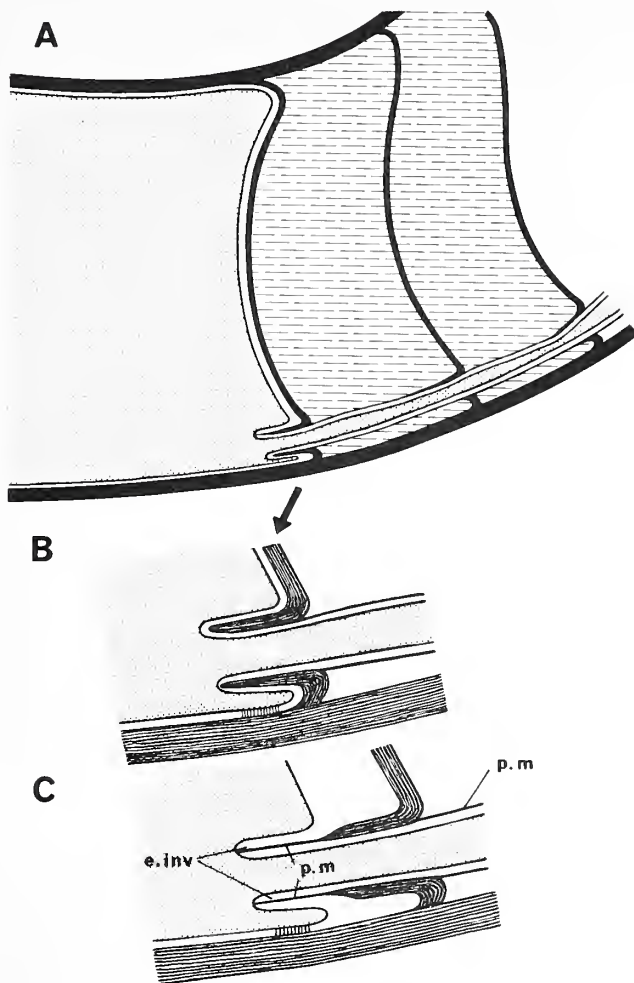
It is unfortunate that the surviving genus of chambered cephalopods comprises species whose shell morphologies are not typical of most members of the class, and in particular the ammonoid branch. In fact the atypical nature of the *Nautilus* shell, with its highly involute shape and large body chamber diameter, may be responsible for obscuring the probable function of the ammonoid shell for so long.

For shells of the ceratitid type, with high, subrectangular whorls and moderately evolute shape, more than half of the chambers of the last whorl, and probably all the lower chambers of the second last whorl, must have been entirely filled with cameral liquid if the shell functioned hydrostatically in the same manner as poised shells of living *Nautilus*. This has certain, albeit minor, consequences for the floating position adopted by the animal in life. Buoyancy adjustments must have been made in the chambers located in the uppermost third of the vertically poised shell, and at least in the last two to three whorls, depending on the nature of the coiling, and the amount of cameral liquid.

THE STRUCTURE AND INFERRED FUNCTION OF THE SIPHUNCLE

The structure of the wall of the siphonal tube. The position of the siphonal tube in most ammonoids tends to be constant. Except for the ontogenetically oldest part of the shell, it is situated close to the ventral (anatomically posterior, outer) side of the whorls. Its diameter is usually small. Characteristic for the majority of Mesozoic ammonoids, as well as several Palaeozoic ammonoids, is that the septal necks change their direction during the ontogenetic growth of the shell. Thus, in the early stages they are directed towards the shell apex; in the later stages they point towards the body chamber. On the basis of their direction, the septal necks are said to be retrosiphonate and prosiphonate, respectively.

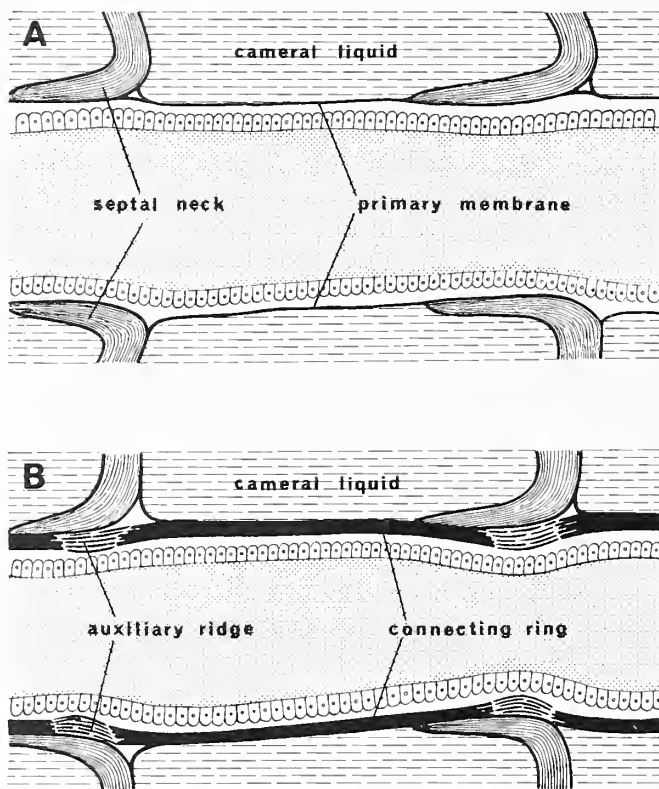
The direction of the septal necks is intimately related to the structure and origin of the connecting rings. In *Nautilus*, which has retrosiphonate septal necks, each connecting ring is composed of an outer spherulitic-prismatic layer and an inner conchiolin layer. The spherulitic-prismatic layer is a direct continuation of that layer in the outer part of the septal neck, whereas the conchiolin layer originates from the nacreous layer of the septal neck (Mutvei 1964a, 1972). On the other hand, the ammonoids with prosiphonate septal necks have connecting rings which seem to be composed solely of a conchiolin layer (Mutvei 1967; Erben and Reid 1971). The calcareous prisms and the carbonate fluorapatite in the connecting rings, reported by Birkelund and Hansen (1968) and Andalib (1972), respectively, are probably of secondary origin. As pointed out in a previous paper (Mutvei 1967), the conchiolin layer of the connecting rings does not originate from the nacreous layer of the septal neck, but constitutes a separate shell unit which is secreted after the adjacent septal necks have completed their growth. The latter condition is obvious when we consider the growth of the septal neck. It must have projected into a circular invagination of the body proper (text-figs. 6A, B). The epithelium which lined the outer (peripheral) face of this invagination must have secreted the septal neck, whereas in *Nautilus* the septal neck is secreted by the epithelium on the proximal portion of the siphonal cord (Mutvei 1964a). Under these circumstances, the conchiolin layer of the connecting ring in prosiphonate ammonoids cannot be a



TEXT-FIG. 6. A. Reconstruction to show the relationship between the soft body and the shell in a prosiphonate ammonoid. B. Detail of fig. A in a higher magnification to show the ontogenetically youngest, prosiphonate septal neck immediately after its formation. C. Similar reconstruction as in fig. B, but at a somewhat later growth stage, showing the formation of the primary conchiolin membrane of the siphonal tube. In all figures the soft body is dotted and the cameral liquid stippled. *e. inv.*, circular invagination of the soft body; *p.m.*, primary conchiolin membrane of the siphonal tube.

continuation of the nacreous layer of the septal neck, as it is in *Nautilus* (cf. Mutvei 1964a, 1972). There is, however, a thin conchiolin membrane, here termed the 'primary membrane', which covers the outer face of the septal neck and continues as a thin tube to the succeeding septum, where it is fused to the conchiolin layer covering the dorsal (adapical) face of that septum (Mutvei 1967, and unpublished

scanning electron microscope observations). The primary membrane was probably successively secreted by the epithelium which lined the bottom of the circular invagination of the soft body (*p.m.*, text-fig. 6C). The wall of the siphonal tube in the newly formed chamber was consequently very thin in that it consisted only of the septal neck and the primary membrane (text-fig. 7A). This is in sharp contrast with the condition found in *Nautilus*, where the distal portion of the septal neck and the contiguous connecting ring reach their maximum thickness when only about one-third of the total thickness of the last septum has been attained (Denton and Gilpin-Brown 1966; Mutvei 1972).



TEXT-FIG. 7. A. Reconstruction of an early growth stage in a prosiphonate ammonoid when the wall of the siphonal tube was composed of the septal necks and primary conchiolin membrane only. B. Fully developed wall of the siphonal tube.

Inferred function. The above-mentioned differences in the growth of the wall of the siphonal tube between the retrosiphonate *Nautilus* and the prosiphonate ammonoids have an important functional significance. As demonstrated by Denton and Gilpin-Brown (1966), the new chamber is always completely filled by liquid. This liquid can be pumped osmotically into the siphonal cord through the permeable connecting ring. In *Nautilus*, with its heavy shell, the removal of the liquid from the new chamber

is accomplished at the fastest possible rate, in order to maintain the buoyancy of the animal, because, as the soft body and the shell continue to grow, they increase in weight. However, this cannot take place before the septal neck, and particularly the contiguous, permeable connecting ring have reached their full thickness and strength to withstand the hydrostatic pressure of the sea. Therefore, the wall of the siphonal tube is required to grow faster than the last septum. On the other hand, as just shown, the shell of most ammonoids was considerably more buoyant than that of *Nautilus*, and must consequently have contained much more cameral liquid during life in order to have been in hydrostatic equilibrium with seawater. As a result, there was not the same pressing need for the removal of liquid from the shell chambers and the growth of the connecting rings was retarded (Mutvei 1967). Evidence for the latter condition is that the connecting ring in each chamber was deposited on the inner faces of the two successive septal necks, and consequently secreted by the epithelium of the siphonal cord after the formation of these septal necks and the primary membrane was completed (text-fig. 7B). Both ends of the connecting ring are fused to the adjacent septal necks by a calcareous structure, the auxiliary ridge (text-fig. 7B). The auxiliary ridge is also present in *Nautilus*, but here it only effects the fusion of the distal end of the succeeding connecting ring to the preceding septal neck (Mutvei 1972). As in *Nautilus*, the emptying of cameral liquid in the ammonoids could have taken place only after the connecting rings had reached their full strength. At which stage this has occurred is still obscure. However, the connecting ring of varying numbers of ontogenetically youngest chambers (up to one whorl) are often absent (Trueman 1920; Westermann 1971), which might indicate that there they were not fully developed and were therefore easily destroyed during diagenesis.

Denton and Gilpin-Brown (1966, 1971) have shown that *Sepia* and *Spirula* are capable of regulating the volumes of the liquid in their chambers. This is probably also true for *Nautilus*. For such regulation of the cameral liquid in the ammonoids, a ventral position of the siphonal tube would have been the most advantageous arrangement, and this is supported by the experimental work.

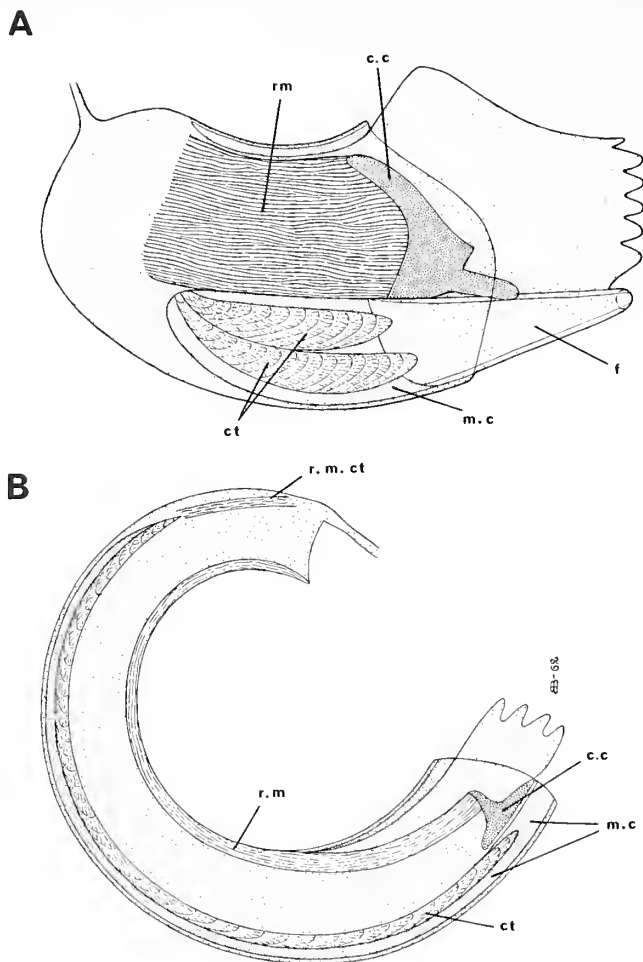
FUNCTIONAL ANATOMY

A comparison between certain shell characters of *Nautilus* and ammonoids allows the following conclusions on the functional anatomy of the latter.

The body chamber of many ammonoids is much longer than that of *Nautilus*. The soft body in these ammonoids must therefore also have been correspondingly longer, and in some forms worm-like (text-figs. 8A and B).

The short-bodied *Nautilus* is well adapted for swimming by jet-propulsion. The mantle fold in *Nautilus* is attached to the shell aperture by the periostracum (Mutvei 1964a). This is a general feature for all molluscs which secrete an external shell. Unlike the dibranchiate cephalopods with internal shells, the mantle fold of *Nautilus* therefore contains only a thin muscular layer, the contractions of which are insufficient to drive out the water from the mantle cavity. The ammonoids certainly had the same relationship between the mantle fold and the shell aperture as *Nautilus*.

The swimming mechanism in *Nautilus* has not yet been fully explained. For an



TEXT-FIG. 8. A. Diagrammatic representation of the anatomy in the recent *Nautilus*. B. Reconstruction of the anatomy in an ammonoid. *c.c.*, cephalic cartilage; *ct.*, ctenidia; *f.*, funnel; *m.c.*, mantle cavity; *r.m.*, paired retractor muscles; *r.m.ct.*, an unpaired muscle, probably representing the retractor muscle of ctenidia.

understanding of this mechanism, the following anatomical features must be taken into consideration. The roof above the spacious mantle cavity is formed by a pair of powerful retractor muscles, which originate from the lateral, inner faces of the shell wall (*r.m.*, text-fig. 8A). These muscles extend to the head, where they are rigidly inserted into the cephalic cartilage (*c.c.*, text-fig. 8A). The function of these muscles is not only to attach the soft body to the shell, and withdraw it into the body chamber, as with the columellar muscles in the gastropods. They are also an important part of the swimming equipment of the animal (Griffin 1900; Mutvei 1964b).

In order to test the latter assumption, experiments with anaesthetized animals

of the dibranchiates, *Sepia* and *Loligo*, were carried out by H. M. in the summer of 1965 at the Marine Biological Station (ARAGO) at Banyuls-sur-Mer, France. Like other dibranchiate cephalopods, *Sepia* and *Loligo* have a highly muscular mantle, the contractions of which are sufficient to produce a powerful water jet. In order to study the action of the mantle musculature, and the retractor muscles of the head and funnel, the mantle of the anaesthetized animals was cut apart so that the mantle cavity was exposed. On touching the hypobranchial ganglia with a needle, rhythmic, simultaneous contractions of all these muscles take place. In all likelihood, similar simultaneous contractions of the muscles in question occur when the animals swim rapidly, as when escaping from an enemy. These experiments make it reasonable to conclude that when *Nautilus* swims rapidly, the retractor muscles do not remain inactive, but by their contractions create the main force for jet-propulsion. This conclusion is in agreement with the above-mentioned 'roof-position' of these muscles above the mantle cavity. During the muscular contractions, the head of the animal is probably slightly withdrawn into the shell, and the roof of the mantle cavity lowered. This would cause a considerable decrease in the volume of the mantle cavity, as a result of which the water is forced out through the funnel (cf. Griffin 1900; Mutvei 1964b). For slow swimming movements, and for respiration, the water is expelled from the mantle cavity by contractions of the funnel (Bidder 1962).

The myo-adhesive scars for the attachment of the paired retractor muscles to the shell wall have been described in several Mesozoic ammonoids by Crick (1898), Jones (1961), and Jordan (1968). These scars have a constant position, in that they are always situated on the dorsal (anatomically anterior) face of the body chamber, irrespective of the shape of the shell. Contrary to this, the scars of the retractor muscles in the fossil 'nautiloids' have a different number and position in different groups (Mutvei 1957, 1964b). As in *Nautilus*, the paired retractor muscles of the ammonoids quite probably extended to the head, where they were inserted into the cephalic cartilage (*r.m.*, *c.c.*, text-fig. 8B; see also Mutvei 1964b, fig. 8). Owing to their dorsal position, and to the curvature of the soft body, these muscles must have been situated in the dorsalmost portion of the body over most of their extension, close to the dorsal (anatomically anterior) wall of the body chamber (text-fig. 8B). One may therefore conclude that their topographic relationship to the main mantle cavity was different from that in *Nautilus*, and this being so, they could not have formed a roof above this cavity (text-fig. 8B; see also Mutvei 1964b, fig. 8E).

To judge from the probable worm-like body shape of many ammonite species, the main mantle cavity in the ammonoids must also have been long and comparatively narrow (*m.c.*, text-fig. 8B), and thus different from the short and broad mantle cavity in *Nautilus* (*m.c.*, text-fig. 8A). The number of the ctenidia is still unknown in the ammonoids, but if they were present, their length would probably have been positively correlated with the length of the mantle cavity. Thus, instead of the rather short ctenidia of *Nautilus* (*ct.*, text-fig. 8A), the ctenidia in the ammonoids may have been long (*ct.*, text-fig. 8B).

Taking into account the shape of the mantle cavity, and the topographic relationship between this cavity and the paired retractor muscles, one may conclude that most ammonoids would have been incapable of efficient swimming by jet-propulsion. Also, the presence of a funnel, necessary for jet-propulsion and steering, is doubtful

for certain ammonoids, which in the adult develop an unpaired, ventral, keel-like projection of the apertural margin. On the other hand, the fossil 'nautiloids' are always provided with an opening for the funnel. The ammonoids were naturally capable of vertical movement in the sea by means of regulation of the volume of the liquid in the shell chambers.

In addition to the paired retractor muscles, the Mesozoic ammonoids also had a small, unpaired muscle in the ventral (anatomically posterior) portion of the body (Jones 1961; Jordan 1968). The myo-adhesive scar for the latter muscle has not yet been found in the Palaeozoic ammonoids (Crick 1898; unpublished observations of H. M.). The extension and function of this unpaired muscle are unknown, but judging from its general position, it may have been homologous with the retractor muscles of the ctenidia in dibranchiate cephalopods (*r.m.ct.*, text-fig. 8B).

POST-MORTAL FATE OF AMMONOID SHELLS

It is now well known that even recently dead *Nautilus* shells do not contain any cameral liquid (Bidder 1962; Denton and Gilpin-Brown 1966). How the post-mortal assimilation and loss of this liquid takes place is still a mystery.

After the death of the animal, the gases deriving from the processes of decomposition of the carcass soon expel water from the body chamber and inflate the decaying soft parts; the dead animal is driven to the surface. The time taken for this is relatively short, usually some few hours. It is therefore clear that at this stage, in the immediate post-mortal phase, the liquid in the chambers remains unaltered in volume. Within a few days at the most, the body parts company with the shell and each passes to its separate fate.

Significant conclusions arising here are that: (1) The ammonoid shell with cameral liquid must have been slightly lighter than water (by analogy with living shell-bearing cephalopods); (2) The density of the body of the ammonoid animal must have been higher than that of water (by analogy with living cephalopods); (3) Irrespective of its structure, the shell and carcass would normally have been forced to the surface shortly after death.

Whether or not the ammonoid lost its cameral liquid during the initial post-mortal phase is a matter for conjecture. There is a reasonable likelihood that at least part of the liquid may have been dissipated during this phase, if the observations made on *Nautilus* have any generality.

There is ample evidence for the vertical embedding of fossil cephalopod shells in sediments (Reyment 1970), and there is little doubt that many shells stranded in semifluid sediment or ooze in their vertical floating positions. In view of the comparative lightness of many ammonoid shells, their relatively high buoyancy, and the necessary requirement of their being lighter than water during life, it is difficult to envisage a situation in which the shell would sink post-mortally without displaying evidence for implosion.

CONCLUDING REMARKS

The structure of the ammonoid siphuncle suggests that it functioned in the same manner as that of living *Nautilus*, albeit with some modification. The development

from retrosiphonate to prosiphonate septal necks tends to be associated with increasing complication of the septa. Secondary simplification of the connecting rings and their retarded growth appears to have been a part of this change. This structural shift could have hardly come about if the ammonoid shell had not evolved in the direction of a buoyancy excess, offset by an increase in the volume of permanent cameral fluid in the living animal. The buoyancy regulation of ammonoid shells probably took place only in those chambers in which the siphuncle had a ventral location, and the cameral liquid, therefore, was in continual contact with the siphuncle. This could be the reason why the majority of the ammonoids had a ventrally located siphuncular tube and why the porous calcareous layers of the siphuncles of many nautiloids, which in living *Nautilus* function in the manner of a 'wick', are absent in ammonoids.

The situation just described is applicable to a large number of ammonoid types. However, extremely evolute shells sometimes have body chambers in excess of one whorl length (Reyment 1973). The effect of this is to offset the uplift of the chambered whorls. It is, we believe, certain that this type of shell must have contained considerably less cameral liquid than other ammonoids, and could therefore have had a specialized mode of life.

Some of our work may cast light on the reason why ammonoids tended to develop complicated cameral sutures with the shell wall. It is no new idea that sutural complications evolved as a means of withstanding water pressure while retaining an optimal thinness of the shell wall. The present study has indicated the strong possibility of the ammonoids having been poorly suited for swimming and more adapted for vertical movement, perhaps connected with a mode of life related to following the diurnal migration of plankton upon which they may have fed. Small size of the prey is indicated by the shape of the jaws (Kaiser and Lehmann 1971). It might therefore be possible that the primary mode of life of the ammonoids involved the need for continual adjustments to a pressure gradient. There is some indirect evidence in support of this interpretation. We know that some ammonites definitely inhabited a shallow-water environment throughout their lives and that they could not have been confronted with the need to adjust to important differences in water pressure. Is this relaxation in the suggested primary mode of life of ammonoids reflected in the suture line?

There are several groups of Cretaceous ammonites that inhabited, permanently, shallow seas. The best known of these is the group of the vascoceratids, the main development of which took place in north-western Africa and the Iberian Peninsula during the Lower Turonian. The vascoceratids have often been said to possess a 'degenerated acanthoceratid suture'. The suture of almost all vascoceratids is indeed greatly simplified in comparison with that of its antecedents and it is not inconceivable that this could have resulted as a genetical response to the pressure-independent mode of life followed by these ammonites in the shallow, epeiric, trans-Saharan sea of the Lower Turonian. This vast inland sea began to develop during the late Cenomanian. At that time it contained the genus *Neolobites*, characterized by a 'pseudogoniatitic' suture. It reached its maximum extension during the Lower Turonian, during which time it stretched from North Africa, across the Saharan region, to Nigeria. The major part of this transcontinental ocean was extremely shallow: its average depth can hardly have exceeded 10 metres, as indicated by the spread of

the sediments in relation to the Upper Cretaceous topography. The shells of most vascoceratid species are more stoutly built than is usual in ammonoids and this would suggest that they were adapted to withstand mechanical damage, resulting from wave action in a shallow environment, rather than the force of water pressure.

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AN UNUSUAL AGGLUTINATING FORAMINIFER FROM THE UPPER CRETACEOUS OF ENGLAND

by C. G. ADAMS, R. H. KNIGHT, and R. L. HODGKINSON

ABSTRACT. *Labyrinthidoma dumptonensis* gen. et sp. nov., belonging to the Superfamily Lituolacea, is described from the Chalk of southern England. It has a distinctive mode of growth, chambers with labyrinthic interiors, and cannot be fitted into any of the existing families of the Lituolacea as presently defined.

THE species described in this paper was first found by one of us (R. H. K.) in the Chalk of Dumpton Bay, Broadstairs, Kent. An intensive search subsequently led to the discovery of numerous additional specimens within the *Micraster coranguinum* Zone in the coastal sections between the Western Undercliff, Ramsgate, and Kingsgate Bay, Broadstairs (text-fig. 1). For details of the local stratigraphy see Peake (1967*a, b*).

The morphological characters of this species do not conform with those of any previously described genus, and the generic characters are such that the species cannot be fitted readily into the subfamilies of the Lituolidae as presently defined. However, since this merely reflects the imperfection of the existing classification, which is based on genera and species described mainly on their external form, a new family or subfamily is not erected here.

It may, perhaps, be thought curious that this relatively large foraminifer should have passed unnoticed in Europe where so much attention has been paid to faunas of Senonian age. However, it has been found in old, undescribed collections in the British Museum (Natural History) under the name *Lituola nautiloidea* (Lamarck), a species to which it bears a superficial resemblance, and we have no doubt that it will also be found in similar collections elsewhere.

All type, described and figured specimens (except Pl. 78, fig. 8) are deposited in the collections of the British Museum (Natural History).

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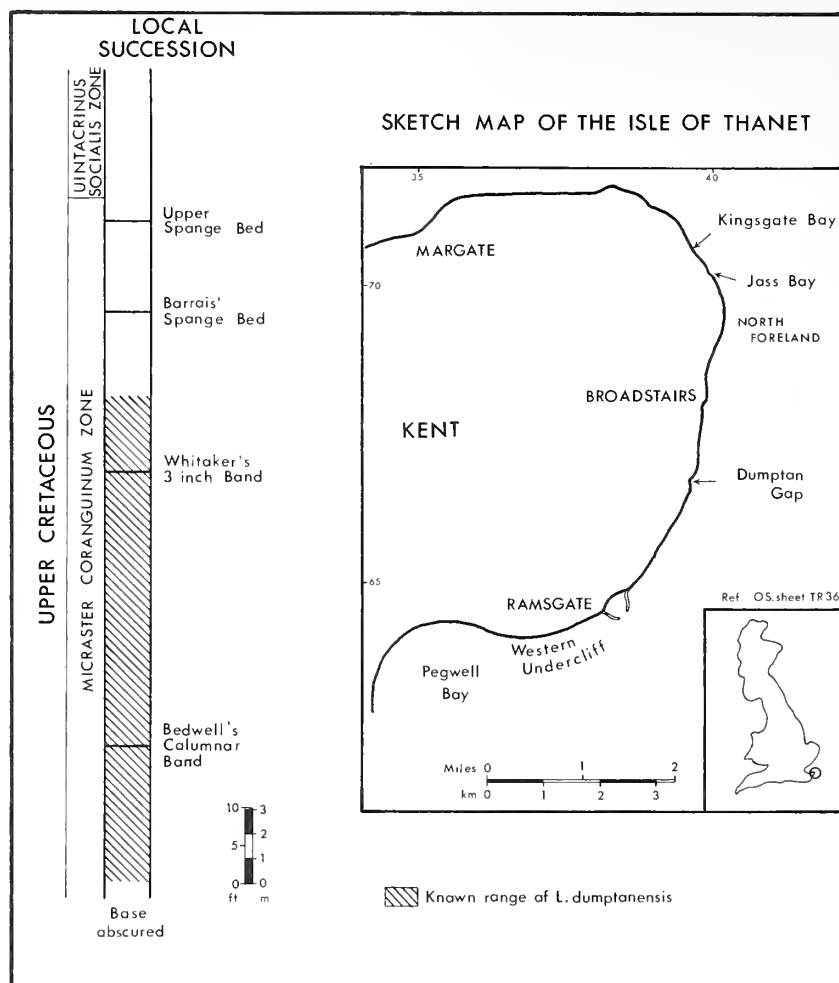
Superfamily LITUOLACEA de Blainville 1825
Genus LABYRINTHIDOMA nov.

Type species. *Labyrinthidoma dumptonensis* nov.

Derivation of name. From the Greek, meaning a labyrinthic house.

Diagnosis. Test free, agglutinating. Initially coiled streptospirally in the megalospheric form, later becoming uncoiled. Microspheric form similar, but with a trochospiral

[Palaeontology, Vol. 16, Part 3, 1973, pp. 637–643, pl. 78.]



TEXT-FIG. 1. Stratigraphy and locality-map, Isle of Thanet.

and/or biserial stage prior to becoming streptospiral. Most chambers labyrinthic; wall canaliculate but non-labyrinthic, not composed of a distinct epidermis and hypodermis. Aperture cribrate.

Remarks. The labyrinthic interior, 'non-labyrinthic walls' (see below), streptospiral coil, and non-adherent habit distinguish this genus from all other described lituolaceans.

Labyrinthidoma dumptonensis sp. nov.

Plate 78, figs. 1-12; text-figs. 2 and 3

Material. More than 300 specimens, of which three are known to be microspheric.

Diagnosis. As for the genus.

Holotype. P. 48623 (Pl. 78, fig. 3); a megalospheric form.

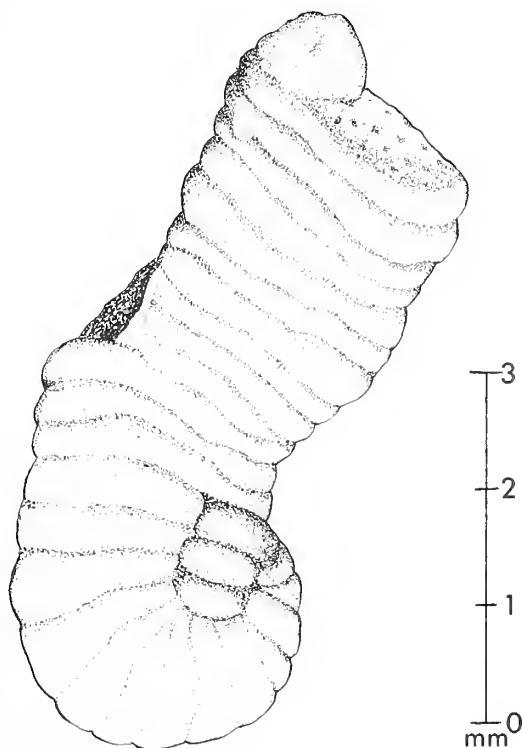
Horizon. Senonian (Upper Coniacian or Lower Santonian: see Barr 1966). Upper *Micraster coranguinum* Zone, Bedwell's Columnar Band (see Peake 1967a).

Locality. North of Dumpton Gap, Dumpton Bay, Isle of Thanet, Kent (exact position unknown).

Description.

Megalospheric form. Test finely agglutinating, with a prominent involute streptospiral initial coil comprising numerous chambers, and a rectilinear portion with up to fifteen chambers; all chambers much wider than high, chambers of uncoiled portion usually subcircular in cross-section. Sutures slightly depressed. Chamber walls thick, composed of agglutinated chalk grains, shell debris and other microfossils,

TEXT-FIG. 2. Typical external appearance of *Labyrinthidoma dumptonensis* gen. et sp. nov.



and characterized by the presence of numerous randomly arranged cytoplasmic canals. These do not open to the exterior except in slightly abraded specimens. Proloculus followed by up to eight simple chambers; all later chambers have labyrinthic interiors. In the rectilinear part of the test, short, stout, irregular vertical partitions project inwards from the wall. The lumen of each chamber is partly occluded with pillars and sinuous partitions of irregular width (Pl. 78, fig. 8). Both pillars and partitions are often perforated by coarse pores. Coil streptospiral, very difficult to see clearly owing to the labyrinthic nature of the chambers. Aperture cribrate with numerous circular or elongate pores, usually on a slightly convex apertural face.

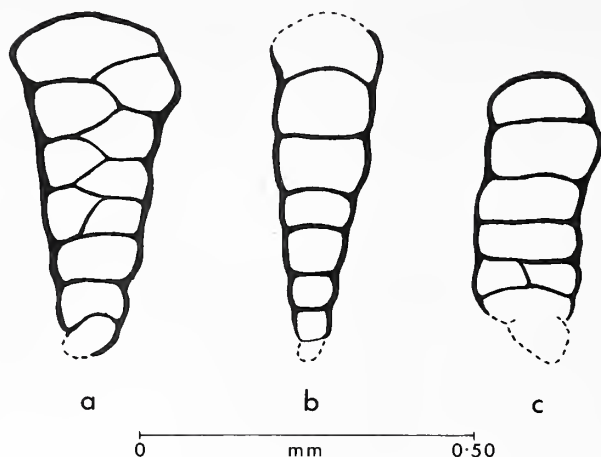
Dimensions of holotype.

Length 4.0 mm.

Width of rectilinear portion 2.2 × 2.8 mm.

Width of coiled portion 2.7 × 2.0 mm.

Height of chambers in rectilinear portion up to 0.50 mm.



TEXT-FIG. 3. Semi-diagrammatic representations of the initial stages of three microspheric individuals. (a) Specimen with a clear trochospiral or biserial stage; (b and c) Two dissected specimens showing some of the early chambers. The uniserial appearance is believed to be an accident of dissection.

Microspheric form. Externally similar to the megalospheric form. Proloculus followed by a high trochospiral coil or biserial stage (up to 0.53 mm in length) comprising at least 11 chambers. This is followed by a streptospiral coil in which the chambers quickly become labyrinthic. The last few chambers are rectilinear as in the megalospheric generation.

The earliest stage of growth is difficult to describe accurately from the three specimens presently available. The best individual (Pl. 78, figs. 4 and 5; text-fig. 3a) starts with a high trochospiral or biserial stage while the other two appear to be uniserial—a condition probably resulting from damage during dissection.

Variation.

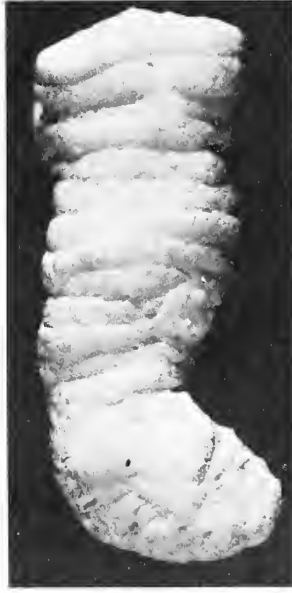
Proloculus. Sectioned and dissected specimens show that the megalospheric form has a large subglobular proloculus. Although accurate measurements have not been possible, the internal diameter appears to be over 0.4 mm in the five specimens in which it is visible.

EXPLANATION OF PLATE 78

Figs. 1–12. *Labyrinthidoma dumptonensis* sp. nov. 1, Dissection of megalospheric form showing streptospiral coil and several uncoiled chambers, $\times 12$. P.48627. Bedwell's Columnar Band, Western Undercliff Promenade, Ramsgate, Kent. 2, External view of large specimen, $\times 10$. P.48628. South of Joss Bay, Broadstairs, Kent. See also fig. 12. 3, Holotype, $\times 10$. P.48623. The partially dissected initial coil shows a cavity which may mark the position of the proloculus. Cf. fig. 1. North of Dumpton Gap, Kent. 4, Thin section of microspheric form showing three phases of growth beginning with a high trochoid spire orbiserial stage, $\times 11.5$. P.48638. South of Dumpton Gap, Kent. 5, Enlargement of initial stage of fig. 4, $\times 33$. 6, Branched specimen with partly abraded surface, $\times 9.5$. P.48630. In flint pebble from beach at Pegwell Bay, Kent. 7, Thin section through uncoiled chambers showing internal partitions and wall structure, $\times 12$. P.48639. 8, Transverse cut through an uncoiled chamber showing vertical internal pillars and short radial plates, $\times 10$. Specimen destroyed during serial sectioning. 9, Internal cast of the uncoiled portion of a test after removal of the wall with dilute acid, $\times 10.5$. P. 48625. 10, Typical apertural view, $\times 12$. P.48626. 11, Part of a septal face showing canals and spongy texture, $\times 130$. P.48947. 12, Apertural face of specimen shown in fig. 2, $\times 10$. P.48628. Note incipient branching. All *in situ* specimens from the Upper Chalk, *Micraster corangium* Zone, Kent.



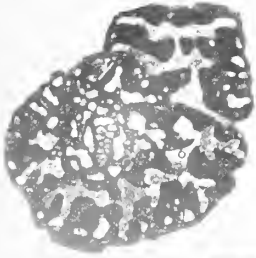
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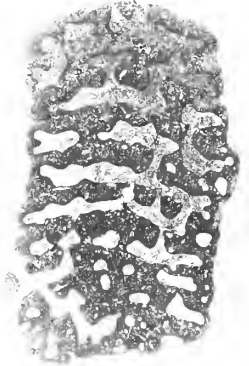
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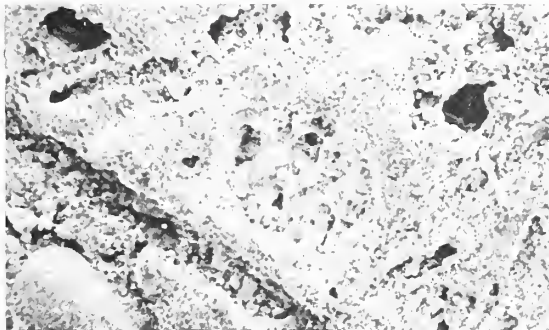
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12

Spire. The initial coil is always tight in the megalospheric form and usually comprises 2–3 streptospiral whorls. However, the plane of coiling appeared to change abruptly by 90° in one specimen, while in another a reversal of coiling was observed. The high trochospiral or biserial stage of the microspheric form has been seen in three individuals and is not the result of fortuitous sections through specimens which happen to have incorporated the shell of another species in the wall. Bartenstein (1952) illustrated a specimen of *Lituola irregularis irregularis* (Roemer) from the Campanian of Hannover which seemed to have grown round a *Heterohelix globulosa* seen in the centre of the spire. He noted that this was quite a common phenomenon, but did not indicate whether the individuals concerned were microspheric or megalospheric. Kaever (1971) described specimens which undoubtedly include a biserial stage in microspheric forms from the Santonian of Dortmund-Eving. The present specimens resemble those described by Kaever in their mode of growth, but not in their internal structure.

Uncoiled portion. This varies considerably in length and may comprise up to eighteen chambers. Some broken specimens, believed to belong to this species but lacking an initial coil, possess up to 26 rectilinear chambers. A few of the larger specimens either branch or show a tendency to branch (Pl. 78, figs. 6 and 12). Branched individuals have the same wall structure and labyrinthic interior as unbranched specimens.

Apertures. Up to 31 (normally 16–18) circular, subcircular or elongate pores have been observed in some of the larger specimens. They are usually irregularly disposed over the apertural face (Pl. 78, fig. 10) which is often slightly convex.

Wall. Finely granular, incorporating shell fragments, spicules, small foraminifera (miliolids, bolivinids, and globigerinids), and chalk grains. Abraded or broken surfaces reveal large numbers of fine cytoplasmic canals from 10–40 µm in diameter. They are randomly oriented and are particularly well seen on broken septal faces. The wall is non-labyrinthic in the sense of Loeblich and Tappan (1964, C61), since it does not contain interlaced dendritic channels perpendicular to the surface. It is, nevertheless, spongy, albeit on a finer scale than in species with typical labyrinthic walls.

Labyrinthic interior. The chamber roofs are supported peripherally by short, stout, radial plates, and centrally by vertical, thick, smoothly finished, sinuous, irregular partitions and pillars. These partially occlude the lumen of each chamber, but leave intercommunicating spaces of irregular size and shape into which the apertures open.

Size. Length 1.9–10.0 mm (mean 4.7 mm).

Length (uncoiled portion) up to 7.2 mm (mean 2.5 mm).

Width (coil) 1.5–4.6 mm (mean 2.8 mm).

Width (uncoiled portion) up to 3.6 mm.

Number of chambers visible in coil 8–22 (mean 15).

Number of chambers visible in uncoiled portion up to 18 (mean 7).

Measurements made on forty well-preserved specimens. Broken individuals suggest that some may have been larger than these measurements indicate.

Affinities.

Labyrinthisma clearly belongs to the Superfamily Lituolacea, but does not fit readily into any of the families or subfamilies as presently defined.

Pokorny (1958) appears to be the only person to have figured specimens which may be conspecific with those described here. He referred his material to *Coscino-phragma cribrosa* (Reuss). However, although there is some doubt about the accuracy of Reuss's original description, *Coscino-phragma* is believed to be an adherent genus lacking an initial coil and possessing labyrinthic walls (Loeblich and Tappan 1964). It gives its name to the subfamily Coscinophragmatinae (family Lituolidae). The types of *C. cribrosa* are from the Upper Cretaceous of Czechoslovakia.

Secondary transverse septa occur in some members of the family Lituolidae, e.g. *Labyrinthisma* Weynschenk, while at least one genus, *Navarella* Ciry and Rat, has a

fully streptospiral initial coil. On the other hand, no known member of this family has a biserial or trochospiral initial stage.

The family Ataxophragmiidae includes *Coprolithina* Marie, a genus with radial partitions and a trochospiral coil but lacking internal pillars. Only in the Pavonitidae is the complexity of the internal structure similar to that of *Labyrinthidoma*, but the mode of growth of the present specimens, particularly in the initial and adult stages, is rather different from anything known in this family.

The fact that the microspheric form of *Labyrinthidoma* combines characters best seen in three different families of the Lituolacea reflects our ignorance of the mode of growth of this generation throughout the superfamily and indicates that the classification is defective. For this reason no attempt is made to assign *Labyrinthidoma* to a family.

The existence of a biserial stage in *Lituola irregularis* prompted Kaeffer (1971) to speculate that it might represent a planktonic phase in the life cycle. While this is possible, it is more likely to indicate that the ancestral form is to be found amongst the numerous small biserial and triserial agglutinating benthic species known from the Mesozoic.

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SCANNING ELECTRON MICROSCOPY OF LATEX CASTS OF FOSSIL PLANT IMPRESSIONS

by W. G. CHALONER and M. M. GAY

ABSTRACT. Rubber latex casts of fossil lycopod stem impressions in fine-grained matrices may be subjected to scanning electron microscopy to reveal details of the original epidermal structure. This technique offers the potential of obtaining microscopic detail from plant impression fossils even if the cuticle is not preserved.

IMPRESSIONS of plant surfaces on a rock matrix are generally regarded as a rather poor and uninformative type of fossil. Where some of the coalified plant material has survived, from which a cuticle may be prepared by maceration (a 'compression fossil'), then this may be subjected to microscopic examination, and the value of the fossil to a palaeobotanist is proportionately greater. In reviews of methods of investigating fossil plants, it is generally suggested that impression fossils will reveal only the outline of the plant material, and perhaps in the case of leaf impressions, the venation pattern. This paper is an account of a method of further investigating such impression fossils by preparing a rubber latex cast of the surface, and photographing the microtopography of the cast by scanning electron microscopy (SEM). Latex replicas have been in use in palaeontology for some years, for preparing casts and moulds of fossils (Rigby and Clark 1965). The application of SEM to such replicas appears to have considerable potential for revealing epidermal features—cell outlines, position and orientation of stomata, hairs, etc., in a class of plant fossils which is not generally rated as susceptible to microscopic examination. The use of SEM in palaeobotany has recently been thoroughly reviewed by Taylor (1968), Muir (1970*a, b*), and Snigirevskaya (1971). These and other authors have emphasized the value of SEM in studies of spores (Leffingwell and Hodgkin 1971; Reyre 1971), of wood (Alvin and Muir 1969), and of cuticles (Boulter 1971), but its application to plant impression fossils does not seem to have been exploited.

MATERIAL AND METHOD

A typical plant 'impression fossil' shows on the rock surface a mould of the outer surface of the organ, with a microtopography which is 'negative' with respect to the original surface, so that stomatal cavities appear as small protrusions, and so on. A rubber latex cast of such an impression or mould gives a replica of the original plant surface. The quality of such a plant impression fossil appears to depend largely on:

1. The extent to which the original plant tissue surface showed a topography reflecting underlying epidermal or subepidermal features. In some cases, as cell contents collapsed post-mortem, the outer surface of the cell walls may even show more of the underlying cell arrangement than was the case in life.
2. The rapidity with which the plant material became incorporated and the accruing

sediment formed a mould in juxtaposition to it, before microbial activity or diagenesis caused collapse and loss of structure of the outer surface of the plant tissue.

3. The particle size of the matrix (whether clastic, or more or less syngenetic in character); the smaller the effective particle size, obviously the greater the fidelity of the mould to the minutiae of the original microtopography. In the latex replicas of plant impression fossils in fine-grained matrices that we have examined, the SEM even at magnifications of up to 10 000 times has revealed surprisingly little detail of the particulate nature of the matrix, and does not resolve any texture induced by the character of the latex itself. The latex, once dried at room temperature for 24 hours, withstands both the exposure to vacuum involved in specimen coating and the electron beam itself. Shrinkage of the latex cast appears to be insignificant; specimens up to 6 months old showed a linear shrinkage of less than 3%. No special study of the possibilities of differential contraction was attempted, but clearly if size or shape differences of this order were consequential, this aspect would need further consideration.

In a preliminary investigation, we have found that Carboniferous argillaceous sediments may retain a high degree of epidermal detail of lycopod stems, capable of being picked up on a latex replica. The most satisfactory results have been obtained from specimens from which the coaly plant material has either been burnt off or removed from the mineral matrix by weathering. Either of these processes reveals a surface of matrix with the highest possible fidelity to the original plant surface microtopography. A less satisfactory result is obtained where the impression has been exposed by a fracture plane running more or less along the interface between matrix and coaly material.

The advantages of the method of SEM examination of latex replicas are:

1. The method reveals epidermal characters on specimens which, lacking a cuticle, would not previously have been rated capable of yielding such detail.

2. In addition, this procedure may reveal cellular character on surfaces which have never had a cuticle (e.g. lycopod leaf abscission scars)—see Pl. 79, fig. 2.

EXPLANATION OF PLATE 79

Replicas in latex of leaf cushions of *Lepidodendron* (fig. 6), showing epidermal detail under the scanning electron microscope (figs. 1–5).

Figs. 1–4, 6. *Lepidodendron subdichotomum* Sterzel, *sensu* Thomas, from old tip heap, Radstock Colliery (Nat. Grid. ref. 696 554), British Museum (Natural History) V 67053. Specimen probably from Radstock Group (Westphalian D) or possibly from the underlying Farrington Group.

Fig. 1. Leaf cushion with scar, $\times 28$.

Fig. 2. Detail of leaf scar surface, with vascular scar, and on either side the two parichnos, $\times 68$.

Fig. 3. Detail of ligule pit, the fissure abutting obliquely on upper edge of leaf scar. (Hole to right of ligule pit is artifact caused by an air bubble in the matrix), $\times 205$.

Fig. 4. Stomata on lower field of the leaf cushion: note clarity with which surrounding epidermal cell walls appear on the latex surface, and the stomatal apertures within the two stomatal depressions, $\times 900$.

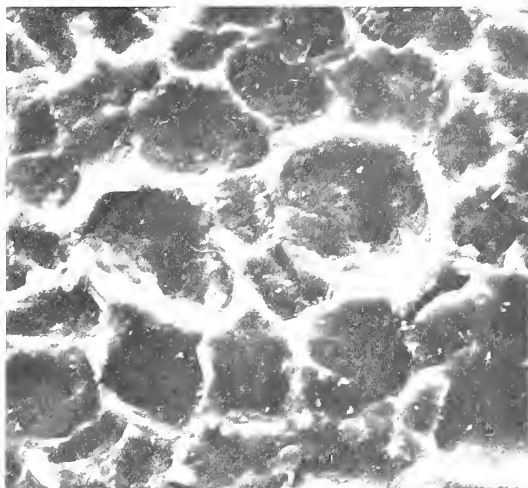
Fig. 5. Single stoma from the leaf cushion just above the leaf scar on a specimen of *Lepidodendron veltheimii* Sternberg (I.G.S., Kidston Collection No. 5115) from the Edge Coal Group, Stirling, Scotland, $\times 600$.

Fig. 6. A photograph, with oblique illumination, of a white latex rubber cast ('positive') prepared from the same specimen of *Lepidodendron subdichotomum* as figs. 1–4, $\times 10$.

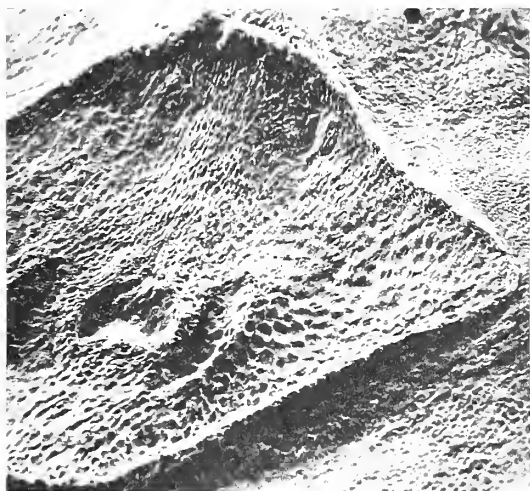
Figs. 1, 4, and 5 were taken on a Cambridge S600; Figs. 2 and 3, on a Cambridge Stereoscan.



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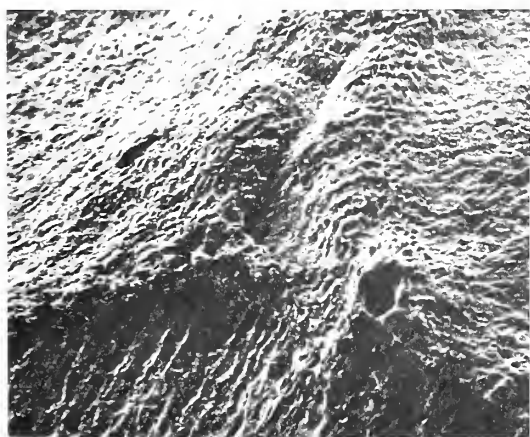
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CHALONER and GAY, latex casts of fossil plants

3. The fossil is left completely intact, which is an obvious advantage in a figured or type specimen.

4. A latex cast may be prepared from a relatively large specimen (e.g. in a museum), which could never itself be subjected directly to scanning microscopy by any other means. The resulting cast may readily be removed, or sent through the post, without needing to move the original specimen.

5. An incidental advantage is the homogeneity of the latex cast, in terms of its secondary electron emission (forming the SEM image). This contrasts with a clastic matrix which, if of petrologically heterogeneous nature, will give a varied secondary emission under the SEM unrelated to the microtopography.

TECHNICAL DETAILS

Casting. We have prepared casts from a number of Devonian, Carboniferous, and Permian plants. The surface of *Lepidodendroid* stems shows a surprising amount of detail; this is evidently because partial collapse of the original epidermal cells of the leaf cushion of these plants produces a surface topography reflecting their underlying structure. General information on the preparation of rubber latex casts is given in Rigby and Clark (1965). We have found that the product marketed as 'Revultex' (Bellman, Ivey, and Carter Ltd., 385b Grand Drive, London, S.W. 20) gives satisfactory results. A first coat is applied using the liquid diluted with an equal volume of water, and is worked into the surface of the fossil with a fine brush to ensure contact with depressions in the surface. Subsequent layers should be applied only after each coat has dried completely. The setting of the latex may be accelerated by placing a table lamp immediately above the latex-covered fossil. For a large surface (greater than 10×10 cm) the latex may be strengthened with gauze bandage or other textile applied to the wet surface of the third or subsequent layer of latex. In some cases (especially with museum specimens) it was found that the first cast carried a good deal of air-borne dust and other extraneous matter, and a second or even third cast gave a cleaner subject for SEM study. However, it was also found that once dry, a latex cast could be washed free of much of this debris with soap and water without loss of cellular detail.

Coating. We found that latex with white pigment (supplied by the manufacturer) gave particularly good results; the white surface is more satisfactory for examination by light microscopy prior to SEM study. Suitable pieces of the latex replica were cut out and mounted on stubs with 'Durofix' cement, painted around the margin with 'silver dag', and coated using carbon-paladium rods in an arc in an Edwards 'Speedivac' 12E6 high vacuum coating unit. Multi-directional coating was achieved by rotating the stubs on an improvised disc mounted eccentrically on the rotating spindle of the unit, set at 6 cm from the arcing source. The stubs were given two coatings in this way, being rotated through about 45° individually (with respect to the rotating disc) between each coating operation. Fifteen 1-second bursts of arcing were found to give an adequate coating under these conditions.

RESULTS

We have used this method successfully on a number of Palaeozoic lycopod stem impressions (*Lepidodendron*, *Sigillaria*, *Lepidodendropsis*, and *Lycopodiopsis*). The type of detail revealed is shown for two species of *Lepidodendron* in Pl. 79, figs. 1–6. The depressed stomata characteristic of the *Lepidodendroids* (Thomas 1966, 1970) show as a particularly clear feature of microtopography on these specimens—probably rather more so than would be the case with other plant groups. A specimen of *Lepidodendron subdichotomum* from the Westphalian C or D of Radstock forms the basis of figs. 1–4 and fig. 6. This specimen had evidently been burnt off, probably by combustion of the tip heap on which it was collected. A white latex cast of part of the stem surface showing leaf scars and cushions is shown in fig. 6, taken with

oblique illumination. Figs. 1–3 show the leaf cushion, the leaf scar, and part of the adjoining cushion surface under SEM at successively higher magnification: these show detail of the cellular pattern on the abscission surface (fig. 2) in addition to the parichnos and vascular cicatricule; the ligule pit is seen as a small fissure abutting on the upper edge of the leaf scar (fig. 3). Stomata show clearly among the epidermal cells on the leaf cushion surface: the orientation of their long axes is evident, and in some cases the stomatal aperture appears in the cast (fig. 4). A single stoma from another species, *L. veltheimii* is shown in fig. 5 for comparison. (This specimen, in the Kidston Collection, No. 5115, is cited in Crookall 1964, p. 302). While this technique has proved successful with a limited number of Palaeozoic plant fossils, it could equally be applied to many types of animal fossils where microtopography is likely to be preserved, such as the chitinous covering of arthropods and the calcareous shells and tests of other invertebrates. No doubt other means of preparing replicas of the surface may give equally good results, but latex has the ability to accommodate to large re-entrant features in the topography, while picking up with equally high precision the microscopic details of the surface.

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Cover illustration: *Ancyrodella* element (Conodont), Cashaqua Shale, Upper Devonian, New York State, $\times 70$.

A NEW SILURIAN ECHINOID GENUS FROM SCOTLAND

by PORTER M. KIER

ABSTRACT. A new genus and species of echinoid, *Aptilechinus caledonensis*, is described from the Silurian (Llandovery) of Scotland. This species, the sixth known from the Silurian, is a flexible echinoid belonging to the family Lepidocentridae. It is unusual in having its largest spines attached to the ambulacra.

A NEW Silurian echinoid is described from the Pentland Hills of Scotland. This discovery is of great importance because of the rarity of echinoids of this age, and the sweeping evolutionary changes which were occurring in echinoids during this time. Only five Silurian echinoids are known: *Echinocystites pomum* Thomson, *Myriastiches gigas* Sollas, and *Palaeodiscus ferox* Salter from Great Britain, *Gotlandechinus balticus* Regnéll from Sweden, and *Koninckocidaris silurica* Jackson from the United States. The addition of the sixth adds considerably to our understanding of the evolution of these primitive species.

Although the specimens are preserved as moulds and are flattened, many minute details of their tests are visible. The most unusual morphological feature, one that would have given it a most 'peculiar' appearance in life, as reconstructed on text-fig. 4, is the presence of the largest spines on the ambulacra, and their absence on most of the interambulacral plates. One of these spines occurs beside each porepair; with presumably a function of protecting the tubefeet from predators. A few of the more adoral of these spines could have been used for locomotion, but probably the echinoid 'walked' mainly on the numerous peristomial spines.

Structurally, *Aptilechinus* possesses many of the characters which would be expected in a Silurian echinoid according to the evolutionary trends described by Kier (1965) for these flexible echinoids. The ambulacra are not expanded adorally, and the porepairs are near the perradial suture as typical in Silurian flexible echinoids. The radial water vessel is covered, as in many early Paleozoic echinoids, but it lacks the groove on the exterior along the perradial suture found in most of the other Silurian echinoids. The regularity of the shape of its plates coincides with that found in some other Silurian echinoids such as *Koninckocidaris* and *Myriastiches*, and its small, high test with few plates is typically primitive.

There appears to be in this genus only a single genital plate lacking genital pores. Although the apical area is not well preserved in any of the specimens, enough of the area is visible on several specimens to convince me that only one genital plate was present. Thus the absence of the other four genital plates and the lack of genital pores in the single madreporitic-genital plate is to be expected in echinoids from the Ordovician and Silurian. The Ordovician genera *Aulechinus*, *Ectinechinus*, and *Eothuria* have only one genital plate with no genital pore as does the Silurian *Echinocystites*. The apical system is not known in the Silurian *Myriastiches*, and the apical system is not clear in *Palaeodiscus*. According to Jackson (1912, p. 286, pl. 20, fig. 5)

there is more than one genital plate in the Silurian *Koninckocidaris silurica* Jackson, but this figure shows no genital pores. However, this species is based on only a fragment showing the interior, and until this specimen has been found and re-examined, the presence and character of these genital plates is not certain. The earliest echinoid which definitely has more than one genital plate is the Devonian *Lepidechinoides whitnalli* in which Cooper (1931, p. 138) found a genital plate at the head of each interambulacrum, and each genital plate had numerous genital pores. This is also the earliest known Paleozoic echinoid that has genital pores. Therefore, it is apparent that the development of genital pores and more than one genital plate in the Paleozoic echinoids occurred at some time in the Silurian or Devonian.

Stratigraphical and geographical occurrence of echinoids. These specimens were collected by Mr. David Hardie from Silurian rocks of the Pentland Hills, Midlothian, Scotland and purchased by the Royal Scottish Museum in Edinburgh in 1897. They are labelled 'Starfish Bed', Gutterborn Burn, Pentland Hills. Dr. Robin Cocks of the British Museum (Natural History) has examined the material and believes that the locality data are correct, and states that these beds belong to the *crenulata* Zone, which is latest Llandovery (Cocks, Holland, Rickards, and Strachan, 1971, fig. 9). The beds and their fauna have been described by Lamont (1947, pp. 193-208, 289-303), who later (1952, p. 27) proposed that they be referred to a new division of the Silurian System called 'Pentlandian'. He also considered them to be Gala-Tarannon (equivalent to latest Llandovery) in age.

Order ECHINOCYSTITOIDA Jackson

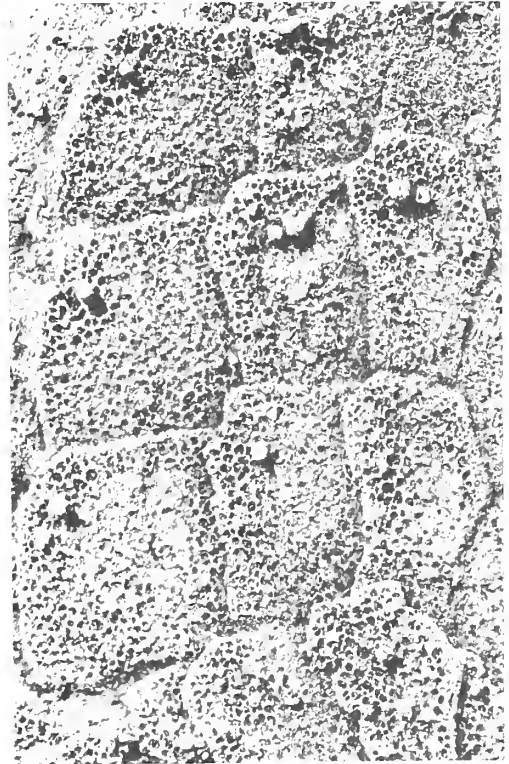
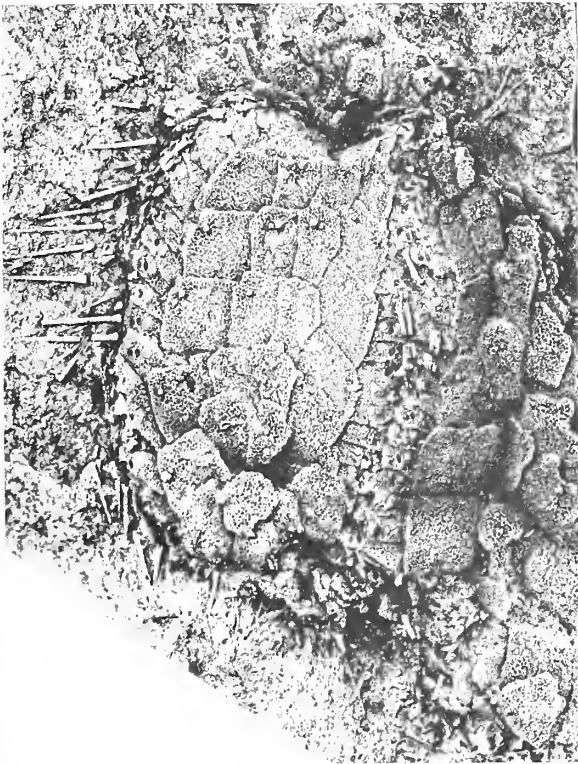
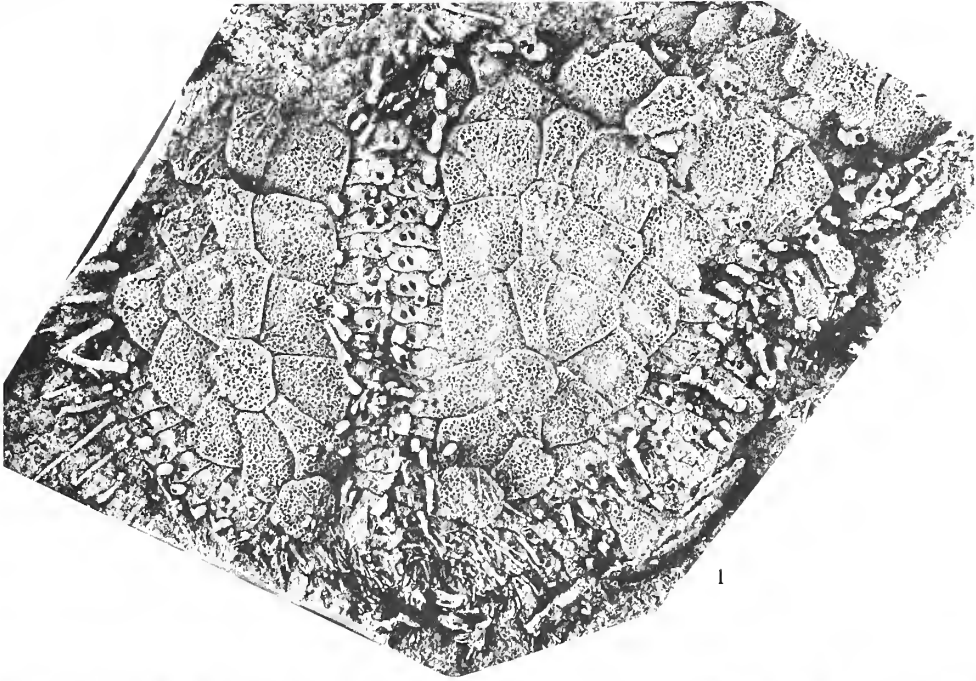
Family LEPIDOCENTRIDAE Lovén

APTILECHINUS gen. nov.

The test is flexible, composed of regularly shaped plates with the interambulacral plates imbricating adapically and laterally, and the ambulacral plates imbricating adorally and under the interambulacra. The apical system has one genital plate lacking genital pores and there are five ocular plates. The ambulacra are composed of two columns of plates in each area, and do not broaden adorally. The porepairs are situated near the perradial suture in well-developed peripodia. On the interior, each ambulacral plate has an elevated process forming an arched covering for the radial water vessel. The interambulacra are composed of four columns of regularly shaped plates. One large spine is attached to each ambulacral plate and to a few of the most adorally situated interambulacral plates. Small spines occur on the ambulacral and interambulacral plates, and pedicellariae were probably present. The surface of the plates are deeply pitted. The peristome is covered with many low, strongly imbricate

EXPLANATION OF PLATE 80

Figs. 1-3. *Aptilechinus caledonensis* sp. nov. 1, Adoral view of latex pull of RSM 1897.32.537A showing portion of two interambulacra and three ambulacra. Note small spines on some of the interambulacral plates, and larger spines on ambulacral plates, $\times 5$. A drawing of the plate arrangement of this specimen is on text-fig. 3. 2, Side view of latex pull of RSM 1897.32.537B (holotype) showing presence of four columns of plates in each interambulacrum with the median column overlapping laterally the others, and the long ambulacral spines, $\times 5$. A drawing of the plate arrangement of this specimen is on text-fig. 2. 3, Interambulacral plates of latex pull in fig. 2 showing the pitted surface of the plates, and the single protuberance or peg on each plate which probably served for attachment of a spine or pedicellaria, $\times 15$.



2

3

ambulacral plates and a few interambulacral plates. Jaws, braces, and longitudinally ridged grooved teeth have been found.

Type species. Aptilechinus caledonensis sp. nov.

Comparison with other genera. This genus clearly belongs in the order Echinocystitoida because of its strongly imbricate plates with the ambulacral plates bevelling under the interambulacra and adorally over each other, and the interambulacral plates imbricating adapically. It is referred to the family Lepidocentridae because it has only two columns in each ambulacrum. *Aptilechinus* is easily distinguished from the Silurian genera of this family, *Palaeodiscus*, *Myriastiches*, and *Koninckocidaris*. *Myriastiches* has many more plates, lacks larger spines on the ambulacra, and has a much less developed covering over its radial water vessel. *Palaeodiscus* is easily distinguished by the external groove in its ambulacra, lack of covering over the radial water vessel, and wider ambulacra with lower plates, lacking larger spines. Too little is known of the Silurian species of *Koninckocidaris* to compare it with *Aptilechinus*. The holotype and only known specimen of *K. silurica* Jackson is a fragment showing only part of the interior of the test, and it is not possible from Jackson's figures to discern the character of the interior of the ambulacral plate. Unfortunately, this holotype is not at the University of Rochester, as reported by Jackson, and is presumably lost.

Aptilechinus differs from the Ordovician genera *Aulechinus*, *Ectinechinus*, and *Eothuria* in having more regularly arranged interambulacral plates, its porepairs more distant from the median suture, its pores completely divided from each other, and well-developed spines. It differs from the Devonian *Lepidechinoides* in having its radial water vessel covered, its porepairs much nearer the perradial suture, larger ambulacral spines, and smaller interambulacral spines. The Devonian *Albertechinus* and *Lepidocentrus* have primary tubercles on the interambulacra, and *Porechinus* is easily distinguished by its ambulacral plates which have the inner pore of each pair open.

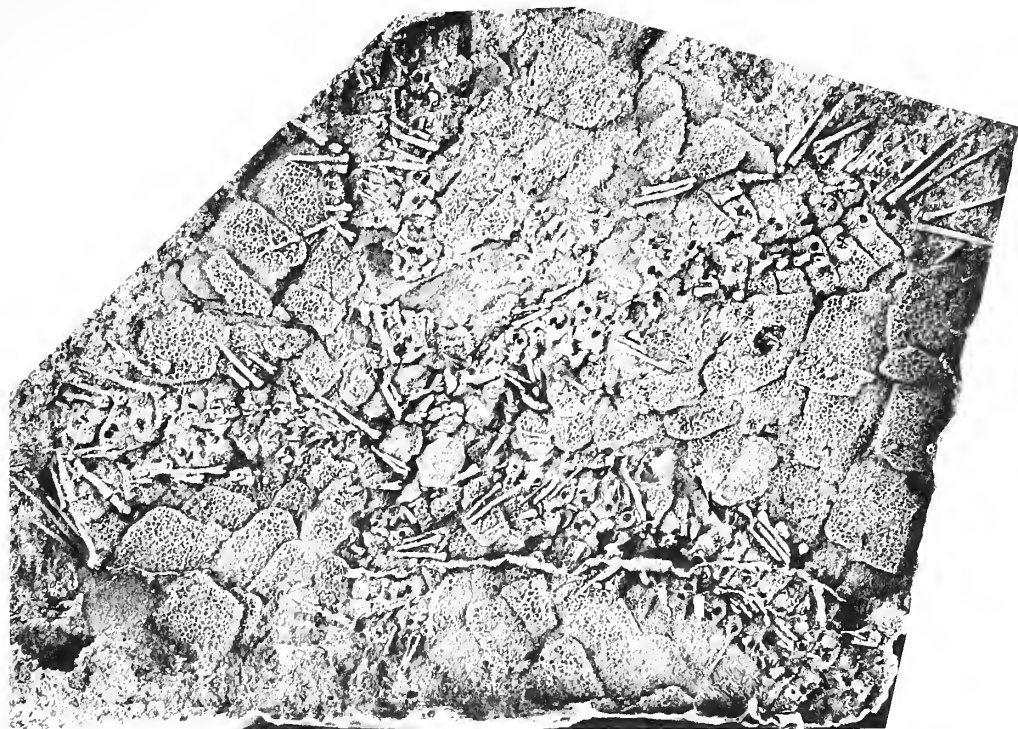
Aptilechinus caledonensis sp. nov.

Material. The specimens are preserved as impressions in a silty shale whose grains are small enough to preserve minute details of the test. All the specimens are flattened, with the plates somewhat shifted but not disassociated. There are impressions of twenty-one specimens, six of which have been collected with their counterparts. Both the interior and exterior of portions of the echinoids are visible, but none of the calcite of the tests is preserved.

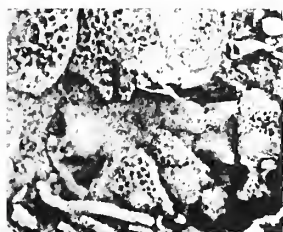
Presumably, the echinoids were covered and killed by the sediment in which they now occur. Although

EXPLANATION OF PLATE 81

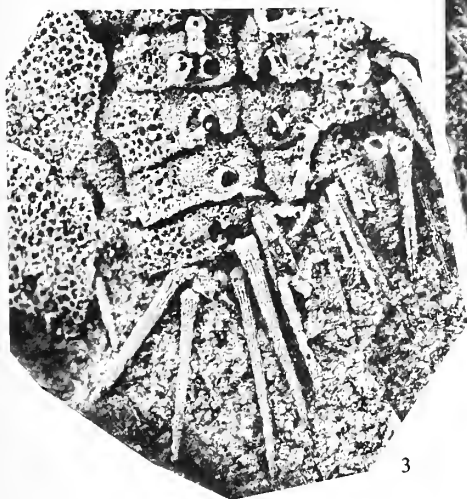
Figs. 1-3. *Aptilechinus caledonensis* sp. nov. 1, Adapical view of latex pull of RSM 1897.32.538B showing the small apical system. Several of the ocular plates are visible; the single large plate is probably the madreporite, $\times 5$. 2, A brace on specimen in fig. 1, $\times 10$. 3, View of portion of ambulacrum of specimen in fig. 1 showing position of porepairs near perradial suture, and greater height adradially of each plate when not overlapped by adjacent plates. Note long striated spines with deep concavity at their bases. These spines were evidently attached to the single nodes occurring on each ambulacral plate visible slightly adradial and adapical to the outside pore of each porepair, $\times 10$. 4, Side view of latex pull of RSM 1897.32.551 showing two interambulacra and three ambulacra, $\times 5$.



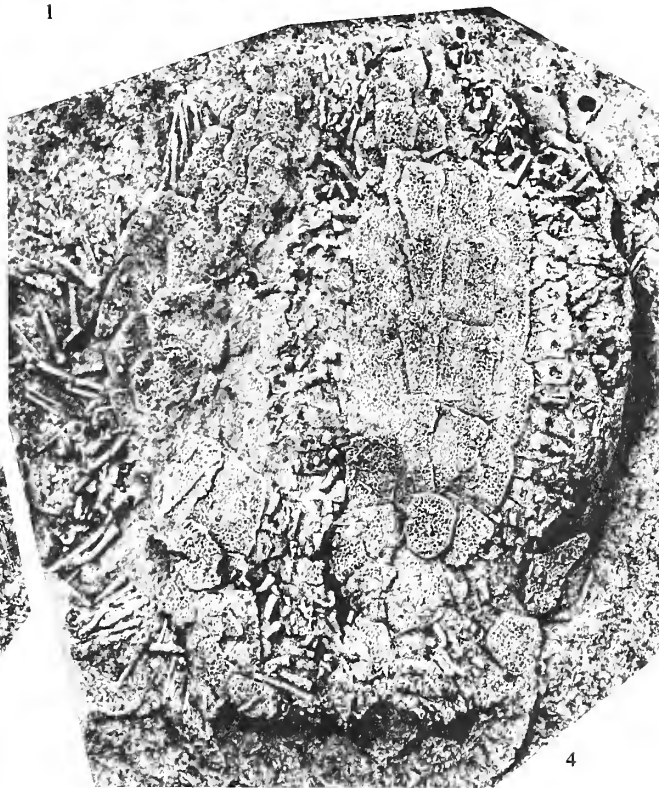
1



2



3



4

KIER, Silurian echinoid

the spines have shifted slightly, they are still very near to where they were attached to the individual echinoid. Most of the ambulacral spines extend vertically from the ambulacra, showing that the echinoids were not disturbed after death by predators or currents.

Size. It is difficult to estimate the original size of the specimens because many are only partially preserved, and all are flattened. A rough estimate was possible on twelve of the twenty-one specimens, with the smallest estimated to have been 14 mm high, the largest 30 mm and the average 20 mm. These estimates are probably accurate to within 20%.

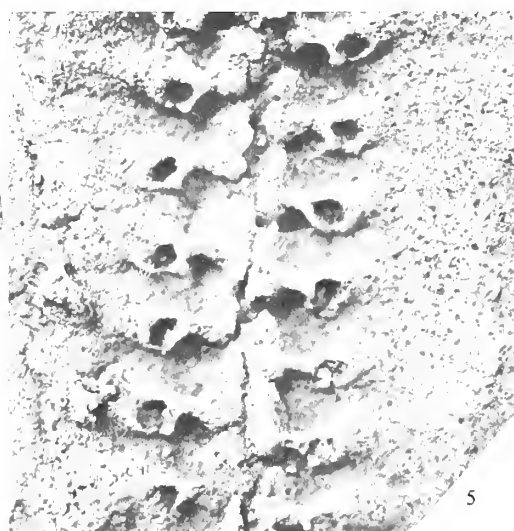
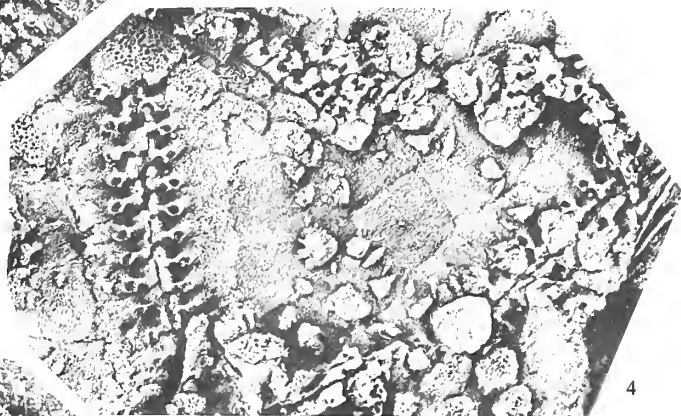
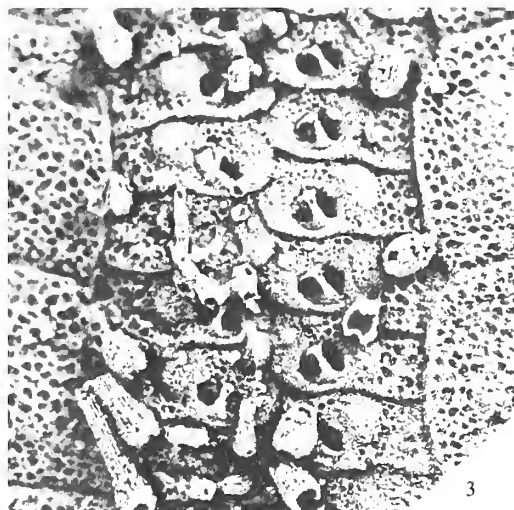
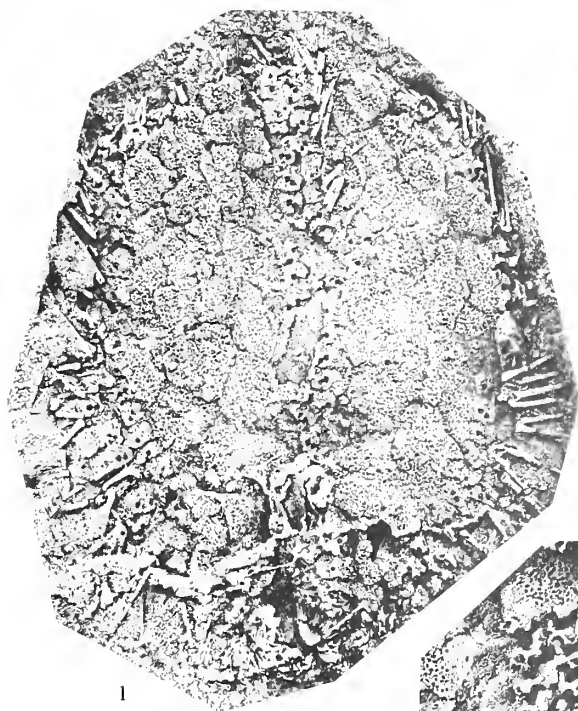
Shape. Three specimens are flattened sideways with little oblique distortion, therefore preserving what appears to be the original profile (Pl. 80, fig. 2; Pl. 82, figs. 1, 2). The test is higher than wide with a width approximately 80% of the height. A reconstruction of the original shape of the test is given on text-fig. 4.

Apical system. In none of the specimens is the apical system well preserved, but on three specimens portions of it are present. The system was very small, with a diameter equal to approximately 25% of the diameter of the test. There were five ocular plates but probably only one genital plate. Four ocular plates are preserved on specimen RSM 1897.32.5388 (Pl. 81, fig. 1). These plates are wider than high, approximately 1.1 mm wide, and have a smoothly curved dorsal margin, and a straight ventral margin. The dorsal part of the plate is thin with coarse-lattice structure, whereas the ventral part is thickened, prominently elevated, and lacks this coarse-lattice structure. A single indentation on the ventral portion of each plate may be the ocular pore. There is a single larger plate, 1.5 mm wide, on this specimen which is probably a genital plate and may be the madreporite. The indentations on the surface of this plate are smaller than the coarse-lattice structure on the interambulacral plates and are probably madreporic pores. No genital pores are visible. No similar plates are preserved on this specimen and probably this species, like the Silurian *Echinocystites pomum* Thomson, had only a single genital plate. Many small narrow angular plates occur in the centre of the apical system, and presumably they are the periproctal plates.

Ambulacra. The greatest width of each ambulacrum in specimens in which the plates are in position is 37–45% of the width of the interambulacrum. Each ambulacrum is approximately the same width above and below the midzone until near the apical system (Pl. 83, fig. 2) and peristome where they narrow gradually. Each has two columns of low plates (Pl. 82, fig. 3; text-fig. 2) which strongly imbricate adorally over each other, but are overlapped by the interambulacra. The height of each plate is approximately 40% of the width when the plates in proper position; the transverse

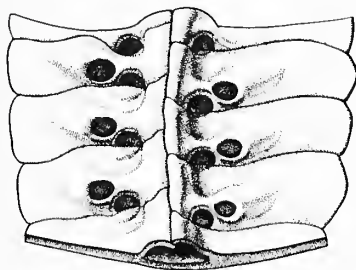
EXPLANATION OF PLATE 82

Figs. 1–5. *Aptilechinus caledonensis* sp. nov. 1, 2, Side views of latex pulls of RSM 1897.32.540B and 1897.32.540A in which most of exterior of the specimen is preserved, $\times 5$. 3, Portion of ambulacrum of latex pull of RSM 1897.32.537A showing the well-developed peripodia, position of porepairs near periradial suture, imbrication of plates, and node for attachment of large spine, $\times 15$. 4, View of interior of portion of test of latex pull of RSM 1897.32.552 showing the lack of pits on the inner surfaces of the plates and the interior structure of the ambulacrum, $\times 5$. A more enlarged view of this ambulacrum is on fig. 5. 5, Interior of ambulacrum of specimen in fig. 4 showing arched covering over radial water vessel, $\times 15$. A reconstruction of this structure is on text-fig. 1.



KIER, Silurian echinoid

sutures are parallel. However, on specimens in which some of the ambulacral plates are isolated by post-mortem distortion and not overlapped by the adjacent interambulacra (Pl. 81, fig. 3), it can be seen that the ambulacral plates expand greatly in height adradially. When in proper position approximately 40% of the surface area of each ambulacral plate is covered by the overlapping interambulacral plate and adapical ambulacral plate. Due to the nature of the preservation, it is not possible to count the number of ambulacral plates in a full column on most of the specimens, but on two specimens a fairly accurate estimate can be made. One specimen, approximately 20 mm high has at least fifty plates in an ambulacrum (excluding the peristomial ambulacral plates), and another with a height estimated at 24 mm has sixty plates in an ambulacrum, plus another sixteen to twenty extending on to the peristome. The peristomial ambulacral plates are lower (Pl. 83, fig. 3) than the other ambulacral plates, more imbricate, and have peripodia approximately one-half as large. Approximately three ambulacral plates occur opposite each adjacent interambulacral plate. The porepairs are situated near the perradial suture (Pl. 82, fig. 3) approximately one-third the distance from the perradial to the adradial suture. The pores of a pair are oblique with the outer pore more adapical. This outer pore is



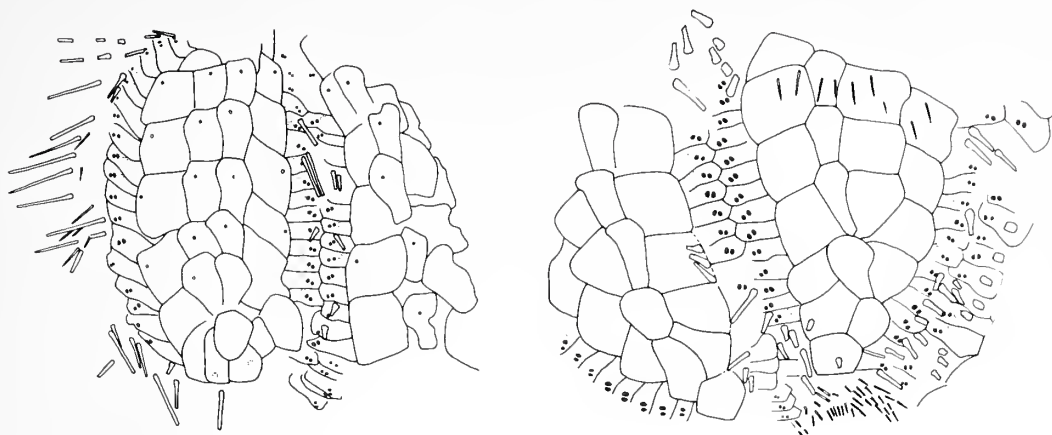
TEXT-FIG. 1. *Aptilechinus caledonensis* sp. nov. A reconstruction of the interior of part of an ambulacrum showing the arched covering which extends along the perradial suture, and served as a passageway for the radial water vessel.

narrower than its partner on some of the plates, but the same width on others, but this narrowing may be due to post-mortem distortion. The porepairs occur in well-developed peripodia (Pl. 82, fig. 3) with a high ridge separating the pores, and with a rim surrounding the porepair. This rim is absent on the adradial side of each outer pore but is well developed curving around the inner pore.

Interior. The interior of each ambulacral plate has a prominent elevated process forming an arched covering extending along the perradial suture, and no doubt serving as a passageway for the radial water vessel (Pl. 82, fig. 5; text-fig. 1). A ridge extends transversely on each plate from this passageway and forms a high rim along the adapical edge of each porepair.

This ridge extends approximately one-half the width of each plate. A deep depression occurs between this ridge and the adjacent porepair with a small gap extending from the inner pore and leading into the covered passageway presumably for the entrance of the side branch joining the tubefoot to the radial water vessel.

Interambulacra. Four columns of thin plates are present in each interambulacrum. They strongly imbricate adapically and laterally and are more or less regularly shaped. The median column (text-figs. 2, 3) is composed of narrower plates than in the other columns with a width equal to approximately only one-half the height. These plates are hexagonal with their greatest width adapical, and they imbricate laterally over the columns on their right and left. This median column varies in position on the same specimen and between different specimens. On some specimens (Pl. 81, fig. 1) all the median columns (as viewed from above) have two columns on the left of the



TEXT-FIG. 2. *Aptilechinus caledonensis* sp. nov. Plate arrangement of a latex pull of the holotype, RSM 1897.32.537B, showing four columns in each interambulacrum, two in each ambulacrum. The dotted circles on the ambulacral plates and a few of the adoral interambulacral plates mark the location of nodes where probably were attached the larger spines, $\times 5$. A photograph of this specimen is on Pl. 80, figs. 2, 3.

TEXT-FIG. 3. *Aptilechinus caledonensis* sp. nov. Plate arrangement of a latex pull of RSM 1897.32.537A showing adoral plate arrangement. Note the fragmental remains of the large spines which were attached to the ambulacral plates and a few of the adoral interambulacral plates. The dotted circles mark the location of nodes where these spines were probably attached, $\times 5$. A photograph of this specimen is on Pl. 80, fig. 1.

median column and one on the right, whereas in other specimens (Pl. 80, fig. 1) one interambulacrum has two columns on the right but another interambulacrum has one on the right.

The plates of the columns which border the ambulacra are less angular in outline and the edge of the plate which overlaps the ambulacra and adapical interambulacral plate is curved. Adorally, the first interambulacral plate is a single plate of the median column (Pl. 80, fig. 1; text-fig. 3), followed by two in the second row, three in the third, and four in the fourth. Approximately thirty-five plates are present in each interambulacrum with approximately ten plates in each column bordering the ambulacra. It is not clear how many interambulacral plates occur on the peristome.

Spines and tuberculation. One of the most unusual features of this echinoid is the presence of large spines on the ambulacra and their absence on the interambulacra, except on a few adoral plates. Two sizes of spines occur on the ambulacra. The largest are up to 3.4 mm long, gently tapering to a sharp point which is not preserved on most of the specimens. They are expanded near their bases where a deep concavity (Pl. 81, fig. 3) is present presumably for the insertion of muscle or ligament. These spines are longitudinally striated with approximately fifteen striations on each spine. One of the spines is attached to each ambulacral plate as indicated by the fact that the number of spines found on any specimen approximates but never exceeds the number of ambulacral plates. These spines were evidently attached to a single node that occurs on each plate slightly adradial and adapical to the outside pore of the porepair (Pl. 81, fig. 3; Pl. 82, fig. 3; text-figs. 2, 3). These nodes lack the coarse meshwork found on

most of the surfaces of the ambulacral plates, and are simple protuberances lacking mamelons. The smaller spines are approximately one-third the size of the larger, are also striated and expanded at their bases, but the presence or absence of the basal concavity cannot be determined. The number of these smaller spines is not clear as most of them were removed during post-mortem sorting. However, they appear to have been attached to a single smaller node that occurs near the median suture adapical to the inner pore of each porepair (Pl. 82, fig. 3).

No large spines were attached to the interambulacra except adorally where a single large node similar to those found on the ambulacra is present on the first three plates of some specimens (Pl. 80, fig. 1; text-fig. 3) indicating that a large spine was attached there. Small spines approximately 0.9 mm long appear to have been attached to most of the interambulacral plates. They are slender, tapering to a sharp point, striated, and have expanded bases. I have not been able to find any nodes or tubercles for the attachment for these spines.

Many of the interambulacral plates bear a single protuberance with sharp sides and a flat upper surface. These pegs occur on the outer adapical corner (Pl. 80, fig. 3; text-fig. 2) of each plate except on the narrow median column where they occur on the middle of the adapical surface. They are approximately 0.2 mm in diameter. Similar but smaller pegs occur on the ambulacral plates (Pl. 82, fig. 3) with two to three on each plate, one between the porepairs and the adradial suture and two between the porepair and the median suture. Perhaps pedicellariae were attached to these pegs: several structures are present which appear to have been pedicellariae but they are too poorly preserved to be certain.

The peristomial region was covered with many small spines (text-fig. 3) which were attached to the narrow ambulacral plates which formed a very flexible surface extending between the end of the interambulacra and the mouth opening. These spines were attached to five or more nodes on each ambulacral plate.

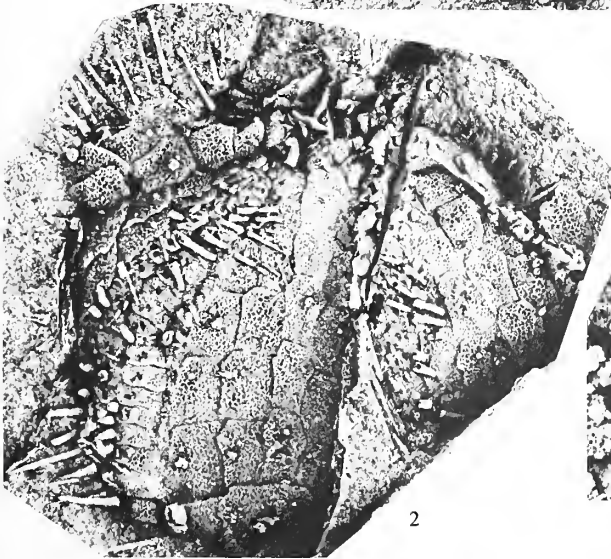
Lantern. The lantern is not well preserved on any specimen, but enough of parts of it are visible on several specimens to show that the pyramids, braces, and teeth were well-developed. Although not enough of a pyramid is preserved on any specimen to be able to determine the depth of the foramen magnum, the height of the pyramid is estimated to have been approximately 2.7 mm. The pyramid appears to be small relative to a tooth which is at least 3 mm long and 0.7 mm wide. The tooth is grooved, and is typical of those found in Paleozoic echinoids. It has four to five longitudinal ridges (Pl. 83, fig. 3). The brace is likewise similar to those found in other Paleozoic echinoids, and is approximately 2.5 mm long, 0.9 mm wide, and expanded at its ends (Pl. 81, fig. 2).

EXPLANATION OF PLATE 83

Figs. 1-3. *Aptilechinus caledonensis* sp. nov. 1, Side view of latex pull of RSM 1897.32.543 showing most of length of two ambulacra with their long spines and part of the interior surface of the other side of the test showing the lack of pits on the interior surface of the plates, $\times 5$. 2, Adapical region of latex pull of RSM 1897.32.541B, $\times 5$. 3, Oral region of latex pull of RSM 1897.32.538A showing portions of pyramids, part of a striated tooth, and several peristomial ambulacral plates, $\times 10$.



1

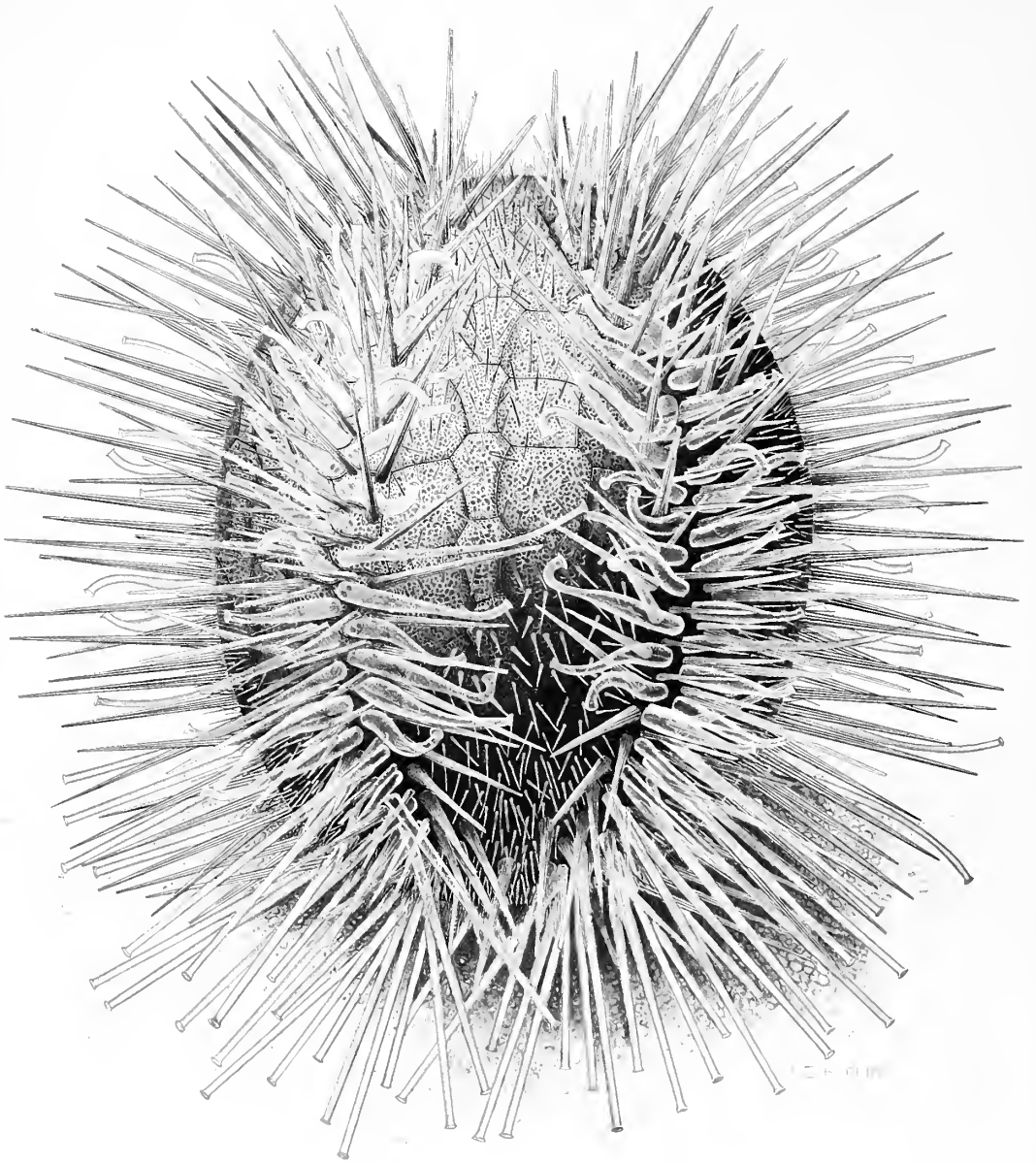


2



3

KIER, Silurian echinoid



EXPLANATION OF TEXT-FIG. 4. A reconstruction of *Aptilechinus caledonensis* sp. nov. as it may have appeared in life.

Surface ornamentation. All of the exterior surface of the interambulacral plates and most of the exterior of the ambulacral plates is deeply pitted (Pl. 80, fig. 3). The largest of these pits are 0.8 mm in diameter, and they are irregularly arranged. At first appearance they appear to be the meshwork structure of the plates themselves but on some specimens parts of the interior of the plates are visible, and it can be seen that the true meshwork is much finer and is regularly structured in a latticework typical of echinoderms (Pl. 83, fig. 1). This pitted surface is absent on the ambulacral plates on the peripodia and on the nodes. Evidently, these pits served no exterior function for they are present on that part of a plate that is covered in life by adjacent plates (Pl. 81, fig. 3).

Type-specimens. Royal Scottish Museum, Edinburgh, Scotland. Holotype RSM 1897.32.537B, figured paratypes RSM 1897.32.537A, 1897.32.538A, B, 1897.32.540A, B, 1897.32.541B, 1897.32.543, 1897.32.551, 1897.32.552.

Acknowledgments. I thank Euan Clarkson who told me of these specimens, and Charles Waterston, the Keeper of the Royal Scottish Museum, who kindly lent them for study. Both Ivor Henrichsen and William James Baird of the Royal Scottish Museum provided me with data on the specimens, and Robin Cocks examined the material and gave me his opinion on their occurrence and age. Larry B. Isham, scientific illustrator, made the excellent reconstruction of the echinoids on text-figs. 1 and 4, and Thomas F. Phelan, museum specialist, did the photography, made the latex pulls and gave me his valuable opinions on the morphology. J. Wyatt Durham and David L. Pawson critically read the manuscript. Robert W. Lamond prepared and studied this material and recognized that it represented a new genus, but was unable to complete his study because of subsequent commitments.

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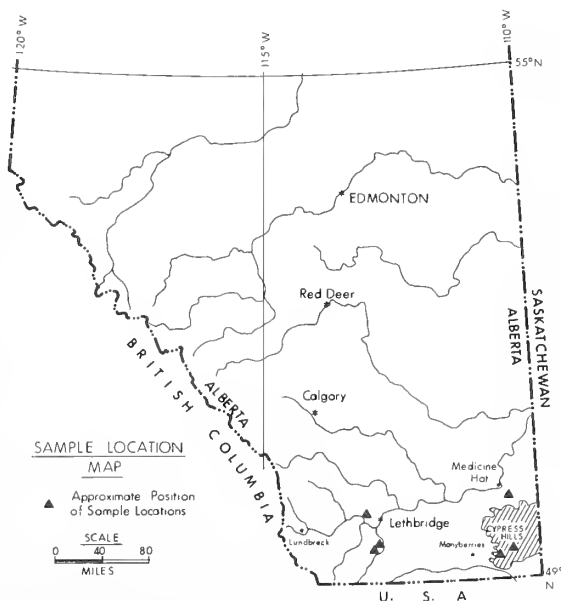
Typescript received 27 October 1972

DINOFLAGELLATE CYSTS AND ACRITARCHS FROM THE BEARPAW FORMATION (UPPER CAMPANIAN) OF SOUTHERN ALBERTA, CANADA

by REX HARLAND

ABSTRACT. Fifty-three species of dinoflagellate cysts and six species of acritarchs are reported from the upper Campanian Bearpaw Formation of southern Alberta. These include *Diconodinium firmum* sp. nov., *Lejeunia parva* sp. nov., *L. ampla* sp. nov., *Spinidinium clavum* sp. nov. and *Hystrichosphaeridium dowingii* sp. nov. The Bearpaw Formation is divided into three informal assemblage zones. A parameter called the gonyaulacacean ratio is used as a possible guide to the salinity of the Bearpaw sea or to the proximity of the coastline. Three periods of open marine conditions are postulated. These open marine conditions are intimately connected with the assemblage zones erected for the formation. Comparisons are made with Campanian assemblages of other areas.

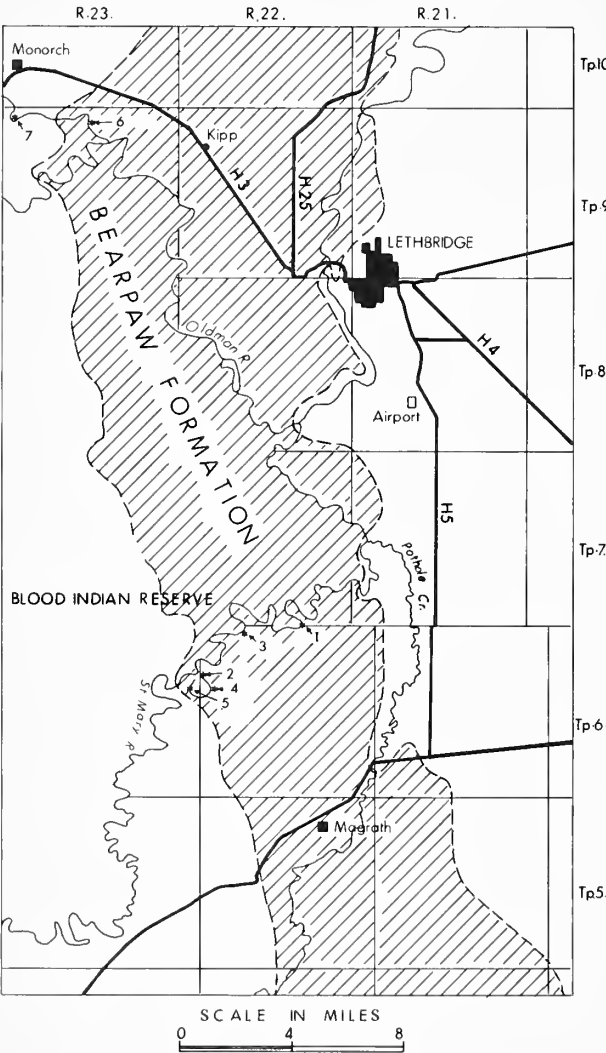
THE Campanian Bearpaw Formation is unique in being firmly placed in the geological time-scale by virtue of its ammonite faunas and its radiometric dating. Since there is a lack of knowledge of Campanian organic-walled microplankton, the Bearpaw was an ideal body of rock on which to study these microfossils. Such a reliably dated assemblage should be valuable in any further work on Campanian or suspected Campanian strata from other areas. The Bearpaw Formation is best known from southern Alberta, so this area was chosen for the study.



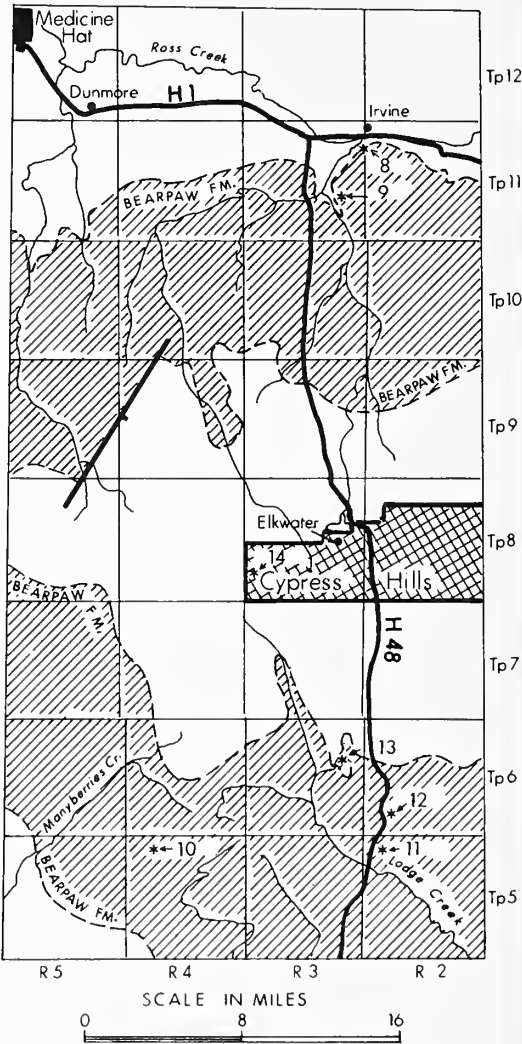
TEXT-FIG. 1. Sketch map of southern Alberta showing the approximate positions of the sample localities and the extent of the Cypress Hills (above 2500').

STRATIGRAPHY OF THE BEARPAW FORMATION

The Bearpaw Formation was named by J. B. Hatcher and T. W. Stanton (1903) from localities in the vicinity of the Bearpaw Mountains, north-central Montana. The first biostratigraphic zonation was that of Russell and Landes (1940), and Loranger and Gleddie (1953) were the first to attempt a micropalaeontological zonation. Potassium-argon radiometric dates are available for the Bearpaw Formation



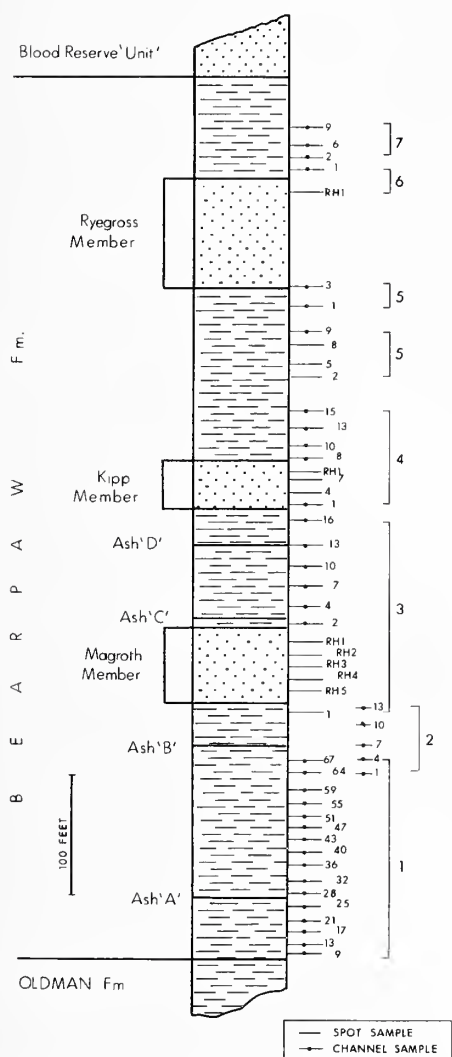
TEXT-FIG. 2. Detailed map of the Lethbridge area with the approximate outcrop pattern of the Bearpaw Formation and the positions of the sample localities. (Geology after GSC Calgary Sheet, 1928.)



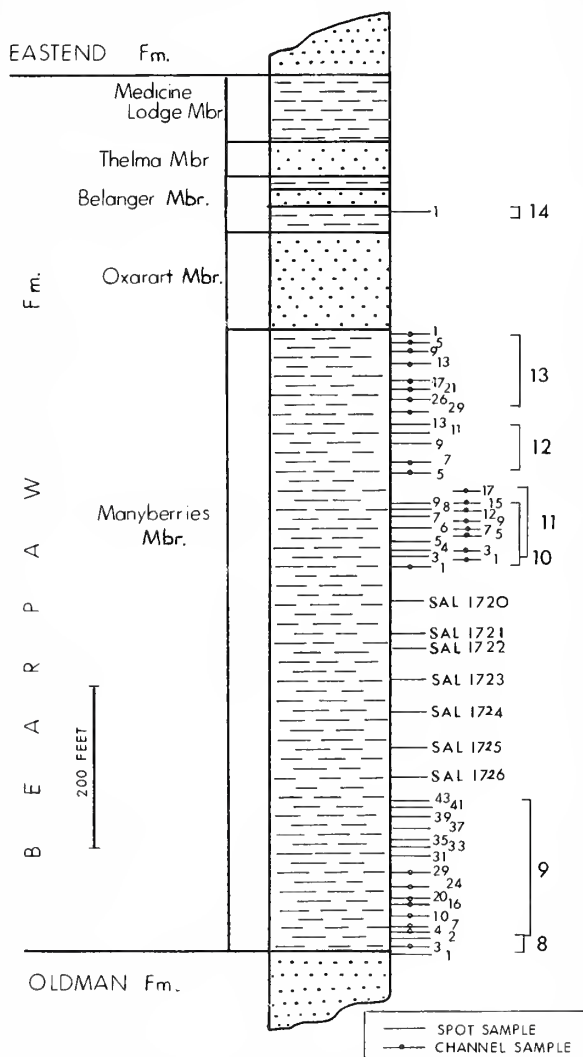
TEXT-FIG. 3. Detailed map of the Cypress Hills area with the approximate outcrop pattern of the Bearpaw Formation and the positions of the sample localities. (Geology after GSC Calgary Sheet, 1928.) The cross-hatched area indicates the Cypress Hills Provincial Park.

at 75 ± 4 million years from a thin bentonite 65 feet above the base of the formation at Lethbridge (Folinsbee *et al.* 1960, 1961).

The Bearpaw Formation is for the most part a sub-horizontal unit except where it has been affected by the Sweetgrass Arch uplift. A maximum thickness of 1170 feet has been recorded in the Cypress Hills (Lines 1947, *in litt.* 1963), but at Lethbridge it is only 726 feet thick (Link and Childerhose 1931). The lithology of the formation is predominantly one of shales with intercalated sandstones, minor bentonites, carbonate bands, and ironstone nodule horizons. Detailed lithological descriptions



TEXT-FIG. 4. Composite stratigraphical section for the Bearpaw Formation of the Lethbridge area showing sample distribution and coding. (After Link and Childerhose 1931.)



TEXT-FIG. 5. Composite stratigraphical section for the Bearpaw Formation of the Cypress Hills area showing sample distribution and coding. (After Lines 1963.)

are given by Williams and Dyer (1930); Link and Childerhose (1931); Russell and Landes (1940); Furnival (1950); and Caldwell (1968). The base of the formation in southern Alberta is generally regarded as being isochronous (Lines 1947, *in litt.* 1963) but it becomes diachronous to the east (Caldwell 1968). The upper boundary is markedly diachronous (Russell 1950).

The age of the formation in southern Alberta is upper Campanian, for the most part lying within the zones of *Baculites compressus* sensu stricto, *B. cuneatus*, *B. reesidei*, *B. jenseni* and *B. eliasi* (Caldwell 1968). The fauna consists mainly of molluscs and foraminiferans, but full descriptions are given in Warren (in Fraser *et al.* 1935); Dowling (1917); Williams and Dyer (1930); Russell and Landes (1940); Warren (1931, 1934, 1937); Douglas (1942); and Caldwell (1968).

The deposition of the Bearpaw Formation was accomplished during the last major marine transgression in western Canadian geological history (Warren and Stelck 1958). A connection with the Arctic is indicated by the work of Martin (1960) in addition to a link with the Gulf of Mexico (Reeside 1957).

Bearpaw Formation of southern Alberta. The Bearpaw Formation of the Lethbridge area has been described by Link and Childerhose (1931) and is exposed in the valley of the St. Mary River (fig. 2), especially in the cut bank sides of meanders. The regional dip of the formation is less than 10 degrees in a westerly direction. Locally, however, there are normal faults and open folds. The Cypress Hills, a plateau remnant, is capped by the Cypress Hills Formation of Oligocene age and is ringed by successively older strata including the Bearpaw Formation. The latter is essentially flat-lying and no complete section of the formation is exposed here. Lines (1947, *in litt.*, 1963) gives the most complete description (see fig. 5). The regional dip is less than 10 degrees in an easterly direction, little faulting has occurred, but there is much slumping and deep weathering.

Treatment. The distribution and type of sampling of the two sections is illustrated in figs. 4 and 5. The samples are stored at the Research Council of Alberta, at Edmonton. A standard palynological preparation technique was used but beyond the hydrofluoric acid stage all the samples were handled using the filtration system of Neves and Dale (1963). A Leitz Laborlux microscope 595949 was used with the slide label to the right of the observer. A reference co-ordinate for the upper left corner of the slide is given on the slide labels, following Pierce (1959). A set of slides is in the Department of Geology, University of Alberta. Specimens were photographed under Leitz Ortholux microscope 594209, equipped with an Orthomat camera attachment. Adox KB 14 film was used. All holotypes and figured specimens are in the Palynological Collections of the Research Council of Alberta at Edmonton.

SYSTEMATIC DESCRIPTIONS

The abbreviations O.D. and S.D. are used to indicate original and subsequent designation. In the dimension sections the figure in parenthesis is the arithmetic mean of the measured morphological parameters. The geological ranges given for the species and genera are after Sarjant (1967) unless otherwise stated, and the affinities are after Wall and Dale (1968).

Division PYRRHOPHYTA Pascher
Class DINOPHYCEAE Pascher
Order PERIDINIALES (Schutt) Lindemann

Cyst-Family GONYAULACYSTACEAE Sarjeant and Downie 1966
Genus APTEODINIUM Eisenack 1958

Type species. Apteodinium granulatum Eisenack 1958; O.D.

Apteodinium sp. A

Plate 84, fig. 2

The specimens compare quite favourably with *A. maculatum* Eisenack and Cookson (1960), except in the possession of a large prominent apical horn and in the style of 'ornamentation'; and with *A. tamboviensis* Vozzhennikova (1967), except in lacking a sulcus. Its affinities are gonyaulacacean with the apteodinioid lineage.

Figured material. Loc. 11, 7 (2) at 104.0–40.6. The last two figures refer to the sample number at the locality and the slide on which the specimen is to be found.

Dimensions. Range: Length 98.0 (112.5) 127.0 μ ; breadth 98.0 (99.0) 100.0 μ . Two specimens observed.

Cyst-Family Uncertain
Genus DICONODINIUM Eisenack and Cookson 1960

Type species. Diconodinium multispinum (Deflandre and Cookson) Eisenack and Cookson (1960); O.D.

Wall and Dale (1968) regard the genus as having a precingular archeopyle and affinities with the Gonyaulacaceae, whereas Davey (1969*b*) prefers to include it with the Cyst-Family Deflandreaceae (of peridiniacean affinities). A precingular archeopyle is demonstrated here.

Diconodinium firmum sp. nov.

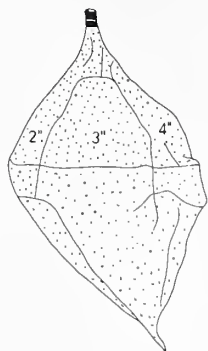
Plate 84, figs. 8, 9, 15, text-fig. 6

Derivation of name. Latin *firmum*—meaning solid, with reference to the structure of the distal extremity of the apical horn.

Diagnosis. Proximate cyst, commonly fusiform in shape, consisting of autophragm or two wall layers very closely adpressed. Test finely granulate. Epittract extends into an apical horn having a solid distal tip which may be oblate, acuminate, or bifurcate. The antapical horn always acuminate, and hollow throughout. The cingulum conspicuous and takes the form of a slight laevorotatory helicoid. Tabulation not usually seen. Archeopyle precingular of the P type (Evitt 1967), and rounded polygonal in shape. (Pl. 84, figs. 5, 6.)

Description. The granules on the walls are of variable size, usually fairly fine, but always conspicuous. The solid apical tip appears to have a definite structure (Pl. 84, fig. 15). It was often seen to be banded but its exact nature must await further study.

The cingulum is displaced by less than one-quarter of its width. Very little variation was seen in this cyst species except as documented in dimensions and in the nature of the apical tip.



TEXT-FIG. 6. *Diconodinium firmum* sp. nov.
Semidiagrammatic sketch of the holotype.
 $\times c. 1000$.

Figured material. Holotype: Loc. 3, 7 (2) at 98.0–32.9; Bearpaw Formation, Campanian, southern Alberta. Loc. 2, 39 (1) at 108.0–30.3.

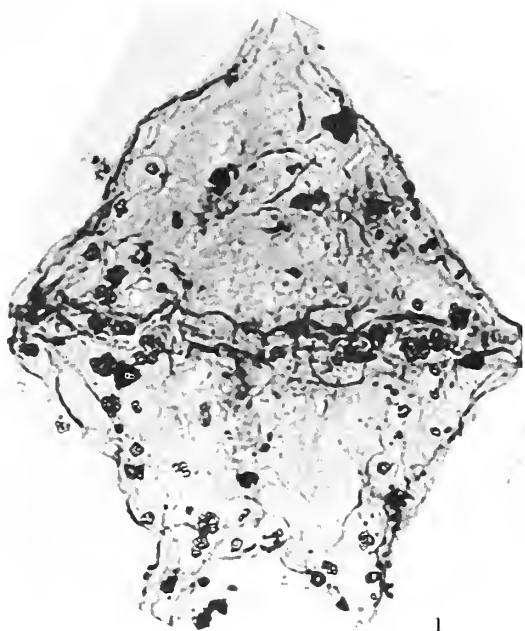
Dimensions. Holotype: Length 42.0 μ ; breadth 29.0 μ . Range: Length 36.0 (42.7) 50.0 μ ; breadth 18.0 (29.3) 32.0 μ . Fifty specimens measured, out of a studied population of sixty-four.

Remarks. This species is characterized by its shape and the solid structure at the distal extremity of the apical horn. It appears close to *Diconodinium rhombiformis* Vozzhennikova 1967 but is different in its lack of a distinct tabulation and the lack of small gonal processes in the cingular region. Although the archeopyle was rarely observed the conspicuous nature of plate 3" also suggests that the archeopyle is formed by the loss of this plate. The species has gonyaulacacean affinities with apteodinioid lineage.

EXPLANATION OF PLATE 84

All figures at a magnification of $\times 600$ unless otherwise stated.

Fig. 1. *Lejeunia ampla* sp. nov., holotype, dorsal view. Fig. 2. *Apteodinium* sp. A, oblique dorsal view, showing the archeopyle and surface ornamentation. Fig. 3. *Lejeunia parva* sp. nov., detail of specimen with the tabulation. $\times c. 1800$. Fig. 4. *Lejeunia tricuspis* (Wetzel) comb. nov., dorsal view. Fig. 5. *Spinidinium clavum* sp. nov., dorsal view. Fig. 6. *Spinidinium clavum* sp. nov., holotype, dorsal view. Fig. 7. *Lejeunia ampla* sp. nov., holotype, detail of apex with the ?apical archeopyle. $\times c. 1800$. Fig. 8. *Diconodinium firmum* sp. nov., holotype, dorsal view. Fig. 9. *Diconodinium firmum* sp. nov., dorsal view showing the archeopyle. Fig. 10. *Spinidinium clavum* sp. nov., a specimen with two well-developed antapical horns. Fig. 11. *Diconodinium arcticum* Manum and Cookson, dorsal view. Fig. 12. *Lejeunia parva* sp. nov., lateral view showing a lack of an antapical horn. Fig. 13. *Lejeunia parva* sp. nov., dorsal view of specimen showing tabulation. Fig. 14. *Lejeunia parva* sp. nov., holotype, ventral view. Fig. 15. *Diconodinium firmum* sp. nov., holotype, detail of the apex. $\times c. 1800$.



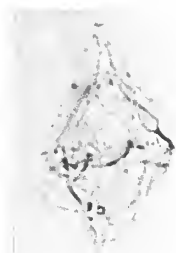
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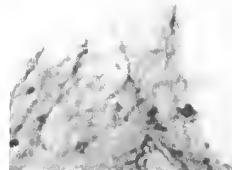
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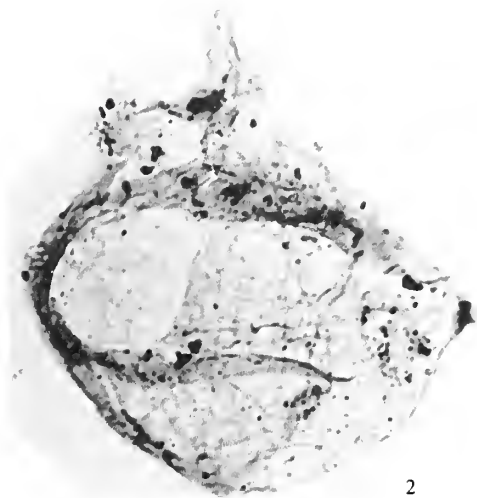
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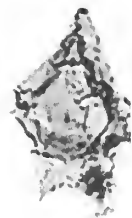
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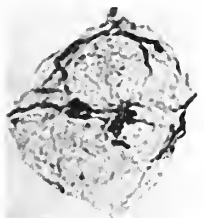
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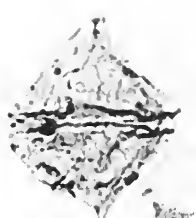
9



10



11



12



13



14



15

Diconodinium arcticum Manum and Cookson 1964

Plate 84, fig. 11

1964 *Diconodinium arcticum* Manum and Cookson; 18-19, pl. 6, figs. 1-4.

The granulation on the surface of the test varied from coarse to fine in the specimens observed. It was also noted that they are smaller than those described by Manum and Cookson (1964). They cannot be compared to *D. glabrum* Eisenack and Cookson (1960) because they lack a clearly defined sulcus and differ in the nature of the 'ornamentation'. *D. arcticum* has an Upper Cretaceous range. Its affinities are gonyaulacacean with the apteodinioid lineage.

Figured material. Loc. 3, 1 (2) at 103·6-37·1.

Dimensions. Range: Length 30·0 (41·1) 57·0 μ ; breadth 20·0 (26·3) 37·0 μ . Fifty specimens measured, out of a studied population of seventy-three.

Genus LEJEUNIA Gerlach 1961

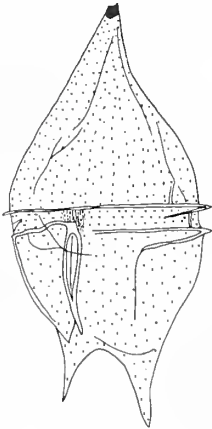
Type species. *Lejeunia hyalina* Gerlach 1961; O.D.

Lejeunia parva sp. nov.

Plate 84, figs. 3, 12-14, text-fig. 7

Derivation of name. Latin *parva*—meaning small, with reference to the size of the cyst.

Diagnosis. Proximate cyst, elongate to rhomboidal, made up of autophragm. Test granulate. Epitract elongated into an apical horn which is distally oblate or indented.



TEXT-FIG. 7. *Lejeunia parva* sp. nov. Semidiagrammatic sketch of the holotype. $\times c. 1200$.

Hypotract carries two antapical horns, one of which larger than the other; both distally acuminate. Cingulum, delimited by raised sutures, is planar to a slightly laevorotatory helicoid. Tabulation ?4', 1a, ?7'', 4-?''', 2'''. Archeopyle not observed.

Figured material. Holotype: Loc. 3, 3 (2) at 99·0-31·9; Bearpaw Formation, Campanian, southern Alberta. Loc. 3, 3 (1) at 97·0-49·2. Loc. 3, 1 (1) at 103·0-36·7.

Dimensions. Holotype: Length 45.0 μ ; breadth 30.0 μ . Range: Length 34.0 (44.4) 57.0 μ ; breadth 25.0 (35.5) 41.0 μ . Twenty specimens measured, the number of specimens studied.

Description. Apical horn has a thickened structure which may or may not be solid, but invariably shows a suture apparently bisecting the horn. The antapical horns may be well developed or one may appear as a swelling. The tabulation variously developed and where present is delimited by raised sutures. One specimen seen with a complete tabulation. The cingulum, usually conspicuous and approximately three microns wide, may contain granular elements that appear aligned parallel to the longitudinal axis of the cyst. Plate 3" of the tabulation large and conspicuous. Range of variation within this species is not great. The specimen with the tabulation not typical for this species and so not chosen as the holotype.

Remarks. This species is similar to that of *L. tenella* Morgenroth 1966. His specimens, however, lack all trace of tabulation and are larger and more rhomboidal in shape. It is also similar to *Palaeoperidinium cretaceum* Pocock but differs in being smaller and in not having an endoblast. It has possible peridiniacean affinities.

Lejeunia tricuspis (Wetzel) comb. nov.

Plate 84, fig. 4

1933 *Peridinium tricuspis* Wetzel; 166, pl. 2, fig. 14.

The Bearpaw specimens compare well with those of Wetzel (1933). The author considers that *Lejeunia kozlowskii* Gorka 1963 is a junior synonym. Gorka (1963) figures both *L. kozlowskii* and *L. cf. tricuspis*. It appears that any difference between the two can be accommodated by specific variation. *L. tricuspis* has a geological range of Santonian-Maestrichtian, and its affinities may be peridiniacean.

Figured material. Loc. 13, 13 (1) at 99.0–29.9.

Dimensions. Range: Length 80.0 (104.3) 135.0 μ ; breadth 52.0 (73.8) 95.0 μ . Sixteen specimens measured, the number of specimens studied.

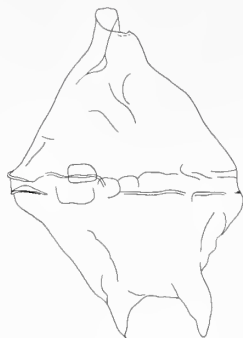
Lejeunia ampla sp. nov.

Plate 84, figs. 1, 7, text-fig. 8

Derivation of name. Latin *ampla*—meaning large, with reference to the overall size of this species.

Diagnosis. Proximate cyst, rhomboidal in shape, probably made up of autophragm only. Test granulate, scabrate and/or reticulate. No tabulation visible. Cingulum usually conspicuous, planar, approximately 5 microns wide, delimited by raised sutures. Single apical horn, distally oblate; two antapical horns one of which generally larger than the other. Archeopyle apical.

Figured material. Holotype: Loc. 3, 13 (1) at 95.8–37.0; Bearpaw Formation, Campanian, southern Alberta.



TEXT-FIG. 8. *Lejeunia ampla* sp. nov. Semidiagrammatic sketch of the holotype. $\times c. 300$.

Dimensions. Holotype: Length $149.0\ \mu$; breadth $108.0\ \mu$. Range: Length 70.0 (116.3) $154.0\ \mu$; breadth 68.0 (97.0) $108.0\ \mu$. Fifty specimens measured out of a studied population of eighty-nine.

Description. It is possible that a second wall layer, closely adpressed, is present. Only one or two specimens show an apical archeopyle. Norris (*pers. comm.*) has observed transapical archeopyles in specimens with the same gross morphology. The Bearpaw specimens appear to have had one or two antapical plates making up the operculum. The antapical horns distally evexate and one was seen to carry small spinules.

Remarks. This species differs from *L. tricuspis* in lacking the vertical striations, the acuminate antapical horns, and the coarse 'ornamentation'. Doubt is expressed in the generic assignment because of uncertainties in the nature of the archeopyle in this species and in the genus. The archeopyle as seen in the holotype is perfectly clear and does not appear to be of accidental origin. Evitt (*pers. comm.*) has commented on the resemblance of the small folds, often observed on the test of these cysts, to growth lines such as those exhibited by *Palaeoperidinium pyrophorum* (Ehrenberg). Its affinities are unknown.

Genus SPINIDINIUM Cookson and Eisenack 1962b

Type species. *Spinidinium styloniferum* Cookson and Eisenack 1962b; O.D.

Spinidinium is characterized by the possession of 'spines'. It is, however, morphologically similar to *Deflandrea* in that the genus is cavate and possesses an intercalary archeopyle. Wilson (1967) has placed certain spiny specimens in the genus *Deflandrea* and certainly a review of the situation is indicated as *Deflandrea* is presently defined to include only forms with smooth or granulate tests.

Spinidinium clavum sp. nov.

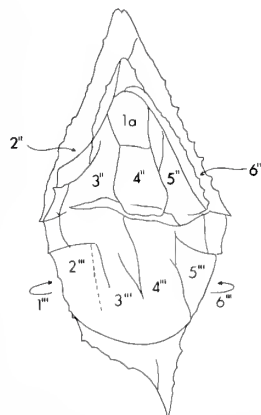
Plate 84, figs. 5, 6, 10, text-fig. 9

Derivation of name. Latin *clavum*—meaning spike, with reference to the development of short, acuminate processes along the sutural crests.

Diagnosis. Cavate cyst, fusiform in shape, made up of two wall layers closely adpressed except at the apex and antapex where pericoels may be evident. Test usually smooth with the presence of occasional discrete granules. Epittract slightly more conical than

the hypotract. Prominent apical horn, tapering with a bifid tip; antapical horns acuminate. Sutural ridges, up to $5\ \mu$ tall, carry short oblate and acuminate processes. Certain plate areas of the tabulation may be delimited due to sutural development. A tabulation ?4', 1a, ?7'', ?4c, 5-6''', ?2'''' indicated. Cingulum planar, sulcus conspicuous extending on to both the epitract and hypotract. Archeopyle indeterminate, but it is almost certain that loss of the conspicuous intercalary plate forms the archeopyle.

Description. Cavate cyst often appears proximate because of poor pericoel development. The apex appears to be made up of four apical plates which are separated by large sutural ridges, characteristic of this species. These ridges add to the prominence of the apex. The crests of the ridges carry small oblate and acuminate processes. The precingular plate series appears to consist of five to seven plates, of which plate 4'' is conspicuous and polygonal in shape; directly above this plate there is a single rectangular anterior intercalary plate. The cingulum is often the focus for folding and crumpling of the cyst. The post-cingular plate series appears to comprise five or six plates but only certain indeterminate plate boundaries were seen. The hypotract is more rounded than the epitract. The sutural crests are better developed on the epitract than on the hypotract. The range of variation of this species is seen in Plate 84. The most variable feature is the size of the endoblast in relation to periblast.



TEXT-FIG. 9. *Spinidinium clavum* sp. nov. Semi-diagrammatic sketch of the holotype. $\times c. 1000$.

Figured material. Holotype: Loc. 11, 1 (1) at 95.0-40.1; Bearpaw Formation, Campanian, southern Alberta. Loc. 5, 1 (2) at 94.7-38.0. Loc. 5, 1 (1) at 104.0-32.0.

Dimensions. Holotype: Length $51.0\ \mu$; breadth $29.0\ \mu$. Range: Length 40.0 (45.3) $60.0\ \mu$; breadth 20.0 (26.0) $35.0\ \mu$. Seventeen specimens observed.

Remarks. This species is characterized by the nature of the large sutural ridges. It is similar to *Palaeoperidinium caulleryi* Deflandre 1934 which Deflandre (1966) considers to be a member of the genus *Diconodinium*. It was not, however, formally combined (re Article 33 of I.C.B.N.). It has peridiniacean affinities with the deflandreoid lineage.

Cyst-Family MICRODINIACEAE Eisenack emend. Sarjeant and Downie 1966

Genus MICRODINIUM Cookson and Eisenack emend. Sarjeant 1966

Type species. *Microdinium ornatum* Cookson and Eisenack 1960; O.D.

Microdinium cf. *irregulare* Clarke and Verdier 1967

Plate 85, figs. 15, 16

1967 ?*Microdinium irregulare* Clarke and Verdier; 65-66, pl. 7, figs. 5-8, text-fig. 27.

Description. Proximate cyst, spheroidal to ovoidal in shape, composed of periphragm and endophragm. The periphragm makes up the large and conspicuous sutural crests.

Cyst microgranulate to granulate except for the crests which are smooth. Tabulation present. Cingulum 3–4 microns wide, planar or weakly helicoidal in nature. Epittract small in comparison to the hypotract, the tabulation difficult to decipher because of the granules and crests but plates 6''', 1p, 1'''' were observed. Epittractal details are especially difficult to see. The archeopyle apical of \bar{A} type, and probably formed by the loss of three or four apical plates (Evitt, *pers. comm.*).

Figured material. Loc. 11, 1 (2) at 100.0–43.3. Loc. 10, 4 (2) at 94.0–32.6.

Dimensions. Range: Length 24.0 (34.5) 39.0 μ ; breadth 26.0 (32.6) 38.0 μ . Thirty-six specimens observed.

Remarks. These specimens compare well with those described by Clarke and Verdier (1967). This species has a geological range Cenomanian–Santonian. It has gonyaulacacean affinities with the lithodinioid lineage.

Cyst-Family Uncertain Genus DINOGYMNium Evitt, Clarke and Verdier 1967

Type species. *Dinogymnium acuminatum* Evitt, Clarke and Verdier 1967; O.D.

Dinogymnium cf. *albertii* Clarke and Verdier 1967

Plate 85, fig. 18

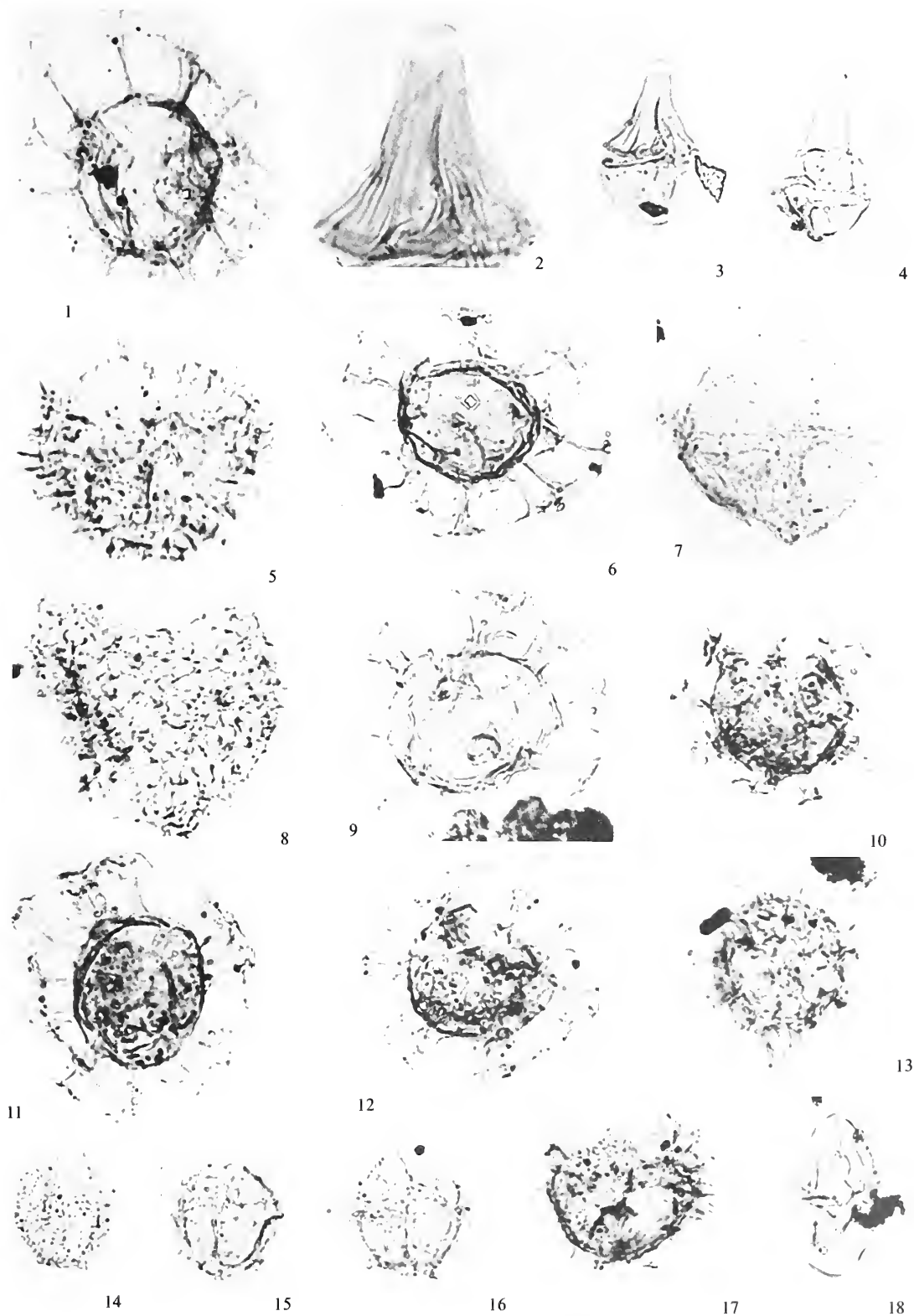
1967 ?*Dinogymnium albertii* Clarke and Verdier; 33, pl. 17, figs. 3, 4, text-fig. 13.

Description. Proximate cyst, subspheroidal to ovoidal in shape, the epittract more conical than the hypotract, made up of two wall layers closely adpressed. Test carries a number of longitudinal grooves, that are commoner on the epittract than on the hypotract. In addition, the test perforated by many punctae (wall canals). Tabulation not present except for a very conspicuous deep cingulum which is 4 microns wide,

EXPLANATION OF PLATE 85

All figures at a magnification of $\times 600$ unless otherwise stated.

Fig. 1. *Hystrichosphaeridium dowlingsii* sp. nov., ventral view, holotype, showing the archeopyle and the nature of the processes. Fig. 2. *Dinogymnium longicornis* (Vozzhennikova) comb. nov., detail of the apex. $\times c. 1800$. Fig. 3. *Dinogymnium longicornis* (Vozzhennikova) comb. nov., ventral view of a specimen with a low cingulum index. Fig. 4. *Dinogymnium longicornis* (Vozzhennikova) comb. nov., lateral view of a specimen with a high cingulum index. Fig. 5. *Canningia senonica* Clarke and Verdier, dorsal view. Fig. 6. *Hystrichosphaeridium* cf. *arborispinum* Davey and Williams, lateral view. Fig. 7. ?*Uvatodinium* cf. *nasutum* Vozzhennikova, dorsal view. Fig. 8. *Canningia senonica* Clarke and Verdier, lateral view. Fig. 9. *Hystrichosphaeridium salpingophorum* (Deflandre) emend. Davey and Williams, lateral view. Fig. 10. *Hystrichosphaeridium tubiferum* var. *brevispinum* Davey and Williams, lateral view. Fig. 11. *Hystrichosphaeridium* cf. *arborispinum* Davey and Williams, ventral view. Fig. 12. *Hystrichosphaeridium salpingophorum* (Deflandre) emend. Davey and Williams, lateral view. Fig. 13. ?*Coronifera oceanica* Cookson and Eisenack, lateral view. Fig. 14. ?*Membranosphaera* cf. *maastrichtica* Samoylovich ex. Norris and Sarjeant emend. Drugg, lateral view. Fig. 15. *Microdinium* cf. *irregulare* Clarke and Verdier, lateral view. Fig. 16. *Microdinium* cf. *irregulare* Clarke and Verdier, lateral view showing well-developed smooth sutural crests. Fig. 17. *Cleistosphaeridium* sp. A, lateral view. Fig. 18. *Dinogymnium* cf. *albertii* Clarke and Verdier, lateral view.



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and takes the form of a laevorotatory helicoid. The test is often crumpled along this feature. Displacement approximately equal to half the width of the cingulum. Sulcus also present but only on the hypotract. Archeopyle apical, regarded as miscellaneous by Evitt (1967), formed by loss of a ? single plate at the very tip of the epittract.

Figured specimen. Loc. 9, 37 (1) at 105.7–42.0.

Dimensions. Range: Length 40.0 (41.3) 42.0 μ ; breadth 20.0 (22.0) 25.0 μ , cingulum index 50.0 (52.3) 55.0. Three specimens observed.

Remarks. This species is compared to *D. albertii* Clarke and Verdier 1967 by virtue of the presence of punctae and in its general form, but it is smaller in size. It was previously recorded from the Santonian by Clarke and Verdier 1967. In general morphology the genus closely resembles the modern genus *Gymnodinium*, with which it has often been confused. The affinities of this cyst are as yet unknown.

Dinogymnium longicornis (Vozzhennikova) nov. comb.

Plate 85, figs. 2–4

1967 *Gymnodinium longicornis* Vozzhennikova; 46, pl. 1, fig. 8, pl. 3, fig. 6, pl. 4, figs. 6a, 6b, 7.

Description. Proximate cyst, ovoidal to markedly elongate, made up of two closely adpressed wall layers. Test carries some longitudinal grooves and a fine micro-punctuation which is better developed in some specimens than others. The epittract conical to very elongate, drawn out into a long apical horn. The hypotract always hemispheroidal. A conspicuous cingulum always present, approximately 2 microns wide, in the form of a laevorotatory helicoid which is displaced by up to twice its width. A sulcus is present on the hypotract only. Faint sutural ridges are sometimes present, delimiting a possible tabulation; a possible reflected plate 1p was observed in one specimen. Archeopyle apical, typical for the genus.

Figured material. Loc. 9, 20 (3) at 102.0–29.3. Loc. 9, 24 (3) at 107.9–36.3.

Dimensions. Range: Length 39.0 (49.4) 59.0 μ ; breadth 19.0 (27.3) 33.0 μ , cingulum index 58.0 (65.75) 75.0. Eleven specimens studied.

Remarks. This species is very similar to that figured by Vozzhennikova (1967); there can be no doubt that the species belongs to the genus *Dinogymnium* as in Vozzhennikova's figures the archeopyle is perfectly evident. The specimens from the Bearpaw Formation seem more variable than those of Vozzhennikova (1967) and are generally smaller. The Russian specimens are Senonian in age and were recovered from western Siberia. Its affinities are unknown.

Cyst-Family FROMEACEAE Sarjeant and Downie 1966

Genus MEMBRANOSPHERA Samoylovich ex. Norris and Sarjeant emend.
Drugg 1967

Type species. *Membranosphera maastrichtica* Samoylovich ex. Norris and Sarjeant, 1965; S.D.

?*Membranosphaera* cf. *maastrichtica* Samoylovich ex. Norris and Sarjeant emend.
Drugg 1967

Plate 85, fig. 14

- 1961 ?*Membranosphaera maastrichtica* Samoylovich (in Samoylovich *et al.* 252, pl. 83, figs. 1, 2.
1965 ?*Membranosphaera maastrichtica* Samoylovich ex. Norris and Sarjeant; 40.
1967 ?*Membranosphaera maastrichtica* Samoylovich ex. Norris and Sarjeant emend. Drugg;
29–30, pl. 5, figs. 12, 13.

Description. Proximate cyst, spheroidal to ovoidal in shape, composed of endophragm and periphragm. The endophragm makes up small cylindrical capitate processes that appear to support an outer membraneous periphragm. A faint trace of the cingulum observed; it appears planar, approximately three microns in width and is delimited by areas devoid of endophragmal processes. No other tabulation discernible. The archeopyle apical, possibly of a type formed by loss of a single apical plate; the sulcal notch was observed.

Figured material. Loc. 10, 5 (3) at 103·0–34·4.

Dimensions. Range: Length 28·0 (30·0) 32·0 μ ; breadth 27·0 (27·5) 28·0 μ . Two specimens observed.

Remarks. The Bearpaw specimens differ from those of Drugg (1967) in possessing a faint cingulum and a smaller apical archeopyle. This species had a previous geological range of Maestrichtian–Danian (Drugg 1967). Its affinities are unknown.

Cyst-Family CANNINGIACEAE Sarjeant and Downie 1966
Genus CANNINGIA Cookson and Eisenack 1960

Type species. *Canningia reticulata* Cookson and Eisenack 1960; O.D.

Canningia senonica Clarke and Verdier 1967

Plate 85, figs. 5, 8

- 1967 *Canningia senonica* Clarke and Verdier; 20, 21, pl. 1, figs. 12–14, text-fig. 7.

It was noticed in the specimens attributed to this species that there was considerable variation with regard to process development and the apparent reticulation. This species was previously reported from the Senonian of the Isle of Wight, England, by Clarke and Verdier (1967). It has gonyaulacacean affinities with the lithodinioid lineage.

Figured material. Loc. 11, 7 (3) at 103·0–30·0. Loc. 9, 39 (1) at 109·0–28·2.

Dimensions. Range: Length 36·0 (48·0) 67·0 μ ; breadth 40·0 (51·5) 63·0 μ , the processes range in length from 2·0–8·0 μ . Four specimens observed.

Cyst-Family PYXIDIELLACEAE Sarjeant and Downie 1966
Genus UVATODINIUM Vozzhennikova 1963

Type species. *Uvatodinium nasutum* Vozzhennikova 1963; O.D.

?Uvatodinium cf. nasutum Vozzhennikova 1963

Plate 85, fig. 7

1963 *?Uvatodinium nasutum* Vozzhennikova; 182, figs. 13a, 13b.

Description. Proximate cyst, subspheroidal in shape, composed of periphragm and endophragm closely adpressed; the former makes up the 'ornamentation'. Test granulate. Epitract bears an apical horn, which is distally evexate, and a distinct 'shoulder'. The hypotract carries a slight antapical boss. The cingulum conspicuous, delimited by raised sutures, takes the form of a laevorotatory helicoid and displaced by half the width of the cingulum which is four to five microns wide. A sulcus present, delimited by raised sutures, and confined to the hypotract. No other tabulation present. Archeopyle intercalary of the I type.

Figured material. Loc. 11, 7 (1) at 99·0–29·6.

Dimensions. Range: Length 61·0 (68·0) 75·0 μ ; breadth 54·0 (57·6) 60·0 μ . Three specimens observed.

Remarks. These specimens compare quite well with those illustrated by Vozzhennikova (1967) but lack the coarse reticulation; although in pl. 8, fig. 4 of Vozzhennikova (1967) the reticulation is not at all obvious. This species has previously been recorded from the Palaeocene (Vozzhennikova 1967). Its affinities are unknown.

Cyst-Family HYSTRICHOSPHAERIDIACEAE Evitt emend. Sarjeant and Downie 1966

Genus HYSTRICHOSPHAERIDIUM Deflandre emend. Davey and Williams 1966b

Type species. *Hystrichosphaeridium tubiferum* (Ehrenberg) Deflandre 1937; O.D.

Hystrichosphaeridium cf. arborispinum Davey and Williams 1966b

Plate 85, figs. 6, 11

1966b *?Hystrichosphaeridium arborispinum* Davey and Williams; 61, pl. 9, figs. 5, 10.

Description. Chorate cyst, subspheroidal to ovoidal in shape, made up of both periphragm and endophragm, the former making up the processes. Cyst smooth to microgranulate. The processes intratabular and reflect the tabulation 6'', 6c, 5''', 1''''; they are hollow, slender to latispinous, erect, cylindrical, and distally flared. The distal extremities recurved, digitate to serrate. In many specimens the processes appear fibrous. Additional cylindrical recurved and digitate sutural processes present in many specimens. The archeopyle apical of the \bar{A} type.

Figured material. Loc. 11, 1 (3) at 93·0–30·5. Loc. 9, 39 (2) at 107·0–33·8.

Dimensions. Range: Long axis of cyst 29·0 (40·0) 52·0 μ ; short axis of cyst 30·0 (38·35) 55·0 μ , processes range in length from 11 to 25 μ . Twenty specimens observed.

Remarks. This species is fairly common in the Bearpaw assemblages and may be recognized by the character of its processes. It had a geological range Lower Barremian–Middle Barremian. Its affinities are gonyaulacacean in the hystrichosphaeridioid lineage.

Hystrichosphaeridium dowlingii sp. nov.

Plate 85, fig. 1, text-fig. 10

Derivation of name. Named in honour of D. B. Dowling, one of the first geologists to work in southern Alberta.

Diagnosis. Chorate cyst, spheroidal in shape, made up of periphragm and endophragm. Test microgranulate. Tabulation 6'', 6c, 6''', 1-2p, 1'''. Processes hollow slender to latispinous, erect to curved, cylindrical, distally flared and fenestrate. Archeopyle of the \bar{A} type.



TEXT-FIG. 10. *Hystrichosphaeridium dowlingii* sp. nov.
Semidiagrammatic sketch of the holotype. $\times c. 1300$.

Figured material. Holotype: Loc. 9, 39 (2), at 106·0–33·9; Bearpaw Formation, Campanian, southern Alberta.

Dimensions. Holotype: Long axis of cyst 44·0 μ ; short axis of cyst 38·0 μ , processes range in length from 15 to 24 μ . Range: Long axis of cyst 25·0 (34·4) 46·0 μ ; short axis of cyst 29·0 (34·0) 54·0 μ , processes range in length from 10 to 28 μ . Twelve specimens measured, the number of specimens studied.

Description. The periphragm makes up the processes which do not appear to connect to the interior of the cyst. Test 'ornament' does not extend on to the process shafts. The sulcal area devoid of all processes except for a group of two sulcal processes. A sulcal notch may also be seen in some specimens.

Remarks. This species is easily distinguishable from *H. cf. arborispinum* by the nature of the processes, i.e. fenestrate nature and lack of 'ornamentation' on the processes shafts. The test 'ornamentation' is also much coarser than that of *H. cf. arborispinum*. Its affinities are gonyaulacacean with the hystrichosphaeridioid lineage.

Hystrichosphaeridium tubiferum var. *brevispinum* Davey and Williams 1966b

Plate 85, fig. 10

1966b *Hystrichosphaeridium tubiferum* var. *brevispinum* Davey and Williams; 58, pl. 10, fig. 10.

This variety compares well with those specimens described by Davey and Williams (1966b). The Bearpaw specimens were, however, smaller in size with a slightly more variable process habit. The variety is characterized by process length, and had a range of Eocene (Davey and Williams 1966b). Its affinities are gonyaulacacean with the hystrichosphaeridioid lineage.

Figured material. Loc. 9, 39 (1) at 101·0–31·3.

Dimensions. Range: Long axis of cyst 25·0 (31·2) 38·0 μ ; short axis of cyst 25·0 (30·6) 38·0 μ , processes range in length 6 to 15 μ . Twenty specimens observed.

Hystrichosphaeridium salpingophorum (Deflandre) Davey and Williams 1966b

Plate 85, figs. 9, 12

1935 *Hystrichosphaera salpingophora* Deflandre; 232, pl. 9, fig. 1.1966b *Hystrichosphaeridium salpingophorum* (Deflandre) emend. Davey and Williams; 61, 62, pl. 10, fig. 6.

This species compares well with those specimens figured by Davey and Williams (1966b). There is an obvious morphological overlap with *H. tubiferum* var. *brevispinum* but usually the two species can be recognized. The species has a geological range of Upper Jurassic–Lower Eocene. Its affinities are gonyaulacacean with the hystrichosphaeridioid lineage.

Figured material. Loc. 9, 39 (2) at 99·0–36·0. Loc. 13, 5 (3) at 92·0–40·6.

Dimensions. Range: Length of long axis 31·0 (38·8) 44·0 μ ; length of short axis 29·0 (35·75) 48·0 μ , processes range in length from 10 to 18 μ . Nine specimens observed.

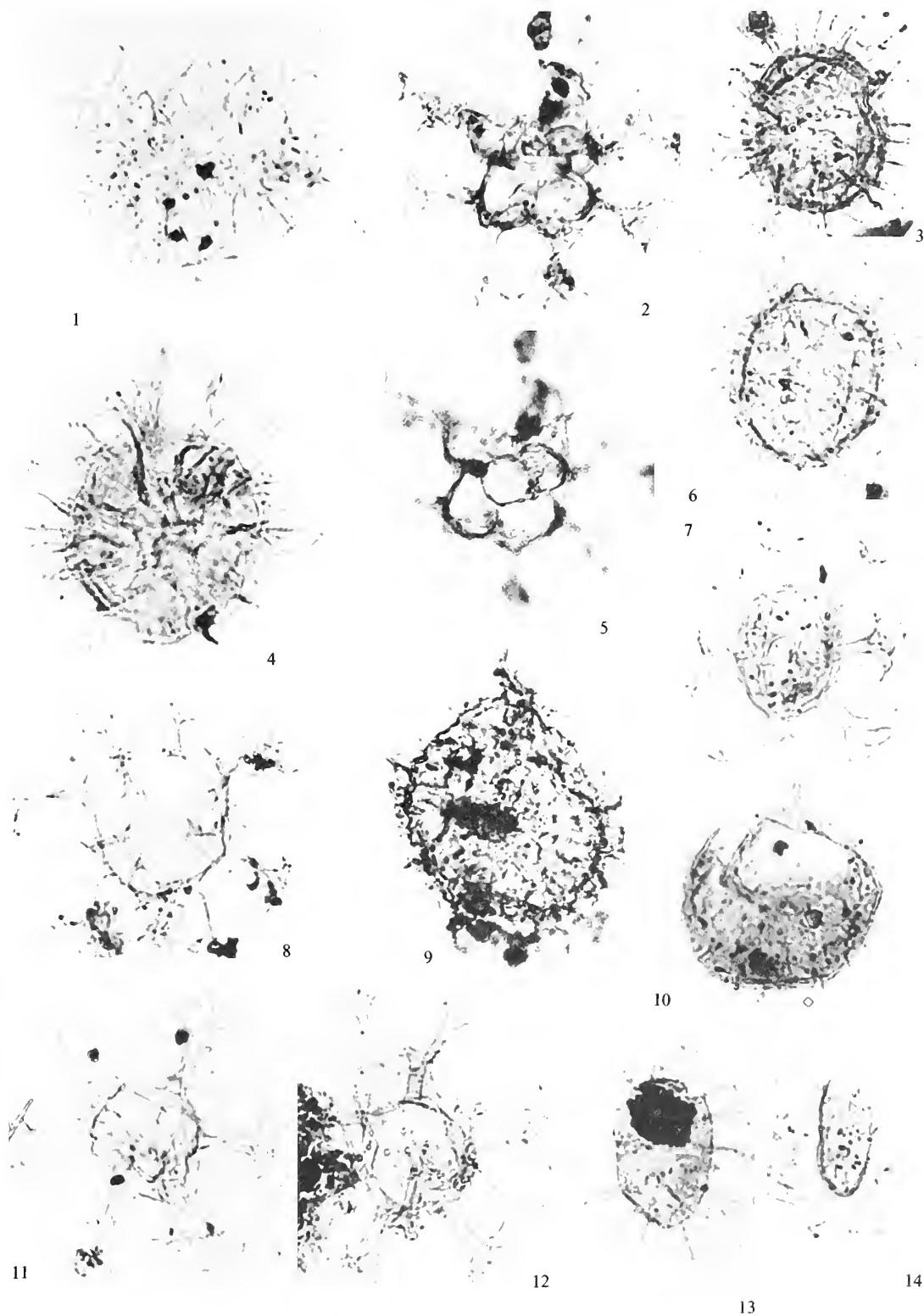
Genus CLEISTOSPHAERIDIUM Davey, Downie, Sarjeant and Williams 1966

Type species. *Cleistosphaeridium diversispinosum* Davey, Downie, Sarjeant and Williams 1966; O.D.

EXPLANATION OF PLATE 86

All figures at a magnification of $\times 600$ unless otherwise stated.

Fig. 1. *Cleistosphaeridium diversispinosum* Davey et al., lateral view. Fig. 2. Forma A, lateral view, showing nature of the archeopyle. Fig. 3. *Polysphaeridium subtile* Davey and Williams, orientation unknown. Fig. 4. *Exochosphaeridium pseudohystrichodinium* (Deflandre) emend. Davey, lateral view. Fig. 5. Forma A, lateral view, showing globular central body. Fig. 6. *Polysphaeridium subtile* Davey and Williams, ?lateral view showing apical boss. Fig. 7. *Oligosphaeridium anthophorum* (Cookson and Eisenack) Davey, lateral view. Fig. 8. *Oligosphaeridium anthophorum* (Cookson and Eisenack) Davey, ventral view. Fig. 9. *Exochosphaeridium* sp. A, lateral view. Fig. 10. *Exochosphaeridium* cf. *phragmites* Davey et al., dorsal view. Fig. 11. *Oligosphaeridium pulcherrimum* (Deflandre and Cookson) Davey and Williams, lateral view. Fig. 12. *Oligosphaeridium pulcherrimum* (Deflandre and Cookson) Davey and Williams, lateral view. Fig. 13. *Tanyosphaeridium variecalamum* Davey and Williams, lateral view of specimen with many processes per plate area. Fig. 14. *Tanyosphaeridium variecalamum* Davey and Williams, lateral view of specimen with few processes per plate area.



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Cleistosphaeridium diversispinosum Davey, Downie, Sarjeant, and Williams 1966

Plate 86, fig. 1

1966 *Cleistosphaeridium diversispinosum* Davey *et al.*; 167, pl. 10, fig. 7.

Considerably more specific variation than that observed by Davey *et al.* (1966) is present within this species. The processes are variable in thickness, sinuosity, length, and in the structural diversity of their extremities. This species was previously recorded from the Eocene. Its affinities are unknown.

Figured material. Loc. 10, 5 (1) at 95·0–43·4.

Dimensions. Range: Length 35·0 (48·75) 57·0 μ ; breadth 43·0 (52·25) 67·0 μ , processes range in length from 5 to 19 μ . Nine specimens observed.

Cleistosphaeridium sp. A

Plate 85, fig. 17

Description. Chorate cyst, subspheroidal in shape, made up of two wall layers; the periphragm makes up the processes. The test carries granules but no trace of tabulation could be discerned, as the processes appear randomly dispersed. The processes slender to latispinous, curved to sinuous, cylindrical to tapering. Most processes end in an equal distal bifurcation but others are acuminate and oblate. Archeopyle apical, of the \bar{A} type.

Figured material. Loc. 3, 3 (1) at 98·0–46·5.

Dimensions. Range: Length 35·0 (39·0) 43·0 μ ; breadth 39·0 (40·5) 42·0 μ , processes range in length from 8 to 11 μ . Two specimens observed.

Remarks. This species is similar to ?*Cleistosphaeridium flexuosum* Davey *et al.* 1966 but differs in process length and in the nature of the process extremities. Its affinities are unknown.

Genus CORONIFERA Cookson and Eisenack emend. Davey 1969a

Type species. *Coronifera oceanica* Cookson and Eisenack 1958; O.D.

? *Coronifera oceanica* Cookson and Eisenack 1958

Plate 85, fig. 13

1958 ?*Coronifera oceanica* Cookson and Eisenack; 45, pl. 12, figs. 5, 6.

Description. Proximate cyst, spheroidal in shape. Test composed of two wall layers closely adpressed of which the periphragm alone makes up the processes. Cyst wall microgranulate and covered by numerous processes, seemingly at random. The processes do not connect to the interior of the cyst and are slender, curved, cylindrical to tapering, and distally acuminate. No tabulation could be discerned. The cyst carries a single large antapical process which is latispinous, erect, distally open with

an entire or denticulate margin. This process is very characteristic of the species and genus. No archeopyle observed.

Figured material. Loc. 1, 28 (1) at 106·7–46·0.

Dimensions. Range: Length 33·0 (37·5) 42·0 μ ; breadth 31·0 (40·5) 50·0 μ , the processes range in length from 4–10 μ . Two specimens observed.

Remarks. The specimens under consideration differ from those of Davey (1969a) in lacking any kind of sutural ridges or clear apical processes. This is probably a consequence of specific variation. Lack of the presence of an archeopyle casts some doubt on the identification of this species. The presence of an \bar{A} archeopyle would suggest that these specimens be placed in the genus *Diphyes* Cookson 1965. *C. oceanica* had a geological range Albian–Cenomanian. It probably has gonyaulacacean affinities by virtue of the single antapical process, suggesting the possession of a single antapical plate. Millioud (1969) reported the presence of a precingular archeopyle in a new species of *Coronifera* from the Upper Hauterivian of Angles, SE. France, indicating that *Coronifera* should be attributed to the hystrichodinioid lineage.

Forma A

Plate 86, figs. 2, 5, text-fig. 11

Description. Chorate cyst, ovoidal to elongate in shape. Test consists of a thick (1·0–1·5 microns) endophragm and a thin periphragm. Test smooth to microgranulate. Endoblast appears made up of discrete chambers giving the cyst a globate appearance. Two whorls of lobes present separated by a cingular groove in the form of a laevorotatory helicoid. Processes intratabular, reflecting a possible tabulation of 7'' and 5 or 6'''. They do not connect to the interior of the cyst and are constructed of periphragm. No antapical processes present. Archeopyle apical with an attached operculum, possibly of the $\bar{A}a$ type.



TEXT-FIG. 11. Forma A. Semidiagrammatic sketch. $\times c. 1200$.

Figured material. Loc. 1, 36 (3) at 107·2–35·9.

Dimensions. Range: Length 32·0 (37·5) 43·0 μ ; breadth 25·0 (29·5) 34·0 μ , processes range in length from 20 to 25 μ . Two specimens observed.

Remarks. These cysts are peculiar in the structure of the central body which appears to be made up of discrete chambers. Two whorls are present, one at either side of the cingulum. A single chamber is centrally placed on the ventral surface of the cyst and it may be equivalent to reflected plate 7''. The laevorotatory helicoidal cingulum divides the two whorls. It is of interest to note that no antapical process is present.

There is, however, a possible accessory sulcul process. Also of interest is the opening in reflected plate 2'''. It appears that the archeopyle has been formed by partial loss of the apical plate series with a single opercular piece remaining. It was difficult to observe the exact relationship of this operculum ? to the archeopyle. Evitt (*pers. comm.*) considers that the lobate nature of this cyst is due to deformation as the result of the growth of pyrite sphaerules. Its affinities are unknown.

Genus OLIGOSPHAERIDIUM Davey and Williams 1966b

Type species. Oligosphaeridium complex (White) Davey and Williams 1966b; O.D.

Oligosphaeridium anthophorum (Cookson and Eisenack) Davey 1969a

Plate 86, figs. 7, 8

1958 *Hystrichosphaeridium anthophorum* Cookson and Eisenack; 43, 44, pl. 11, figs. 12, 13.

1969a *Oligosphaeridium anthophorum* (Cookson and Eisenack) Davey; 147, 148, pl. 5, figs. 1-3.

These specimens compare well with those of Cookson and Eisenack (1958) except that they are smaller and the processes appear to be a little more slender. The species had a previously described geological range Oxfordian-Albian, and has gonyaulacacean affinities with the hystrichosphaeridioid lineage.

Figured material. Loc. 3, 7 (3) at 105.7-39.7. Loc. 9, 37 (1) at 92.0-28.2.

Dimensions. Range: Length of long axis 24.0 (33.3) 45.0 μ ; length of short axis 21.0 (31.8) 43.0 μ , the processes range in length from 12 to 34 μ . Sixteen specimens observed.

Oligosphaeridium pulcherrimum (Deflandre and Cookson) Davey and Williams 1966b

Plate 86, figs. 11, 12

1955 *Hystrichosphaeridium pulcherrimum* Deflandre and Cookson; 270, 271, pl. 1, fig. 8, text-figs. 21, 22.

1966b *Oligosphaeridium pulcherrimum* (Deflandre and Cookson) Davey and Williams; 75, 76, pl. 10, fig. 9, pl. 11, fig. 5.

These specimens agree closely to those of Deflandre and Cookson (1955) except in size; the Bearpaw material being smaller. The geological range of this species is Valanginian-Lower Eocene. It has gonyaulacacean affinities with the hystrichosphaeridioid lineage.

Figured material. Loc. 11, 9 (1) at 103.0-44.6. Loc. 9, 39 (2) at 101-31.9.

Dimensions. Range: Length of long axis 20.0 (34.9) 43.0 μ ; length of short axis 23.0 (32.9) 40.0 μ , processes range in length from 9 to 37 μ . Fifty specimens measured, from a studied population of seventy-four.

Genus POLYSPHAERIDIUM Davey and Williams 1966b

Type species. Polysphaeridium subtile Davey and Williams 1966b; O.D.

Polysphaeridium subtile Davey and Williams 1966b

Plate 86, figs. 3, 6

1966b *Polysphaeridium subtile* Davey and Williams; 92, pl. 11, fig. 1.

These specimens compare well with those of Davey and Williams (1966b) except in the morphology of the distal tip of the processes; those of Davey and Williams (1966b) are more serrate. There is, however, a certain amount of variability in the Bearpaw specimens suggesting that these morphological variations may all be encompassed in the concept of this species. *P. subtile* has a geological range of Coniacian–Middle Miocene, and has gonyaulacacean affinities probably with the hystrichosphaeridioid lineage.

Figured material. Loc. 3, 7 (2) at 107·2–42·6. Loc. 9, 39 (2) at 97·0–32·3.

Dimensions. Range: Length of long axis 22·0 (38·5) 50·0 μ ; length of short axis 30·0 (35·9) 47·0 μ , processes range in length from 5 to 14 μ . Twenty specimens observed.

Genus TANYOSPHERIDIUM Davey and Williams 1966b

Type species. *Tanyosphaeridium variecalamum* Davey and Williams 1966b; O.D.

Tanyosphaeridium variecalamum Davey and Williams 1966b

Plate 86, figs. 13, 14

1966b *Tanyosphaeridium variecalamum* Davey and Williams; 98, 99, pl. 6, fig. 7, text-fig. 20.

A tentative tabulation from specimens where the processes appear to be restricted to one per plate area is 6'', 6c, 6–7''', 1p, 1'''''. These specimens compare well in all respects to those figured by Davey and Williams (1966b). This species had a previously recorded geological range of Albian–Cenomanian. The possession of a single reflected antipical plate suggests a gonyaulacacean affinity for this cyst, probably with the hystrichosphaeridioid lineage.

Figured material. Loc. 9, 39 (3) at 106·0–38·0, and 109·0–40·9.

Dimensions. Range: Length 25·0 (31·4) 37·0 μ ; breadth 15·0 (22·3) 42·0 μ , length of processes ranges from 6 to 13 μ . Seven specimens observed.

Cyst-Family EXOCHOSPHAERIDIACEAE Sarjeant and Downie emend. Davey 1969c

Genus EXOCHOSPHAERIDIUM Davey, Downie, Sarjeant and Williams 1966

Type species. *Exochosphaeridium phragmites* Davey, Downie, Sarjeant, and Williams 1966; O.D.

Exochosphaeridium cf. *phragmites* Davey, Downie, Sarjeant, and Williams 1966

Plate 86, fig. 10

1966 *Exochosphaeridium phragmites* Davey, Downie, Sarjeant, and Williams; 165, 166, pl. 2, figs. 8–10.

Description. Chorate cyst, subspheroidal in shape, made up of periphragm and endophragm closely adpressed; the former makes up the processes. Test granulate.

A large apical process present and is one-sixth to one-fifth the length of the cyst, carries granules, branched, and distally acuminate. The other processes appear randomly distributed on the test and are slender, solid, tapering, and distally acuminate. No tabulation seen. The archeopyle precingular of the P or 2P type.

Figured material. Loc. 9, 39 (3) at 106·0–35·5.

Dimensions. Range: Length 52·0 (62·0) 84·0 μ ; breadth 43·0 (50·3) 63·0 μ , processes vary in length from 2 to 8 μ . Six specimens observed.

Remarks. Except in lacking the pitted nature of the central body and possessing smaller processes, the Bearpaw specimens compare favourably with those of Davey *et al.* (1966). This species had a previously recorded range of Albian–Cenomanian and has possibly gonyaulacacean affinities in the apteodinioid lineage.

Exochosphaeridium pseudohystrichodinium (Deflandre) emend. Davey 1969a

Plate 86, fig. 4

1937 *Hystrichosphaeridium pseudohystrichodinium* Deflandre; 73, pl. 15, figs. 3, 4.

1969a *Exochosphaeridium pseudohystrichodinium* (Deflandre) emend. Davey; 163, 164, pl. 11, figs. 4, 5.

These specimens compare well with those of Davey (1969a) except for the detail of the pitted test. All specimens attributed to this species were granulate. The possession of a slight cingulum in some suggests that this species should be transferred to *Trichodinium* Eisenack and Cookson 1960 but as this is the exception rather than the rule it is assigned as above. It may, however, prove necessary in the future to treat *Exochosphaeridium* as a junior synonym of *Trichodinium*. This species has a geological range of Cenomanian–Eocene, and has possibly gonyaulacacean affinities with the apteodinioid lineage.

Figured material. Loc. 11, 5 (2) at 110·0–31·7.

Dimensions. Range: Length 53·0 (60·1) 71·0 μ ; breadth 44·0 (53·3) 69·0 μ , processes range in length from 10 to 20 μ . Six specimens observed.

Exochosphaeridium sp. A

Plate 86, fig. 9

Description. Chorate cyst, subspheroidal in shape, made up of periphragm and endophragm closely adpressed; the former making up the processes. Test smooth. The apical process large, up to one-fifth of the cyst length and branched. The processes solid to membranous, cylindrical, erect to curved and distally oblate to bifurcate. In plan the membranous processes give a reticulate pattern to the cyst surface. Tabulation not observed nor the archeopyle.

Figured material. Loc. 5, 2 (1) at 101·0–33·6.

Dimensions. Range: Length 50·0 (62·8) 98·0 μ ; breadth 43·0 (49·8) 60·0 μ , processes range in length from 5 to 10 μ . Five specimens observed.

Remarks. These specimens are unlike all other previously described species of *Exochosphaeridium* but the scarcity of specimens precludes the erection of a new

species. The distinguishing feature is the apparent reticulate pattern on the cyst surface. It has possibly gonyaulacacean affinities with the apteodinioid lineage.

Cyst-Family AREOLIGERACEAE Evitt emend. Sarjeant and Downie 1966

Genus CYCLONEPHELIUM Deflandre and Cookson emend. Cookson and Eisenack 1962

Type species. Cyclonephelium compactum Deflandre and Cookson 1955; O.D.

The original diagnosis of this genus was emended by Cookson and Eisenack (1962) and later by Williams and Downie (1966) to correct the interpretation of cyst orientation and to describe fully the range of process structure. The later emendation of Williams and Downie (1966) is nearly word for word the same as that of Cookson and Eisenack (1962).

Cyclonephelium distinctum Deflandre and Cookson 1955

Plate 87, figs. 1, 4

1955 *Cyclonephelium distinctum* Deflandre and Cookson; 285, 286, pl. 2, fig. 14, text-figs. 47, 48.

This species is recorded for the first time from Campanian rocks. Its previously recorded range being Hauterivian–Santonian. A large degree of process variation is observed for this species. *C. distinctum* is characterized by the isolated nature of the process. *C. compactum* Deflandre and Cookson 1955 is very similar except the processes are lamella-like. *C. distinctum* has gonyaulacacean affinities with the areoligeroid lineage.

Figured material. Loc. 13, 5 (1) at 97·0–43·3. Loc. 10, 3 (1) at 108·0–34·6.

Dimensions. Range: Length 37·0 (48·9) 84·0 μ ; breadth 39·0 (51·9) 87·0 μ , processes range in length from 2 to 18 μ . Thirty-eight specimens observed.

Cyst-Family SPINIFERITACEAE Sarjeant 1970

Genus SPINIFERITES Mantell ex Loeblich and Loeblich 1966

Type species. Spiniferites ramosus (Ehrenberg) Mantell 1854; S.D.

Spiniferites ramosus var. *ramosus* (Davey and Williams) Sarjeant 1970

Plate 87, fig. 7

1966a *Hystrichosphaera ramosa* var. *ramosa* Davey and Williams; 33, 34, pl. 1, figs. 1, 6, pl. 3, fig. 1, text-fig. 8.

This variety has a known geological range of Middle Barremian–Ypresian. It has gonyaulacacean affinities with the gonyaulacoid lineage.

Figured material. Loc. 9, 39 (1) at 99·0–38·2.

Dimensions. Range: Length 33·0 (39·2) 46·0 μ ; breadth 22·0 (30·3) 35·0 μ , processes range in length from 6 to 18 μ . Thirteen specimens observed.

Spiniferites ramosus var. *multibrevis* (Davey and Williams) Sarjeant 1970

Plate 87, fig. 3

1966a *Hystrichosphaera ramosa* var. *multibrevis* Davey and Williams; 35-37, pl. 1, fig. 4, pl. 4, fig. 6, text-fig. 9.

This variety compares well with those figured by Davey and Williams (1966a). It is characterized by its short gonial and sutural processes; it has a geological range from Hauterivian-Eocene. Its affinities are gonyaulacacean with the gonyaulacoid lineage.

Figured specimen. Loc. 11, 1 (1) at 103.0-32.4.

Dimensions. Range: Length 20.0 (33.9) 42.0 μ ; breadth 18.0 (26.75) 35.0 μ , processes range in length from 3 to 12 μ . Twenty specimens observed.

Spiniferites ramosus var. *granosus* (Davey and Williams) Sarjeant 1970

Plate 87, fig. 8

1966a *Hystrichosphaera ramosa* var. *granosa* Davey and Williams; 35, pl. 4, fig. 9.

These specimens compare well with those of Davey and Williams (1966a) except in differences of process morphology probably due to specific variability. This variety had previously been recorded only from the Eocene. Its affinities are gonyaulacacean with the gonyaulacoid lineage.

Figured material. Loc. 3, 3 (3) at 96.8-53.5.

Dimensions. Range: Length 39.0 (43.25) 46.0 μ ; breadth 32.0 (34.5) 38.0 μ , processes range in length from 9 to 19 μ . Five specimens observed.

Spiniferites cf. *porosus* (Manum and Cookson) comb. nov.

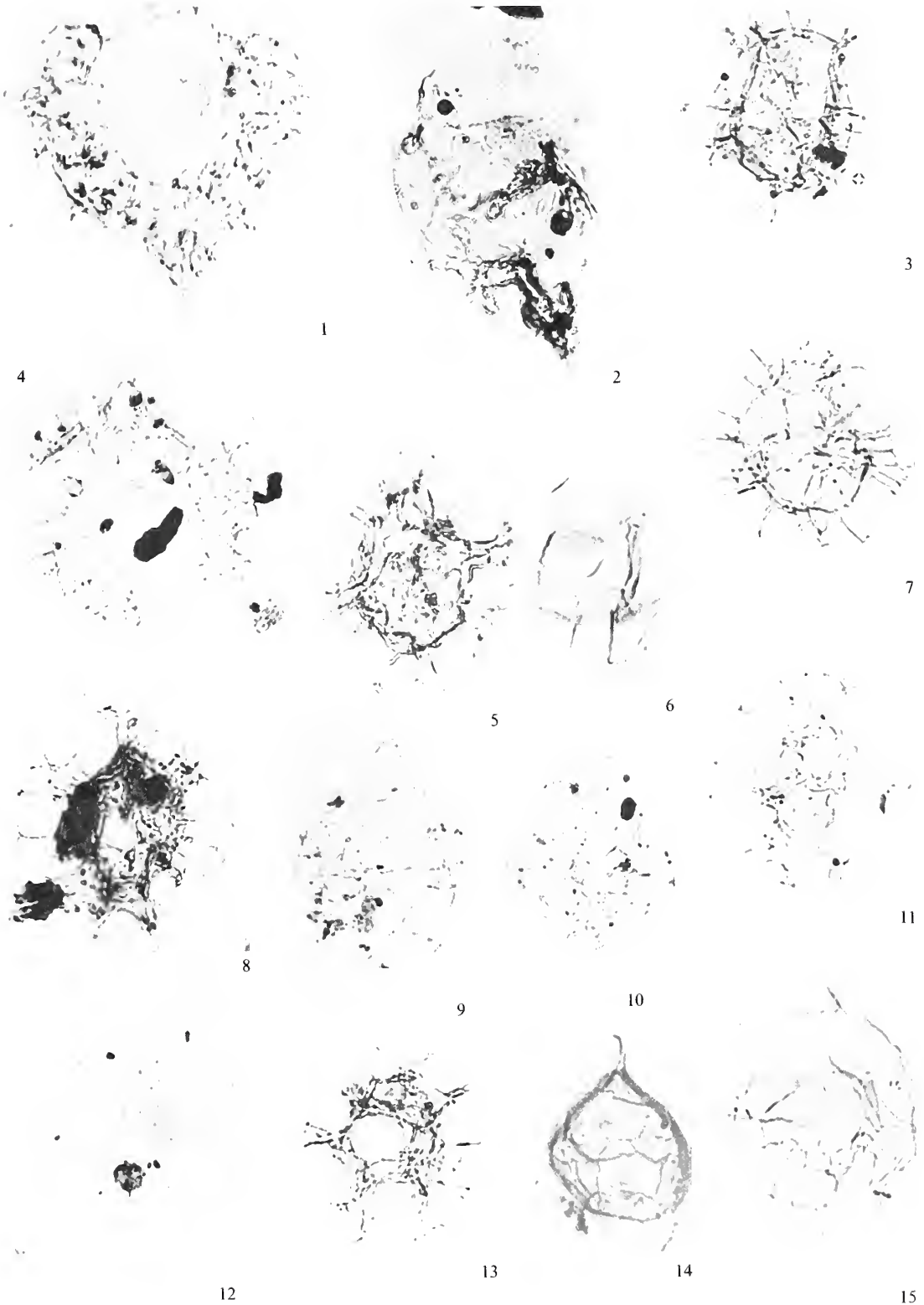
Plate 87, fig. 5

1964 *Hystrichosphaera porosus* Manum and Cookson; 11, 12, pl. 2, figs. 1-5, text-fig. 2.

EXPLANATION OF PLATE 87

All figures at a magnification of $\times 600$ unless otherwise stated.

Fig. 1. *Cyclonephelium distinctum* Deflandre and Cookson, lateral view. Fig. 2. *Deflandrea tripartita* Cookson and Eisenack emend, Cookson and Manum, dorsal view. Fig. 3. *Spiniferites ramosus* var. *multibrevis* (Davey and Williams), lateral view. Fig. 4. *Cyclonephelium distinctum* Deflandre and Cookson, lateral view, showing the operculum. Fig. 5. *Spiniferites* cf. *porosus* (Manum and Cookson), lateral view. Fig. 6. *Deflandrea korojonensis* Cookson and Eisenack, dorsal view. Fig. 7. *Spiniferites ramosus* var. *ramosus* (Davey and Williams), lateral view. Fig. 8. *Spiniferites ramosus* var. *granosus* (Davey and Williams), lateral view. Fig. 9. *Deflandrea spectabilis* Alberti, lateral view of specimen with a conical epittract. Fig. 10. *Deflandrea echinoidea* Cookson and Eisenack, ventral view. Fig. 11. *Spiniferites ramosus* var. *membranaceus* (Rossignol), lateral view. Fig. 12. *Achomosphaera* cf. *hyperacantha* (Deflandre and Cookson) Davey et al., lateral view. Fig. 13. *Spiniferites ramosus* var. *gracilis* (Davey and Williams), lateral view. Fig. 14. *Deflandrea macrocysta* Cookson and Eisenack, lateral view. Fig. 15. *Deflandrea spectabilis* Alberti, dorsal view of specimen with a bell-shaped epittract.



Description. Proximo-chorate cyst, spheroidal to ovoidal in shape, made up of periphragm and endophragm closely adpressed. The endophragm may be thickened; the periphragm makes up the processes. Cyst smooth. Tabulation present with the fields delimited by sutural ridges; no specimen, however, seen in which the tabulation could be deciphered. Processes hollow, latispinous, erect, buccinate, open distally, fenestrate, and digitate. One or two specimens observed in which the cylindrical sutural processes were present. Archeopyle precingular of type P, formed by the loss of plate 3''.

Figured material. Loc. 3, 10 (2) at 109·4–44·8.

Dimensions. Range: Length 33·0 (38·8) 46·0 μ ; breadth 22·0 (32·5) 40·0 μ , processes range in length from 8 to 18 μ . Seventeen specimens observed.

Remarks. This species is morphologically similar to *H. porosa* Manum and Cookson 1964 but in certain specimens a similarity with *H. perforata* Davey and Williams 1966 was apparent. It may be that there is a complete morphological range between these two species. *H. porosa* had a recorded geological range of Aptian–Turonian. Its affinities are gonyaulacacean with the gonyaulacoid lineage.

Spiniferites ramosus var. *gracilis* (Davey and Williams) Sarjeant 1970

Plate 87, fig. 13

1966a *Hystrichosphaera ramosa* var. *gracilis* Davey and Williams; 34, 35, pl. 1, fig. 5, pl. 5, fig. 6.

These specimens compare well with those of Davey and Williams (1966a) except that in the Bearpaw assemblages there is more variability in process length; this may be an indication of a morphological trend from the *ramosus* type to the *gracilis* type. The geological range of this variety is Cenomanian–Miocene. Its affinities are gonyaulacacean with the gonyaulacoid lineage.

Figured material. Loc. 3, 3 (1) at 94·0–47·3.

Dimensions. Range: Length 28·0 (34·5) 49·0 μ ; breadth 21·0 (30·5) 38·0 μ , processes range in length from 7 to 18 μ . Thirteen specimens observed.

Spiniferites cf. *membranaceus* (Rossignol) Sarjeant 1970

Plate 87, fig. 11

1964 *Hystrichosphaera furcata* var. *membranacea* Rossignol; 86, pl. 1, figs. 4, 9, 10, pl. 3, figs. 7, 12.

1966a *Hystrichosphaera ramosa* var. *membranacea* (Rossignol) Davey and Williams; 37, pl. 4, figs. 8, 12.

1967 *Hystrichosphaera membranacea* (Rossignol) Wall; 102, 103, pl. 14, figs. 14, 15, text-fig. 2.

1970 *Spiniferites membranaceus* (Rossignol) Sarjeant; 76.

These specimens compare well with those of Davey and Williams (1966a) but differ from those of Rossignol (1964) in lacking the two large dorsal antapical processes. *S. ramosus* var. *membranaceus* had a previously recorded geological range of Eocene–Recent, and its affinities are gonyaulacacean with the gonyaulacoid lineage.

Figured material. Loc. 11, 1 (1) at 96·0–29·3.

Dimensions. Range: Length 30·0 (35·6) 40·0 μ ; breadth 22·0 (27·8) 38·0 μ , processes range in length from 8 to 18 μ . Ten specimens observed.

Genus ACHOMOSPHAERA Evitt 1963

Type species. Achomosphaera ramulifera (Deflandre) Evitt 1963; O.D.

Achomosphaera cf. hyperacantha (Deflandre & Cookson) Davey and Williams 1969

Plate 87, fig. 12

1955 *Hystrichosphaera hyperacantha* Deflandre and Cookson; 264, 265, pl. 6, fig. 7.

1967 *Hystrichosphaera hyperacantha* (Deflandre and Cookson) Wall; 100, pl. 14, fig. 3.

1969 *Achomosphaera hyperacantha* (Deflandre and Cookson) Davey and Williams; 4.

Description. Proximo-chorate cyst, spheroidal to ovoidal, consisting of two closely adpressed wall layers. Cyst surfaces smooth. Periphragm alone makes up the hollow processes, which do not connect to the interior of the cyst. They are slender and taeniate, erect, cylindrical to tapering; generally trifurcate with bifid tips. The processes are, like the test, smooth. Sutural ridges absent in general although one or two faint lines may be seen in some specimens. Archeopyle not observed.

Figured material. Loc. 13, 13 (2) at 94.0–32.6.

Dimensions. Range: Length 37.0 (38.0) 39.0 μ ; breadth 32.0 (32.5) 33.0 μ , length of processes 6 to 15 μ . Two specimens observed.

Remarks. This species has recently been formally transferred to the genus *Achomosphaera* by Davey *et al.* (1969). The observed specimens were smaller than the original specimens of Deflandre and Cookson (1955). Wall (1967) considers this species as being a robust variety of *H. furcata* (Ehrenberg) Wetzel. It is, however, probably best regarded as a morphotype within the '*Spiniferites* complex'. *Achomosphaera hyperacantha* has a recorded geological range of Lower Miocene?–Holocene. The geological range should only be extended with some reserve on the evidence of only two specimens. It is characterized, in particular, by the nature of its trifurcate processes. It is almost certainly a gonyaulacacean dinoflagellate of the gonyaulacoid lineage.

Cyst-Family DEFLANDREACEAE Eisenack emend. Sarjeant and Downie 1966

Genus DEFLANDREA Eisenack emend. Williams and Downie 1966

Type species. Deflandrea phosphoritica Eisenack 1938; O.D.

Williams and Downie (1966) state that this genus is represented by many species that clearly overlap with regard to their morphology. It is probably best to regard this genus as embracing a complex of morphotypes that show geographical and evolutionary intergradation; but at any one level in the stratigraphic column, a number of morphotypes may be recognized. The species described below are regarded in this light. Vozzhennikova (1967) created two new genera, *Chatangiella* and *Australiella*, and emended the genus *Deflandrea* in her treatment of *Deflandrea*-like cysts. The present author is reluctant to follow this scheme at the present time.

Deflandrea spectabilis Alberti 1959

Plate 87, figs. 9, 15

1959 *Deflandrea spectabilis* Alberti; 99, pl. 9, figs. 7, 8.

This species is common in the Bearpaw Formation, it has a large specific variation

as interpreted from the assemblages studied, and it is not difficult to visualize that with more of a conical epittract it would appear very similar to *D. cooksoni* as figured by Clarke and Verdier (1967); but with a bell-shaped epittract it is closer to the holotype of *D. cooksoni* Alberti (1959). Vozzhennikova (1967) regards this species as a member of the genus *Australiella*. *D. spectabilis* has a geological range of Santonian–Campanian. Manum (1963) reported a peridiniacean tabulation for certain species of *Deflandrea*, and Wall and Dale (1968) place it in the deflandreoid lineage.

Figured material. Loc. 5, 1 (3) at 103·0–44·3. Loc. 11, 1 (1) at 95·0–35·9.

Dimensions. Range: Length 58·0 (65·5) 87·0 μ ; breadth 32·0 (41·7) 50·0 μ . Fifty specimens measured, out of a studied population of seventy-four.

Deflandrea korojonensis Cookson and Eisenack 1958

Plate 87, fig. 6

1958 *Deflandrea korojonensis* Cookson and Eisenack; 27, pl. 4, figs. 10, 11.

This species may be distinguished from *D. spectabilis* by its over-all shape and the absence of any type of tabulation. It forms a distinct morphotype within these assemblages. It is, however, close to *D. bakeri*, Deflandre and Cookson 1955, the major difference being the nature of 'ornamentation', *D. bakeri* having a punctate test. Vozzhennikova (1967) regards this species as a member of the genus *Australiella*. *D. korojonensis* has a geological range of Campanian–Maestrichtian. It has peridiniacean affinities with the deflandreoid lineage.

Figured material. Loc. 13, 5 (1) at 93·0–44·2.

Dimensions. Range: Length 70·0 (97·4) 132·0 μ ; breadth 40·0 (56·6) 82·0 μ . Thirteen specimens observed and measured.

Deflandrea echinoidea Cookson and Eisenack 1960

Plate 87, fig. 10

1960 *Deflandrea echinoidea* Cookson and Eisenack; 2, pl. 1, figs. 5, 6.

This species forms a distinct morphotype within the Bearpaw Formation by virtue of its 'ornamentation', but it is otherwise morphologically similar to *D. spectabilis*. *D. echinoidea* has a geological range of Albian–Campanian. It has peridiniacean affinities with the deflandreoid lineage.

Figured material. Loc. 11, 7 (2) at 102·0–47·7.

Dimensions. Range: Length 60·0 (67·0) 71·0 μ ; breadth 45·0 (48·3) 50·0 μ . Two specimens observed.

Deflandrea tripartita Cookson and Eisenack emend. Cookson and Manum 1964

Plate 87, fig. 2

1960 *Deflandrea tripartita* Cookson and Eisenack; 2, pl. 1, fig. 10.

This species is similar to *D. victoriensis* but differs in that it lacks all traces of tabulation. Vozzhennikova (1967) regards this species as a member of the genus

Australiella. *D. tripartita* has a geological range of Turonian–Campanian. It has peridiniacean affinities with the deflandreoid lineage.

Figured material. Loc. 4, 13 (2) at 107·8–30·9.

Dimensions. Range: Length 75·0 (94·0) 105·0 μ ; breadth 35·0 (48·6) 62·0 μ . Six specimens observed and measured.

Deflandrea macrocysta Cookson and Eisenack 1960

Plate 87, fig. 14

1960 *Deflandrea macrocysta* Cookson and Eisenack; 3, pl. 1, figs. 7, 8.

This species forms a distinct morphological type in Bearpaw assemblages. In general it appears quite close to *Trithyrodinium evittii* Drugg 1967 but differs in possessing an intercalary archeopyle formed by the loss of a single plate. It has peridiniacean affinities with the deflandreoid lineage.

Figured material. Loc. 1, 13 (2) at 99·2–39·0.

Dimensions. Range: Length 44·0 (67·6) 78·0 μ ; breadth 36·0 (47·6) 54·0 μ . Ten specimens observed and measured.

Cyst-Family PSEUDOCERATIACEAE Eisenack emend. Sarjeant and Downie 1966

Genus ODONTOCHITINA Deflandre 1935

Type species. *Odontochitina operculata* (Wetzel) Deflandre 1946 = *Odontochitina silicorum* Deflandre 1935; O.D.

Odontochitina operculata (Wetzel) Deflandre 1946

Plate 88, fig. 1

1933 *Ceratium* (*Euceratium*) *operculatum* Wetzel; 170, pl. 2, figs. 21, 22.

1946 *Odontochitina operculata* (Wetzel) Deflandre; 238, figs. 1016–19.

This was the only species of *Odontochitina* observed in the Bearpaw assemblages. It is distinguished from *O. costata* Alberti emend. Clarke and Verdier 1967, which in many respects it closely resembles, by lack of striations on the horns. It is uncertain whether the horns of *Odontochitina* are equivalent to horns as seen in many modern species of *Ceratium* or whether they should be more correctly termed processes. Its affinities are unknown.

Figured material. Loc. 9, 39 (2) at 99·0–32·9.

Dimensions. Range: Endoblast: length of long axis 42·0 (53·9) 71·0 μ , length of short axis 39·0 (49·9) 68·0 μ . The horns range in length from 54·0–200·0 μ . Thirty-one specimens observed.

In addition to these species the following were noted, but were only represented by single specimens. They are, therefore, not herein described or figured but are included in the primary data and in the range charts.

Cribroperidinium sp.

Pareodinia sp.

Komewuia cf. *glabra* Cookson and Eisenack 1960
Canningia cf. *rotundata* Cookson and Eisenack 1961
Exochosphaeridium bifidum (Clarke and Verdier) Clarke *et al.* 1968
Cyclonephelium cf. *paucispinum* Davey 1969
Spiniferites cornutus (Gerlach) var. A
Deflandrea granulifera Manum 1963
D. sp.
Hexagonifera chlanydata Cookson and Eisenack 1962b

INCERTAE SEDIS

Group ACRITARCHA Evitt 1963

Subgroup ACANTHOMORPHITAE Downie, Evitt, and Sarjeant 1963

Genus BALTISPHAERIDIUM Eisenack emend. Downie and Sarjeant 1963

Baltisphaeridium sp. A. (Pl. 88, fig. 5.) Loc. 11, 9 (1) at 105.0–38.0. Thirty-one specimens.

Genus *Micrhystridium* Deflandre emend. Downie and Sarjeant 1963

Micrhystridium sp. A. (Pl. 88, figs. 2, 3.) Loc. 2, 1 (1) at 93.0–45.4 and Loc. 3, 13 (2) at 108.0–35.6. Twenty-three specimens.

Micrhystridium sp. B. (Pl. 88, fig. 7.) Loc. 3, 13 (2) at 109.0–39.4. Twenty-seven specimens.

Micrhystridium sp. C. (Pl. 88, fig. 4.) Loc. 3, 10 (3) at 93.5–38.1. Seven specimens.

Micrhystridium sp. D. (Pl. 88, fig. 6.) Loc. 3, 10 (2) at 94.6–43.2. Nine specimens.

Subgroup HERKOMORPHITAE Downie, Evitt and Sarjeant 1963

Genus CYMATIOSPHAERA Wetzel emend. Deflandre 1954

Cymatiosphaera sp. A. (Pl. 88, fig. 8.) Loc. 3, 1 (1) at 106.0–47.1. Ten specimens.

INTERPRETATION OF THE BEARPAW PHYTOPLANKTONIC RECORD

The Bearpaw assemblage. The Bearpaw Formation contains a distinct assemblage of dinoflagellate cysts and acritarchs. In particular it is characterized by the presence of the genera *Deflandrea*, *Diconodinium*, and *Lejeunia*. To characterize the assemblage further it is necessary, though difficult, to give some idea of the relative proportions of certain of the cysts present. In a qualitative sense, therefore, the following three categories are used: 'common', 'occasionally common', and 'rare'.

EXPLANATION OF PLATE 88

All figures at a magnification of $\times 600$ unless otherwise stated.

Fig. 1. *Odontochitina operculata* (Wetzel) Deflandre, lateral view, showing the archeopyle and the nature of the horns. Fig. 2. *Micrhystridium* sp. A, general view to show the cyst habit. Fig. 3. *Micrhystridium* sp. A, general view, showing the nature of the processes. Fig. 4. *Micrhystridium* sp. C, general view, showing the nature of the processes. Fig. 5. *Baltisphaeridium* sp. A, general view, showing the cyst habit. Fig. 6. *Micrhystridium* sp. D, general view, showing the nature of the processes. Fig. 7. *Micrhystridium* sp. B, general view, showing the cyst habit. Fig. 8. *Cymatiosphaera* sp. A, general view, showing the polygonal fields on the central body and the nature of the processes.



The Bearpaw assemblages studied always had high proportions of the following cysts: *Deflandrea spectabilis* Alberti, *Diconodinium firmum* sp. nov., and *Oligosphaeridium pulcherrimum* (Deflandre and Cookson) Davey and Williams. These species are regarded as being 'common'. Some of the assemblages, in addition to those mentioned above, contain high proportions of *Canningia senonica* Clarke and Verdier, *Microdinium irregulare* Clarke and Verdier, *Lejeunia ampla* sp. nov., *L. tricusps* (Wetzel), *Odontochitina operculata* (Wetzel) Deflandre, *Cyclonephelium distinctum* Deflandre and Cookson, *Hystrichosphaeridium tubiferum* var. *brevispinum* Davey and Williams and *Deflandrea korojonensis* Cookson and Eisenack. These species are regarded as 'occasionally common'. All other species recovered from the Bearpaw Formation are 'rare'.

Comparisons with other assemblages are difficult to make as little work has been published with respect to Campanian microplankton. Cookson and Eisenack (1960) described some types from Western Australia with some similar *Deflandrea* species to those from the Bearpaw Formation. In addition they recorded a unique collection of species. Clarke and Verdier (1967) recorded very few species of dinoflagellate cysts and acritarchs from the Campanian of the Isle of Wight. Species common to their assemblage and the present assemblage are *Exochosphaeridium bifidum* (Clarke and Verdier) Clarke *et al.* 1968, *Cyclonephelium distinctum*, and *Odontochitina operculata*. Vozzhennikova (1967), in her tables of diagnostic species, lists the following for the Campanian of Kazakhstan: *Gymnodinium kasachstanium* Vozzhennikova, *Australiella cooksoni* (Alberti) Vozzhennikova, *A. granulifera* (Manum) Vozzhennikova, *Albertia curvicornis* Vozzhennikova and *Cooksoniella manumi* Vozzhennikova. Similarities exist to the Bearpaw assemblages especially with regard to the *Deflandrea* species. Oltz (1969) recorded the presence of *Deflandrea* aff. *micrograuulata* Stanley, *Deflandrea* sp., *Hystrichosphaeridium* aff. *tubiferum* (Ehr.) Deflandre, *Hystrichosphaeridium*, cf. *Gonyaulacysta*, Forma 'A', Forma 'B', Forma 'C', and *Paleotetradinium* sp. from the Bearpaw Formation of east central Montana. His assemblage appears similar to that described in this work but a full comparison is not possible as he failed to place his specimens in formal taxa. Recently Davey (1969*b*, 1969*c*) described dinoflagellate cysts from the Campanian of South Africa. His assemblages do not appear comparable except for the presence of *Diconodinium* spp. and *Exochosphaeridium bifidum*.

Local biostratigraphy. The Bearpaw Formation is interpreted as containing a number of informal microplankton assemblage zones. At Lethbridge three informal assemblage zones are recognized from the distribution of the contained microplankton. These have been labelled I to III on fig. 12. The primary data, i.e. number of specimens of each organic-walled microplankton species per assemblage, on which figs. 12 and 13 are based may be obtained from the author on request.

The first assemblage zone encompasses a body of rock contained between 10 feet above the base of the Bearpaw to approximately 160 feet above the base of the formation.

The second informal assemblage zone consists of a body of rock 190 feet above the base of the formation to approximately 260 feet above the base of the formation.

The third assemblage zone consists of a body of rock from 305 feet above the base of the Bearpaw to approximately 540 feet above the base of the formation.

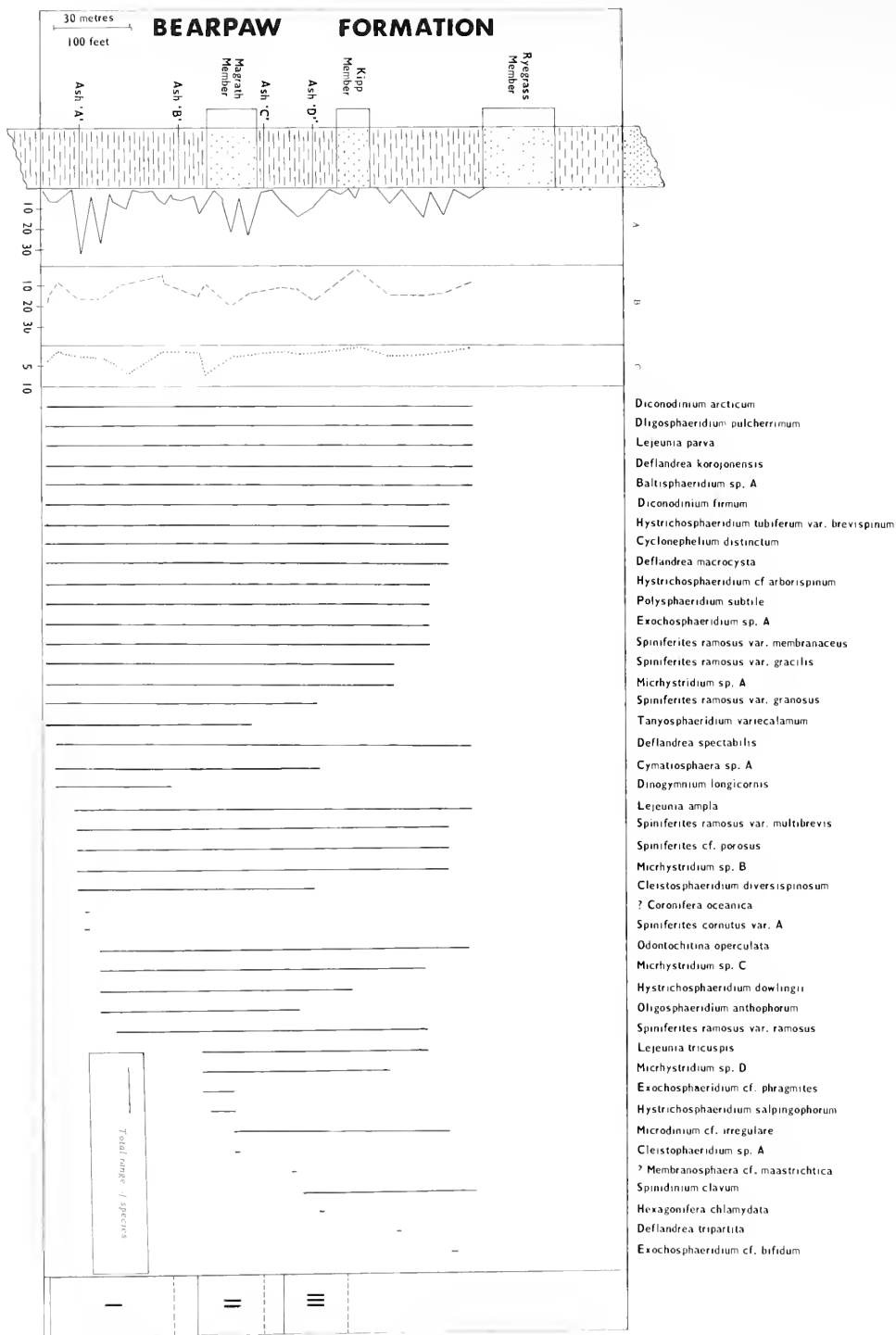
In the Cypress Hills sections only two informal assemblage zones were initially recognized, as part of the Manyberries Member could not be sampled because of poor exposure and lack of stratigraphic control. A lower assemblage zone was recognized (see fig. 13), and an upper assemblage zone was also present although its full limits could not be ascertained.

Recently the author, through the courtesy of Dr. J. H. Wall of the Research Council of Alberta, has examined a part of the core of water borehole RCA Thelma (Lsd 14, Sec. 31, Tp. 6, R. 2, W 4th Mer) to complete that part of the Cypress Hills sections not originally studied. The additional data has been added to all the relevant diagrams and the samples and slides have been deposited in the Palynological Collections at the Institute of Geological Sciences, Leeds, and registered as SAL 1720-SAL 1726. The samples from RCA Thelma confirm the presence of informal assemblage zone II in the Cypress Hills based on the use of the semi-quantitative procedures, i.e. percentages of dinoflagellates and acritarchs, the number of dinoflagellate cyst species and on the gonyaulacacean ratio discussed below, but not on the ranges of the organic-walled microplankton (see fig. 13).

The recognition of the majority of these informal microplankton assemblage zones rests on the vertical distribution of the microplankton in the Bearpaw Formation. A clear correlation by species inspection between these two areas is not possible but both areas do reflect, in the distribution of the dinoflagellate cysts and acritarchs, the transgression and various environmental changes of the Bearpaw sea.

Palaeoenvironment of the Bearpaw. The Lethbridge section of the Bearpaw Formation was examined for its foraminiferan content by Anan-Yorke (1969). He recognized six cycles of water-depth fluctuations and it was suggested that salinity changes accompanied these fluctuations. An attempt has been made to recognize these fluctuations using dinoflagellate cysts and acritarchs.

A record was kept of the percentage of dinoflagellate cysts and acritarchs present in the total palynomorph population in each sample examined. This information is shown in column A of figs. 12 and 13. In addition, in those samples that were studied in detail, i.e. those where the percentage of dinoflagellates and acritarchs rose to 10% or more, a record of the number of dinoflagellate species was kept, and this is shown in column B of the two range charts. Column C records the gonyaulacacean ratio, for each of the samples studied in detail. The gonyaulacacean ratio is simply the number of species that have a gonyaulacacean affinity divided by the number of species having a peridiniacean affinity. If we assume that conditions have not radically altered from today, then it appears that in an open marine environment the number of gonyaulacacean dinoflagellate species is relatively higher than the number of peridiniacean dinoflagellate species (Schiller 1937). We must assume that this is reflected in the cyst populations. In Wall (1967) the calculated gonyaulacacean ratio is 18.0 for cysts collected from deep-sea cores in the Caribbean, and Wall and Dale (1968) has a calculated gonyaulacacean ratio of 0.44 for a near-shore cyst population at Woods Hole, Massachusetts. Freshwater assemblages have high proportions of peridiniacean dinoflagellates and low proportions of gonyaulacacean dinoflagellates



TEXT-FIG. 12. Vertical ranges of the dinoflagellate cysts and acritarchs recovered from the Lethbridge sections of the Bearpaw Formation together with the proposed informal biostratigraphical zonation.

Column A—Percentages of phytoplankton per sample.

Column B—Number of dinoflagellate cyst species per sample.

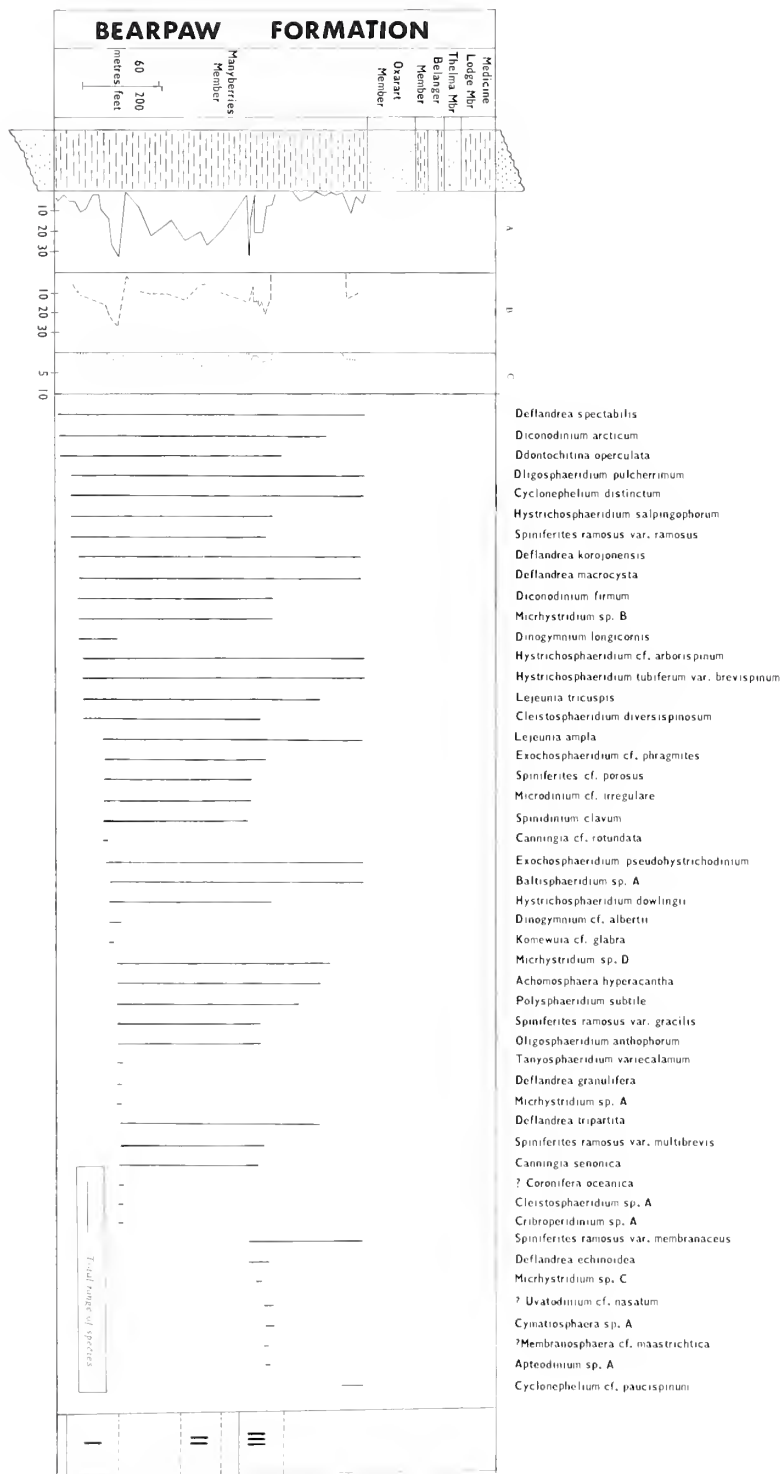
Column C—Gonyaulacacean ratio.

as may be seen in Eddy (1930) and Thompson (1947, 1950). The gonyaulacacean ratio was calculated for each of the samples studied in detail, using cysts for which their natural affinities are known or reasonably assured. The results are shown in column C of the range charts.

An inspection of these three columns (A-C) from the Lethbridge section reveals that an increase in the percentages of the dinoflagellates and acritarchs is accompanied by an increase in the number of species and by an increase in the gonyaulacacean ratio. This relationship may be used to pinpoint the appearance of possible open marine conditions. The author has no justification in setting definite limits on this environment, in terms of salinity, temperature, etc., so the term open marine is used only in a relative sense. These open marine conditions may be indicative of periods of maximum extent of the Bearpaw sea such that the shoreline is distant with the accompanying normal salinity for ocean waters. It might, however, indicate periods when the nutrient content of the sea was optimum for the phytoplankton. Using this information it may be interpreted that an initial flooding or transgression in the Lethbridge area is represented by the lowermost 150 feet of the formation with optimum open marine conditions between 60 and 100 feet above the base of the formation. A second period of open marine conditions is represented from approximately 180-240 feet above the base of the formation and a third period is represented from approximately 310-350 feet above the base of the formation. Many more minor fluctuations are apparent in column A, but on an individual basis these are difficult to explain and may indeed be entirely spurious.

In comparing the results from the dinoflagellate cysts and acritarchs with those from the foraminiferans a close similarity is evident. Anan-Yorke (1969) categorizes his zones as follows: (5) 450 feet to Ryegrass Member—lagoonal. (4) 200-450 feet—deeper water but not as deep as in 2. (3) 115-200 feet—lagoonal, brackish. (2) 56-115 feet—open marine. (1) Basal 56 feet—lagoonal, brackish. Anan-Yorke's zone 2 corresponds quite well with the time of optimum conditions for the initial flooding of the Bearpaw sea as documented by the dinoflagellates and acritarchs. These fossils also pick out a second period of optimum conditions at the level of the Magrath Member which Anan-Yorke unfortunately failed to examine for foraminiferans because of lack of samples. Dinoflagellate and acritarch evidence suggests fluctuating conditions for zone 5 of Anan-Yorke. In the Cypress Hills the period of initial flooding can be recognized together with the other open marine periods. A correlation of the marine palaeoenvironments is thus achieved.

Although the use of the gonyaulacacean ratio appears to be a useful technique it may, in this case, more precisely indicate that the *Deflandrea* spp. prefer a near-shore reduced salinity situation; as the majority of the peridiniacean cysts studied were species of the genus *Deflandrea*. Certain over-all limitations do exist. The palynologist, in studying microplankton, is looking at the cyst and not the motile stage of the life cycle. To what extent does the cyst population reflect the true population of these organisms in their natural habitat? Under what conditions do cysts form and what factors have affected their distributions in the sediments from which they are extracted? These two largely unanswered questions clearly point out the present limitations of all dinoflagellate and acritarch research.



TEXT-FIG. 13. Vertical ranges of the dinoflagellate cysts and acritarchs recovered from the Cypress Hills sections of the Bearpaw Formation together with the possible equivalent informal biostratigraphical units to those proposed for the Lethbridge area. Column explanations the same as those given for text-fig. 12.

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APPENDIX A: SAMPLE LOCALITIES

Sample localities previously mentioned in the text are listed below with their code numbers and geographical locations.

Lethbridge Area. Loc. 1: Lsd. 1, Sec. 2, Tp. 7, R. 22, W.4th Mer.

Loc. 2: Lsd. 9-10, Sec. 33, Tp. 6, R. 22, W.4th Mer.

Loc. 3: Lsd. 15, Sec. 32, Tp. 6, R. 22, W.4th Mer.

Loc. 4: Lsd. 11, Sec. 19, Tp. 6, R. 22, W.4th Mer.

Loc. 5: Lsd. 10-15, Sec. 24, Tp. 6, R. 23, W.4th Mer.

Loc. 6: Lsd. 12, Sec. 34, Tp. 9, R. 23, W.4th Mer.

Loc. 7: Lsd. 1-2, Sec. 32, Tp. 9, R. 23, W.4th Mer.

Cypress Hills Area. Loc. 8: Lsd. 6, Sec. 31, Tp. 11, R. 2, W.4th Mer.

Loc. 9: Lsd. 12, Sec. 14, Tp. 11, R. 3, W.4th Mer.

Loc. 10: Lsd. 6, Sec. 32, Tp. 5, R. 4, W.4th Mer.

Loc. 11: Lsd. 7, Sec. 32, Tp. 5, R. 2, W.4th Mer.

Loc. 12: Lsd. 12, Sec. 5, Tp. 6, R. 2, W.4th Mer.

Loc. 13: Lsd. 5, Sec. 25, Tp. 6, R. 3, W.4th Mer.

Loc. 14: Lsd. 1-2, Sec. 7, Tp. 8, R. 3, W.4th Mer.

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ON THE MODE OF BRANCHING IN A NEW SPECIES OF *CLONOGRAPTUS*

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ABSTRACT. The precise nature of dichotomous branching in pyritized specimens of *Clonograptus aureus* sp. nov. of Tremadocian age is described and is compared with Arenigian species of *Loganograptus* and *Goniograptus* from Scandinavia. The manner whereby new branches are generated is analogous to the proximal end development of *Didymograptus minutus*.

ALTHOUGH the mode of development of first-order stipes has been worked out in considerable detail for several multiramous and pauciramous graptolites, little is known about the precise way in which higher order stipes branch laterally or dichotomously. This new material from the Road River Formation in Yukon Territory is therefore of great interest because its exquisitely pyritized rhabdosome indicates how second-, third-, and fourth-order branches are generated. The absence of bithecae in this species indicates that at least one line of clonograptids lost this dendroid characteristic before the close of the Tremadocian.

SYSTEMATIC DESCRIPTION

Family ANISOGRAPTIDAE Bulman 1950

Genus CLONOGRAPTUS Hall and Nicholson 1873

Clonograptus aureus sp. nov.

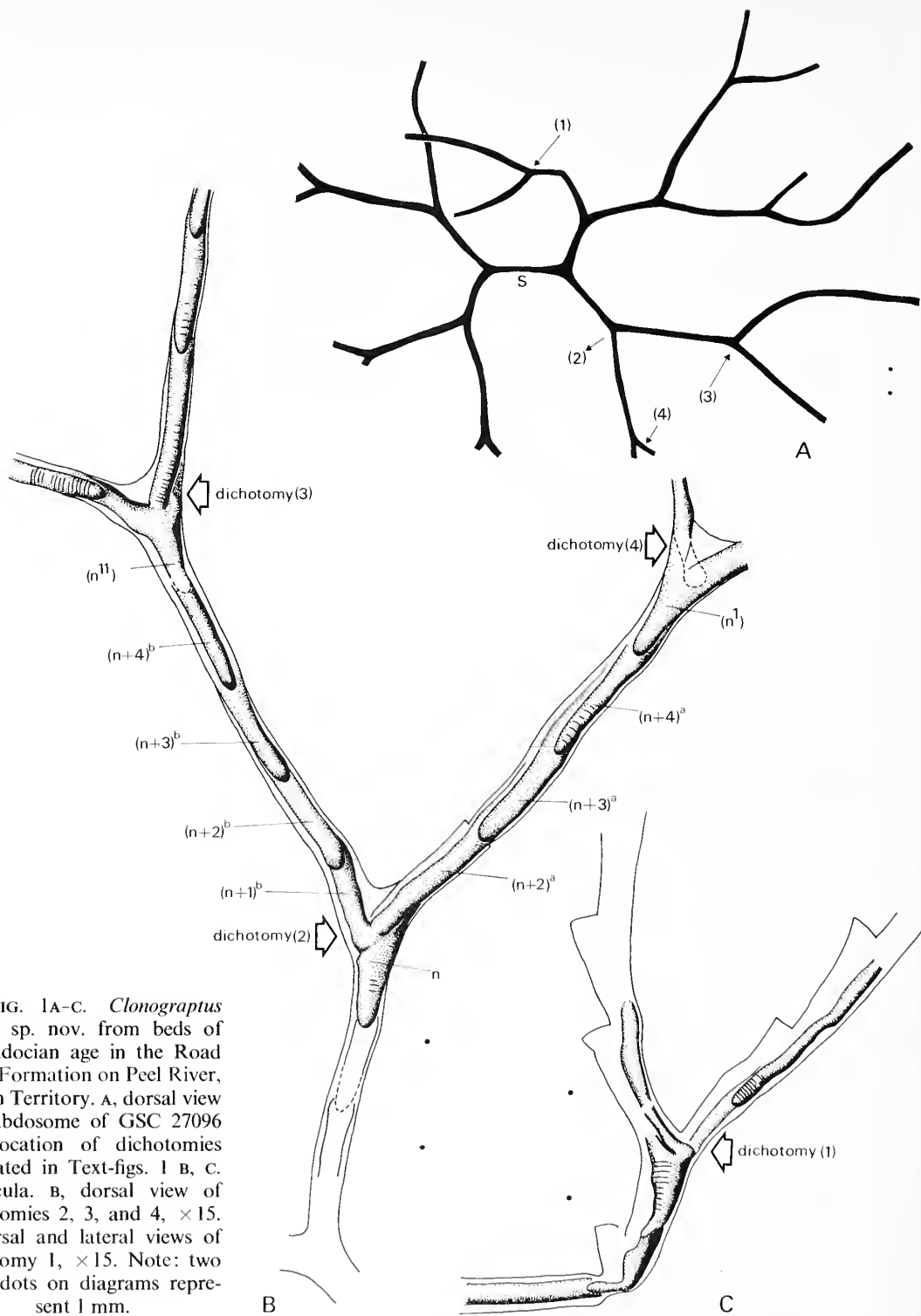
Text-figs. 1 A-C, 2A, 3 A-C

Material. Three incomplete rhabdosomes are available preserved in full relief in pyrite. Illustrated specimens comprising GSC 27096 (Holotype) and 27098 as well as 27097 and 27099 come from the Road River Formation in the Upper Canyon on Peel River, Yukon Territory (65° 56' N., 134° 51' W.).

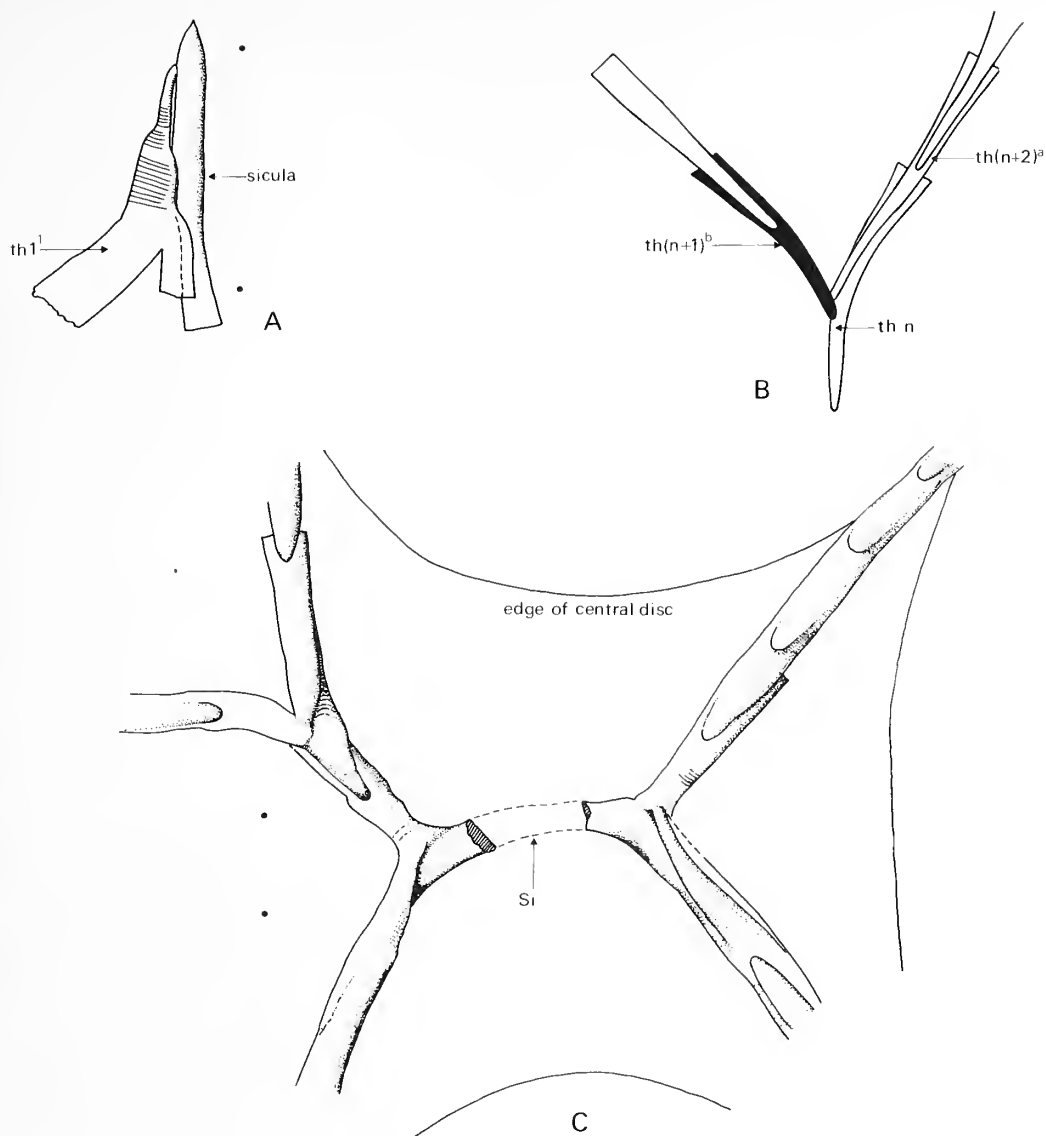
Horizon. Upper part of Tremadocian *Bryograptus-Clonograptus* Zone of Jackson and Lenz (1962, p. 33). The approximate stratigraphic relationship is known to be 60 metres below the base of *Tetragraptus approximatus* Zone and 120-150 metres above the top of the *Staurograptus* Zone. In 1969 the writer recollected at this stratigraphic level and found *Adelograptus* cf. *victoriae* (T. S. Hall), *Adelograptus*(?) *antiquus* (T. S. Hall), *Dictyonema pulchellum* T. S. Hall, and ?*Tetragraptus decipiens* T. S. Hall. Such a fauna is clearly indicative of an La 2 age in Australia.

Derivation of name. From Latin *aureus* = golden; referring to colour of pyritized rhabdosome.

Description. Rhabdosome not seen to exceed 25 mm across with dichotomous branching to 5th-order. The funicle is 2.5-2.9 mm long, details of proximal end development not seen. Second-order branches 2-3 mm long diverge so that distally they enclose angles of 110 to 120°; each branch probably composed of 3-4 thecae (see text-fig. 1B). Third and fourth-order branches 3 mm-5.5 mm long and 0.3 mm wide in dorsal view; one fourth-order branch (Text-fig. 1C) preserved in profile is 0.6 mm across thecal aperture, free ventral wall of thecae 1.0 mm long, concave, and inclined at 20°-30°. The thecal rate on third-order stipes is 4 in 4 mm. Associated



TEXT-FIG. 1A-C. *Clonograptus aureus* sp. nov. from beds of Tremadocian age in the Road River Formation on Peel River, Yukon Territory. A, dorsal view of rhabdosome of GSC 27096 and location of dichotomies illustrated in Text-figs. 1 B, C. S = sicle. B, dorsal view of dichotomies 2, 3, and 4, $\times 15$. C, dorsal and lateral views of dichotomy 1, $\times 15$. Note: two small dots on diagrams represent 1 mm.

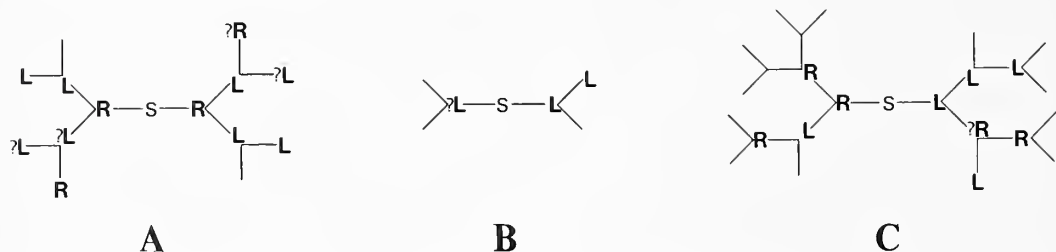


TEXT-FIG. 2A. Pyritized sicula GSC 27098 associated and possibly conspecific with *Clonograptus aureus* sp. nov.; $\times 33$. B, Schematic thecal diagram illustrating dicalycal nature of $th(n+1)^b$; C, proximal end of *Loganograptus kjerulfi* Herrmann from Galgeberg, paratype 73123, Palaeontological Museum Oslo, $\times 13$.

fragmented stipes on same bedding plane believed to belong to this species have a profile width of 0.8 mm across thecal apertures and 11 thecae in 10 mm. Bithecae are apparently absent in all specimens. The details of the sicula are somewhat uncertain. Specimen GSC 27098 may represent the sicula of this species (Text-fig. 2A) in which case it is typically dendroid, consisting of a parallel-sided tube with $th1^l$ originating near apex presumably in the prosicula.

Mode of branching. The precise way in which stipes undergo dichotomous division is best illustrated at points 1, 2, and 3 of text-fig. 1A. Text-figs. 1B, C are enlarged sketches of these branching points and the process is perhaps most clearly shown in dichotomy 2. The third theca on this second-order stipe which is here labelled 'n' (analogous to Jaanusson's 'accessory theca' in *Goniograptus*) is slightly fatter than the preceding theca and in mid-length curves to the right through about 40° . About one-third of the way along the convex side of theca n arises theca $(n+1)^b$ which immediately diverges from theca n to form an angle of about 60° with it. Theca $(n+2)^a$ is derived from the base of theca $(n+1)^b$ and in nearly all cases the junction is marked by a constriction (see text-fig. 1B). Theca $(n+1)^b$ also gives rise to $(n+2)^b$ and is therefore dicalycal. Recognition of dicalycal thecae elsewhere on the rhabdosome is facilitated by the fact that theca $(n+2)^b$ lies considerably closer to the point of dichotomy than does theca $(n+3)^a$ and also by the tendency for the $(n+1)^b$ bearing stipe to diverge at a slightly greater angle from the parent stipe. The paired stipes arising from theca n are of unequal length due to their thecal composition. For example the left stipe which develops from theca $(n+1)^b$ is composed of $(n+1)^b + (n+2)^b + (n+3)^b + (n+4)^b + \frac{1}{3}(n^{11}) = 4\frac{1}{3}$ thecae, whereas the right stipe is composed of $(n+2)^a + (n+3)^a + (n+4)^a + \frac{1}{3}(n^1) = 3\frac{1}{3}$ thecae (excluding the metathecal portion of theca n).

The position of the dicalycal theca in each dichotomy can be on either the left or right side of thecae n, n^1 , n^{11} , etc. The dispositions of these dicalycal thecae on individual specimens are plotted in text-fig. 3.



TEXT-FIG. 3A-C. Dispositions of dicalycal thecae in specimens of *Clonograptus aureus* sp. nov. A-C are GSC 27096, 27097, and 27099 respectively. S = sicula, L = left-handed, R = right-handed.

Although GSC 27096 indicated a highly organized pattern in the direction the dicalycal thecae were distributed in each of the four quadrants of the colony it does not apparently hold true for GSC 27099.

Comparisons. The mode of branching observed by the writer in *Loganograptus kjerulfi* Herrmann from the Arenigian at Galgeberg, Norway (see text-fig. 2B) is of identical type. However, the pattern of the positioning of the dicalycal thecae in PMO Paratype 73123 can be seen to be left-handed for second-order stipes and left-handed for one-third-order stipe. This is comparable to GSC 27097 but not to GSC 27096 or 27099.

The described mode of dichotomous branching also closely resembles that suggested by Jaanusson (1965) for *Goniograptus* sp. from Jämtland. However, two

important differences in stipe anatomy exist. Firstly, in *Goniograptus* the positions of the dicalyca thecae are alternately right-handed and left-handed along each main stipe whereas in *Clonograptus* the pattern is not regular. A second difference is that whereas in *Clonograptus aureus* sp. nov. the prothecal segment of $(n+2)^a$ (see text-fig. 1B) is abnormally long by comparison to $(n+1)^b$ the relationship in *Goniograptus* sp. is reversed.

In summary, the manner of stipe dichotomy in *Clonograptus*, *Loganograptus*, and *Goniograptus* and perhaps many other multiramous genera can be compared with proximal end development in dichograptids. When theca n is made analogous to theca 1^1 then the development is of isograptid type in which the dicalyca theca $(n+1)^b = th1^2$ and theca n , like $th1^1$, forms from the first theca of the other stipe. Among the three subtypes of development discussed by Bulman (1955), *Didymograptus minutus* with its single crossing canal seems to afford the best comparison.

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NOTES ON OPEN NOMENCLATURE AND ON SYNONYMY LISTS

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ABSTRACT. Rudolf Richter's proposals on practice in open nomenclature and on annotated synonymy lists are described and briefly criticized.

Plus quam leges valent boni mores

Tacitus, quoted by Richter in 1930

AUTHORS of palaeontological papers can discover a great deal of instruction in the International Code of Zoological Nomenclature (Stoll and others 1961). But the Code sets a limit on its provisions: it does not intend in any way to impinge on the individual taxonomist's exercise of his judgement (see the 'Preamble' to the Code). It is therefore necessary to seek elsewhere for guidance on matters such as open nomenclature (a device whereby an author expresses his judgement of his own material) and synonymy lists (the means by which an author concisely expresses his judgements of earlier opinions on the taxonomic problem he is handling). A highly explicit set of recommendations on these matters is available in Rudolf Richter's (1948) 'Einführung in die Zoologische Nomenklatur'. His proposals have never been as well known as they deserve among English-speaking palaeontologists. A French translation, it may be noted, is available as Traduction no. 1448, prepared by Département Documentation du B.R.G.M., B.P. 6009, 45—Orléans—02, France. This present article, intended to bring Richter's views to a wider public, draws freely on what Richter wrote in 1948 (especially pp. 45–56). It is not a direct translation (some things are deleted, and there are certain interpolations) and it makes no claim to carry anything of the authority of Richter's original. It is offered in order to promote discussion of two points of nomenclatural technique, in the hope that authors might become more familiar with the nature of certain devices they commonly employ, and hoping too that greater consistency of practice might emerge. Richter's proposals are recommended by the fact that they have to a large extent become standard in the German palaeontological literature—this article may have some incidental usefulness in explaining the meaning of a system of annotation which regularly appears in papers published in the major German palaeontological journals, but whose significance is not widely understood in other countries.

Those who are entirely unfamiliar with Richter's work may find it useful to read Stubblefield (1957).

OPEN NOMENCLATURE

Richter introduced his discussion of open nomenclature by considering the problem of dealing with a specimen whose identity cannot exactly be determined. If it is too hastily referred to a known species or genus, a previously clear taxonomic

concept may be diminished. If one refuses altogether to identify it, potentially useful information may be left unemployed. If one decides to propose a new species or genus to contain the specimen (a lesser error, in Richter's view, than would arise by referring the specimen to a previously well-established taxon—Richter, epigrammatic here as elsewhere in his writings, observed that though spoiling the work, this procedure would not damage the tool, the standard form) a feeble name might result, and proposals of feeble new names should not be encouraged.

Open nomenclature was developed as a remedy against such weaknesses of the taxonomic method. It operates by attaching to known species or genera those specimens whose identity is uncertain. The method offers a clear expression of the fact of uncertainty, and also some indication of the degree of uncertainty involved. This is not a matter of abdicating taxonomic responsibilities. It is instead an especially perspicacious form of nomenclature that is involved. In contrast to closed nomenclature, with its firmly established and strictly defined names, it remains open to whatever possibility of improvement future findings might bring. By giving taxonomy a means of stretching (in an entirely honest and proper way) the limits of existing knowledge, it by itself indicates where improvements are needed and in which direction they might be sought. It permits us to build any such improvements into nomenclature left open for that purpose, and this without any upset of established names.

The signs. The signs employed in open nomenclature are in essence nomenclatural and make up an integral part of the name. It should therefore be understood that they are fundamentally different from signs attached to synonymy lists (see below).

1. Signs for uncertainty at family or higher level.

The highest category touched by uncertainty, and above which certainty begins, has the designation 'incerta'. Examples:

Incertae familiae:	Family uncertain
Incerti subordinis:	Suborder uncertain (order known)
Incerti ordinis:	Order uncertain (class known)
Incertae sedis:	Class uncertain

The requirements at other levels are handled in the same way: *Incertae subfamiliae*; *Incertae superfamiliae*.

2. Signs for uncertainty at genus or subgenus level.

If the attribution to an established genus is uncertain a ? is placed behind the name of the genus. Examples:

Agenus? album Anton (?Anton)
Agenus? album (Anton) (?Anton)
Agenus? album (Anton) (?Bruno)

In the first case it was Anton himself who, at the time of the establishment of the species *album*, attributed it with a question mark to the genus *Agenus*; for behind the species-name, the name of the author is not in parentheses, and this, according to ICZN Article 11, signifies that the original generic assignment has remained unaltered. In the second and third cases Anton had originally assigned the species without

question to the genus *Agenus*, and it was in later publications that the assignment came into doubt. In the second case it was Anton himself who expressed this doubt, and so added to his authorship of the name *album* also the authorship of the open nomenclature. In the third case it was Bruno who was responsible, and he is the author of the open nomenclature. Because in these latter two cases the generic assignment is no longer unequivocally the one proposed by Anton when he established the species, the name of the author of the species-name appears in parentheses (Article 11).

Uncertainty surrounding the subgenus can be dealt with in a corresponding way. Example:

Agenus (Agenus?) album (Anton) (?Bruno)

3. Signs for uncertainty at species or subspecies level.

(i) When attribution to an established species is possible, but cannot be thought certain, a ? is placed behind the name of the author of the species. In a subsequent citation, the author of the open nomenclature, with the sign he introduced (here: ?), is added in parentheses. Examples:

Agenus album Anton? (?Anton)

Agenus album Anton? (?Bruno)

In the first case, Anton himself had assigned a specimen, with some question, to his species *album*, and in the second case it was Bruno who did this. There are no circumstances in which it would be correct to place a ? between a species-name and the name of its author. These two names (species + author) make up a nomenclatural entity, which nothing should be allowed to divide.

Year of publication is also relevant, e.g. in the case where a certain author has at different times made distinctions between forms but has given them all the same name, assigning each of them, with a ?, to some particular species. These forms, which could of course eventually prove to be specifically different from one another and must be cited individually, may be distinguished for one another by the year.

The corresponding treatment can be given where it is attachment not to the species but to a subspecies that is to be shown to be uncertain. Example:

Agenus album striatum Caesar? (?Bruno)

It also happens (especially in ornithology and herpetology) that the subspecies can be firmly fixed even although the attribution to a species remains under question (in most cases lateral replacement of species is involved). Examples:

Agenus album? striatum Caesar (?Caesar)

Agenus album? striatum Caesar (?Bruno)

(ii) If instead of attribution to an established species, only a possibility of comparison with that species should be indicated, cf. (abbreviation of the Latin word confer) is placed in front of the species-name. Authors' names, repetition of the sign introduced (here: cf.), year, and distinction between several forms can be inserted as in (i). Example:

Agenus cf. *album* Anton (cf. Bruno)

The corresponding treatment may be given to a subspecies where this is the subject of a comparison only, as compared with the species attribution, which is firm. Example:

Agenus album cf. *striatum* Caesar (cf. Bruno)

(iii) If a specimen shows itself to represent a new species, whose formal establishment is, however, not yet justifiable, one can, in the interim, associate it with some related, known species, before whose name *n. sp.*, aff. (abbreviation of nova species, affinis) will be inserted. Authors' names, restatement of the sign inserted (here: *n. sp.*, aff.), and distinction of several forms can be introduced as in (i). Example:

Agenus n. sp., aff. *album* Anton (*n. sp.*, aff. Bruno).

Association with a known subspecies can be done in the same way. Example:

Agenus album n. subsp., aff. *striatum* Caesar (*n. subsp.*, aff. Bruno).

If any author has several different forms to compare with a known species in this way, it is useful practice to identify each of them by a lower-case letter. These letters have an advantage over names in that they introduce no question of priority and so impose no burden. They can be used, with just as much exactitude as resides in a species-name, for temporary characterization of a particular form. They are placed, together with *n. sp.*, behind the genus-name, or in the case of subspecies, together with *n. subsp.*, behind the species-name. Examples:

Agenus n. sp. a, aff. *album* Anton (*n. sp. a*, aff. Bruno)

Agenus n. sp. b, aff. *album* (*n. sp. b*, aff. Bruno)

Agenus album n. subsp. a, aff. *striatum* Caesar (*n. subsp. a*, aff. Bruno)

If the form is to be treated as a new species, not yet to be defined, and incapable of being associated with any established species, then one writes simply *n. sp.*, or if several forms are involved, *n. sp. a* and *n. sp. b* (there are, quite possibly, many people to whom 'open nomenclature' means no more than this particular provision).

(iv) If, again, the question of a relationship with some established species is unclear, and yet an indication of the possibility of such a relationship is desirable (on taxonomic, geographic, or stratigraphic grounds) then *n. sp. aff. ?* is placed in front of the name of the established species. Example:

Agenus n. sp. aff. ? album Anton (*n. sp. aff. ? Bruno*)

An unclear relationship with a subspecies can be treated likewise. Example:

Agenus album n. subsp., aff. ? *striatum* Caesar (*n. subsp.*, aff. ? Bruno)

(v) If the form might equally well belong to a known as to a new species, *sp.* (or more fully, *sp. inc.*, or *sp. indet.*—abbreviations of: species incerta, indeterminabilis)

[Editorial note: it is the practice in *Palaontology* to put the noun before the adjective, e.g. *sp. nov.*, *subsp. nov.*]

is placed behind the genus-name. The corresponding practice at subspecies level is to place subsp. inc. behind the species name. Examples:

Agenus sp. Anton, or *Agenus* sp. inc. Anton
Agenus album Anton subsp. inc. Bruno

4. Signs for uncertainty of both genus and species.

If both the genus and the species are uncertain, the appropriate signs all appear. Examples:

Agenus? cf. *album* Anton (cf. Bruno)
Agenus? *album* Anton? (?spec. Bruno)
Agenus? n. sp., aff. *album* Anton (n. sp., aff. Bruno)
Agenus? n. sp., aff. ? *album* Anton (n. sp., aff. ?Bruno)
Agenus? sp. inc. Bruno

SYNONYMY LISTS

Non-nomenclatural signs. The signs attached to entries in a faunal list or synonymy list are not integral parts of the zoological names and have nothing to do with formal nomenclature. They stand to the left of the name and belong neither to the name itself nor to the author of the name. Nor do they belong among the signs that stand within or to the right of the name. They express the judgements of the author of the list.

Signs attached to the synonymy list. The author of a synonymy list uses his signs to make qualifying comments on these cases he cites in his list as synonyma of the species whose name appears at the head of the list.

Anyone who wishes to carry forward a piece of research must check the existing information. He needs the whole literature on the subject. In order to assist such an inquirer one must strive to make the synonymy lists as near complete as possible, and yet at the same time try to find means of making them as serviceable and as readable as possible. By such means one can rid one's text of pointless information and discussion. The following signs, first proposed in 1924, have subsequently had much use.

1. Signs which should obviate needless searches.

1881 Year in italics: this work has a mention of the species, but without description or illustration. It may be ignored by anyone who wishes to check merely the morphological information, rather than the total data arising out of the occurrence.

1881 Year in roman: the work contributes to our knowledge of the species. If such a reference includes an illustration, it may help a later inquirer to give an indication of the anatomical parts figured, e.g. in arthropods \ominus = illustration of the whole carapace, \frown = cephalon, \smile = abdomen.

[cop. Anton 1856]: the illustration is not a new one, merely a repetition of one already produced by Anton in 1856. Someone who is familiar with the figure in the earlier work need not feel obliged to examine the repeat.

2. Signs which indicate the degree of confidence with which particular items in the list are referred to the species under discussion:

- *1881 * in front of the year: with publication of this work the species can be regarded as valid under the terms of Article 11 of the ICZN (earlier mentions of this name are to be regarded as *nomina nuda*).
- .1881 . in front of the year: we accept responsibility for attaching this reference to the species under discussion.
- 1881 No sign in front of the year: we have no right expressly to accept responsibility for attaching this reference to the species under discussion; but at the same time we have no cause to doubt such an allocation.
- ?1881 ? in front of the year: the allocation of this reference must be subject to some doubt because of the way in which it was presented (e.g. if the species-name concerned included at that time several forms now treated as separate species).
- v1881 v in front of the year: *vidimus!* We have checked the deposited specimens that relate to the work cited, and on their evidence we have chosen the additional sign used. v*1881: we have seen the type of the species. v.1881: because of the evidence of the deposited specimens we are able to take responsibility for this assignment, or v1881: we do not accept responsibility. v?1881: the condition of the original specimens is such that no clear decision is possible.
- (1881) year in parentheses: the year of publication is uncertain.

An example of a synonymy list:

Agenus album ANTON, 1900.

- v . 1895 *Agenus viride* AULUS. — BRUNO, Monogr. Agenidae, S. 12 Taf. 3 Fig. 2.
- ? 1907 *Agenus nigrum* ANNA. — BERTA, Bibl. Ind., S. 20.
- v* 1900 *Agenus album* n. sp. — ANTON, Fauna Bras., S. 35 Taf. 2 Figs. 1-4 ∩ .
- v 1902 *Begenus* cf. *cinereum* AULUS. — CAESAR, Reiseber., S. 10 [vix S. 12].
- 1908 *Agenus album* ANTON. — ANTON, Neue Beob., S. 25, Tabelle 4.
- v . 1910 *Agenus?* *album* ANTON (?BRUNO). — DAVID, Orientierung, S. 30 Taf. 9 Fig. 3 ∩ [kop. ANTON 1900 Fig. 1].
- v ? 1914 *Agenus caeruleum* n. sp. — EMIL, Übersicht, S. 6 Taf. 5, Fig. 2 ∩ . [non Fig. 1 = *Agenus fuscum* FELIX.]

A critical synonymy list like this one, Richter observed, may be in itself a piece of scientific work, approaching the state of a detailed monograph in its critical completeness as well as in the range of information on which it draws. A compilatory synonymy list, which brings together every mention of a zoological name available in the literature, but involves no expense of effort on deposited material nor any exercise of judgement, is not a scientific work, although it could usefully supply raw material for one. A transcriptive synonymy list, which does nothing other than repeat earlier lists, serves merely to put a surface gloss, easily penetrated, on something that is quasi-scientific, and in effect no more than a waste of paper. Once a dependable list has been published, it is sufficient at a later date simply to make a reference to it, adding any necessary supplementary material. The supplementary entries will then serve toward preparation of a revised synonymy list.

Concluding comment. It is now twenty-five years since the second edition of Richter's 'Einführung' appeared. Much of what he suggested then has become firmly established in Germany. One or two of his proposals have faltered. His practice of citing the name of the author of a piece of open nomenclature, for example, is not often seen in the literature. His method of recording anatomical parts figured in references (see 'synonymy lists' above) could be applied in a simple way in the case of arthropods, but it would be difficult to contrive similar schemes for other groups—it would certainly be difficult to think of anything that could conveniently be rendered in type. The annotations he proposed for synonymy lists have otherwise proved acceptable and practicable. Rabien (1954) has proposed two additional signs. These are

(?)1881 (?) before the year: it is probable that the reference applies to the species under discussion, but this cannot be established with certainty (e.g. in a case in which the originals could not be checked, and the illustrations and descriptions were insufficient to justify firm identification, yet in which the identification could be considered probable for reasons stated in detail in remarks which would follow).

p.1881 p before the year: partim: the reference applies only in part to the species under discussion. If attached to any of the other signs of the synonymy list, p would indicate that the sign applies only up to a certain limit to the work cited. Example: vp before the year: the deposited specimens have been checked, and some only of them belong to the species under discussion.

Struve (1966, p. 125) too has made some supplementary proposals. These have not achieved any great currency, but they may, like Rabien's, be found useful in cases where it is necessary to make more specific comment than is provided for in Richter's own system.

Acknowledgements. The author is grateful to Professor Dr. D. Meischner (Göttingen), Professor Dr. K. Krömmelbein (Kiel), and Professor S. Simpson (Exeter) for their comments on a draft of the paper. P. M. Sadler has kindly joined in discussions of many of the points involved.

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WYLEYIA: A NEW BIRD HUMERUS FROM THE LOWER CRETACEOUS OF ENGLAND

by C. J. O. HARRISON and C. A. WALKER

ABSTRACT. An imperfect humerus found in the Weald Clay (Lower Cretaceous) of Henfield, Sussex, represents the earliest British bird known, *Wyleyia valdensis* gen. et sp. nov. It is compared with other reptile and bird humeri from the Jurassic and Cretaceous.

IN July 1964 Mr. J. F. Wyley found an imperfect humerus in the Weald Clay (Lower Cretaceous) at Henfield, Sussex. It is reminiscent of certain advanced archosaur humeri; but, having compared it with the humeri of pterosaurs (from which it is completely distinct) and of small dinosaurs such as *Hypsilophodon* Huxley 1869 and *Deinonychus* Ostrom 1969, we are confident that it represents a bird. The particular bird-like characters which it shows are as follows:

1. There is a transverse ligamental furrow on the palmar surface just below the articulating area of the proximal end.
2. The deltoid crest is blade-like, large, and very thin.
3. There is some indication of a capital groove on the anconal surface.
4. The shaft is slender, hollow, and thin-walled.
5. There is a distinct groove (brachial depression) for the insertion of the brachialis anticus muscle.

The only other Lower Cretaceous bird remains known are *Gallornis straeleni* Lambrecht 1931 from France (assigned by Brodkorb in 1963 to the Phoenicopteridae), the gaviiform *Enaliornis* Seeley 1876 from the Cambridge Greensand of England, and indeterminate feathers from Australia.

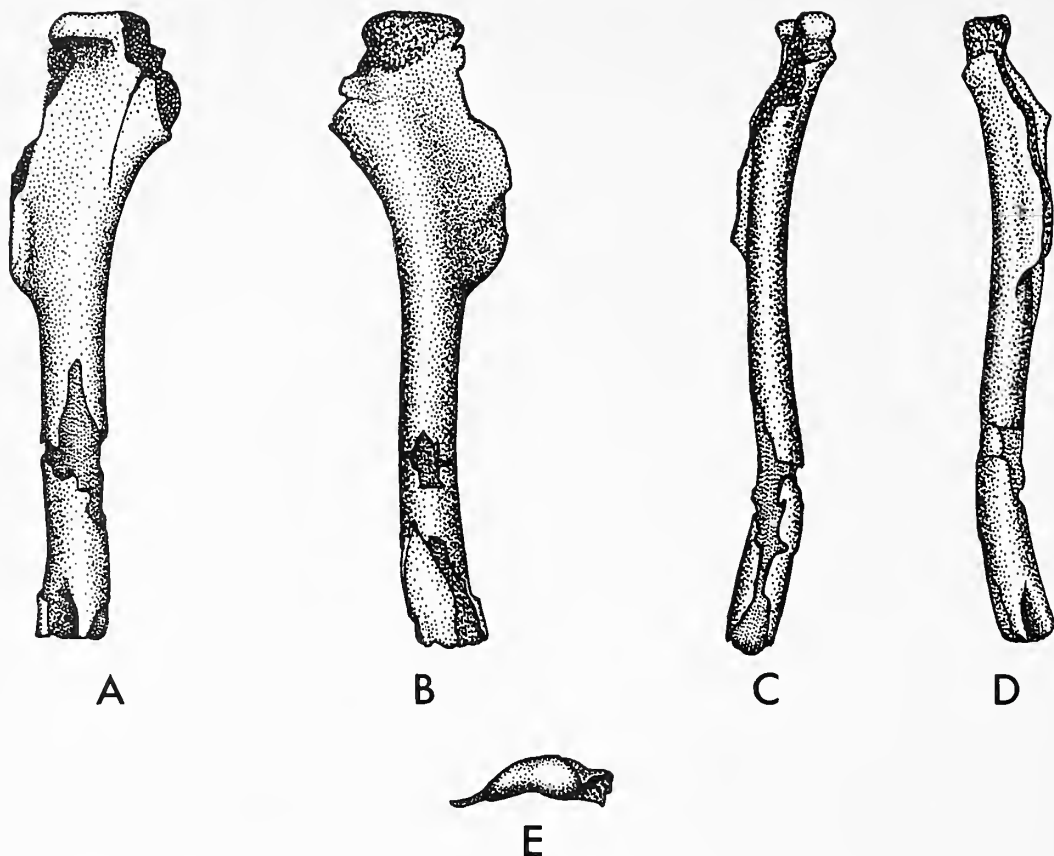
SYSTEMATIC DESCRIPTION

Wyleyia valdensis gen. et sp. nov.

Plate 89; text-figs. 1-2

Holotype. Unique specimen in British Museum (Nat. Hist.) No. A 3658: an imperfect right humerus.

Diagnosis. Humerus similar in character to both *Archaeopteryx* von Mayer and *Ichthyornis* Marsh, but smaller. Proximal end of humerus relatively smooth and flattened. Deltoid crest extending for nearly one-third of length of humerus apparently making only slight angle with plane of the proximal palmar surface; palmar surface of crest itself with small longitudinal ridge on distal half and a very small curved depression at distal end; lower profile of crest forming angle of about 45° with external profile of shaft. No evidence of prominent bicipital surface. Bicipital crest large, relatively thick, and rounded along internal edge. Ligamental furrow present just below head on palmar surface. Shaft curved with some torsion (may be due to



TEXT-FIG. 1. *Wyleyia valdensis* gen. et sp. nov. Holotype: right humerus (BMNH A 3658). $\times 2$. A, palmar aspect; B, anconal aspect; C, internal aspect; D, external aspect; E, proximal aspect.

crushing), widening distally. Impression for brachialis anticus muscle nearer external side of shaft, fairly deep, broad (half as wide as shaft), and elongated.

Description. The specimen is a damaged right humerus, with the distal end missing altogether. The proximal end also is eroded and the outer part of the deltoid crest and the proximal part of the bicipital crest have been broken away. The head itself is damaged, but appears to have been prominent and rounded; there is some indication of a capital groove. Just below the head, on the palmar surface, there is a broad, shallow, transverse depression which is probably the remains of the ligamental furrow. The palmar surface is relatively smooth and slightly concave; the anaconal surface is rounded, especially towards the internal side, but tapers down on the

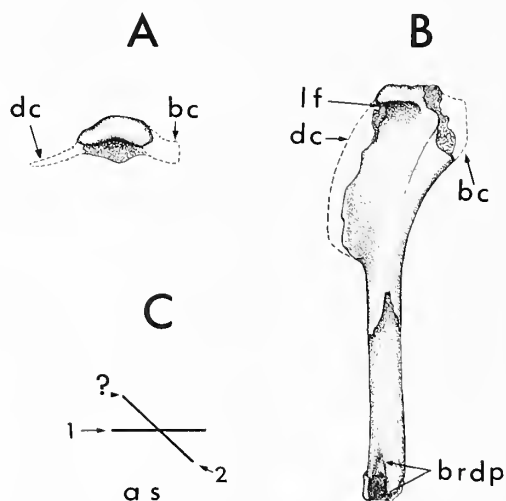
EXPLANATION OF PLATE 89

Wyleyia valdensis gen. et sp. nov. Holotype: right humerus (BMNH A 3658). Stereopairs, $\times 2$. A, palmar aspect; B, anconal aspect; C, internal aspect; D, external aspect; E, proximal aspect.



external side into the thin flange of the deltoid crest. The deltoid crest is long, about a third of the probable total length of the bone, and distally curves in rather abruptly to the shaft; its outer edge is broken, but on the palmar surface a small longitudinal ridge is apparent distally, running near and parallel to the edge. There is also a very small curved depression at the distal end of the crest, just next to the shaft. On the internal side the bone curves out evenly to form a bicipital crest, but lacks any prominent bicipital surface. The bicipital crest is thick and is curved on the anconal surface with no suggestion of a narrow flange indicated in the illustrations of the humeri of *Ichthyornis*. There is a small ridge where a median crest would be expected to occur, but no suggestion of a pneumatic fossa or foramen.

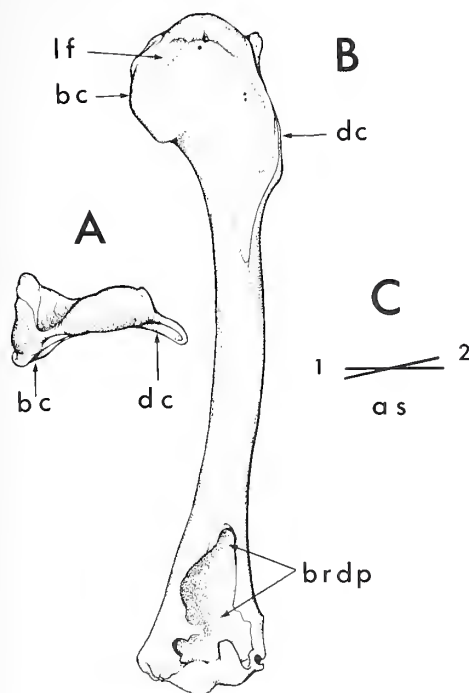
The centre of the shaft is slightly crushed, but allowing for this, its anconal profile is still slightly convex in lateral view; the shaft begins to widen towards the distal break. Also visible in this area, near the external side of the shaft, is the scar of the brachialis anticus muscle. It is fairly deep, broad (half as wide as the shaft), and elongated; its edges are relatively steep and the impression tapers proximally, appearing to terminate in a smaller and slightly deeper pit. There is some torsion in the shaft, so that the two ends of the bone were inclined to each other at a considerable angle (text-fig. 2C); some of it might be due to crushing, but it was in any case much greater than in a modern bird (text-fig. 3C).



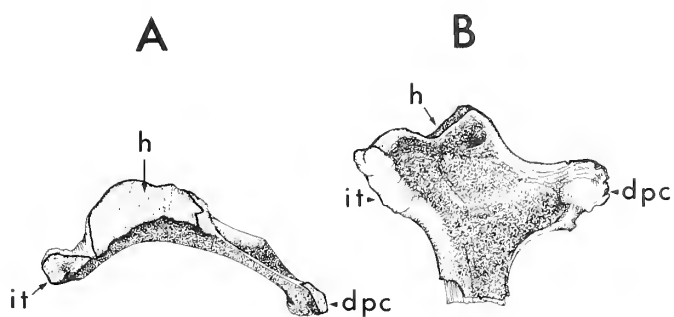
TEXT-FIG. 2. *Wyleyia valdensis* gen. et sp. nov. Holotype: right humerus. A, reconstruction of proximal aspect; B, reconstruction of palmar aspect, $\times 1\frac{1}{4}$; C, diagram showing approximate angle between proximal (1) and distal (2) articulations. Abbreviations used in this and other text-figures: as, anconal; bc, bicipital crest; brdp, brachial depression; dc, deltoid crest; dpc, deltopectoral crest; h, humeral head; it, internal tuberosity; lf, ligamental furrow.

Measurements (in millimetres):

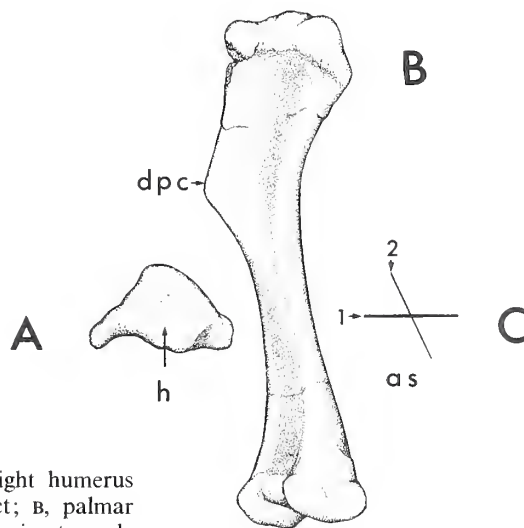
Total length as preserved	42.4
Length of deltoid crest	17.4
Length of bicipital crest	10.3
Width of shaft just distal to deltoid crest (internal-external)	4.5
Width of shaft just distal to deltoid crest (palmar-anconal)	3.3
Greatest width preserved at distal end	5.3



TEXT-FIG. 3. *Cathartes aura* (Turkey Vulture). Left humerus. A, proximal aspect; B, palmar aspect, \times approx. $\frac{1}{2}$; C, diagram showing approximate angle between proximal (1) and distal (2) articulations. Abbreviations: see legend to text-fig. 2.



TEXT-FIG. 4. *Ornithocheirus clifti*. Proximal part of left humerus (BMNH 2353). A, proximal aspect; B, palmar aspect, $\times \frac{2}{3}$. Abbreviations: see legend to text-fig. 2.



TEXT-FIG. 5. *Hypsilophodon foxii*. Right humerus (BMNH R 196). A, proximal aspect; B, palmar aspect, $\times \frac{2}{3}$; C, diagram showing approximate angle between proximal (1) and distal (2) articulations. Abbreviations: see legend to text-fig. 2.

Occurrence. Weald Clay, Lower Cretaceous, Henfield, Sussex. The ostracods in the Henfield deposits indicate that they lie about 500–600 feet below the top of the Weald Clay. This would establish the horizon as being in the middle of the Reeves Group II, in the Barremian Substage of the Neocomian Stage.

COMPARISONS

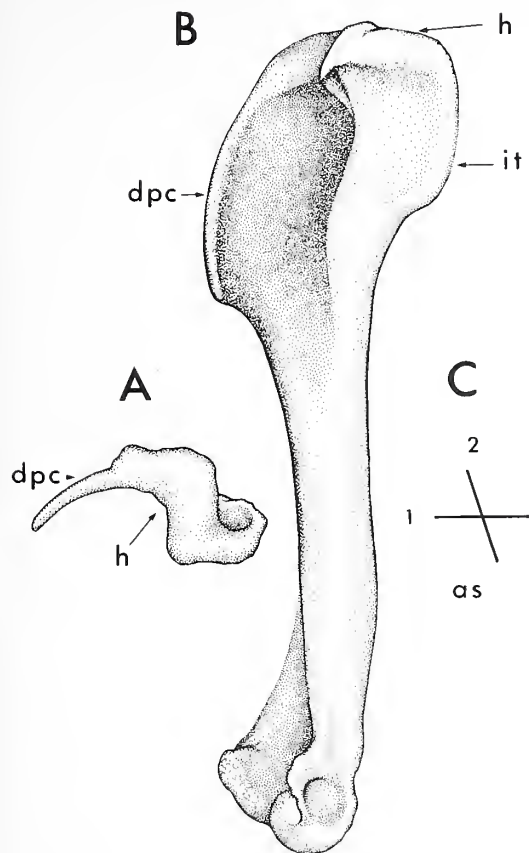
Because of the early Cretaceous age of *Wyleyia* it was felt necessary to compare it with humeri of certain archosaurs and early birds.

?Ornithocheirus clifti (Mantell). The humerus compared (BMNH 2353 and 2353a; text-fig. 4) is from the Wealden of Sussex. It resembles a bird humerus in having a thin wall and a hollow interior, but differs considerably in its general anatomy. The shaft is shorter and more massive with a large distal articulation. The articular head is fundamentally different in being saddle-shaped and concave in lateral view. The deltopectoral crest (deltoid crest in birds) also differs in being a thick projection rather than a thin blade, projecting at a much more acute angle to the plane of the proximal end.

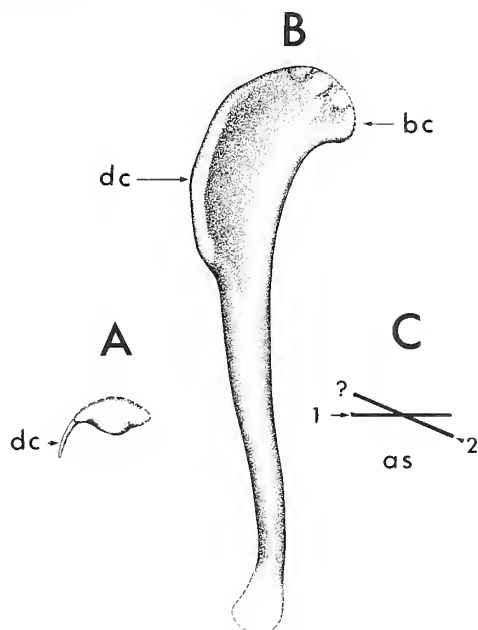
Hypsilophodon foxii Hulke. The humerus of this Wealden ornithopod from the Isle of Wight belonged to a small specimen (BMNH R 196; text-fig. 5). It differs from *Wyleyia* in several characters. Seen from above, the articulating area of the humeral head is more massive and triangular and not crescentic in shape. The bone lacks the transverse ligamental furrow on the palmar surface, the capital groove on the anconal surface, and the well-marked brachial depression at the distal end. The shaft is rather short and stout and has undergone a considerable amount of torsion, rather more than in *Wyleyia*, so that the two ends of the humerus are almost at right angles to each other. The deltopectoral crest is not blade-like but thick and blunt. Although there is some torsion present in *Wyleyia* which is certainly more than is found in modern birds, it is much less than is found in the majority of archosaurs. Some of the torsion present in the shaft of *Wyleyia* could be due to crushing.

Deinonychus antirrhopus Ostrom. Comparison was made with a cast of a humerus (AMNH 3015; text-fig. 6) of this Lower Cretaceous theropod from Montana. Like *Hypsilophodon*, it lacks the ligamental furrow of *Wyleyia* and the well-marked brachial depression; indeed, the brachialis anticus muscle has left no indication of its presence. Further, the deltopectoral crest lies in a different plane.

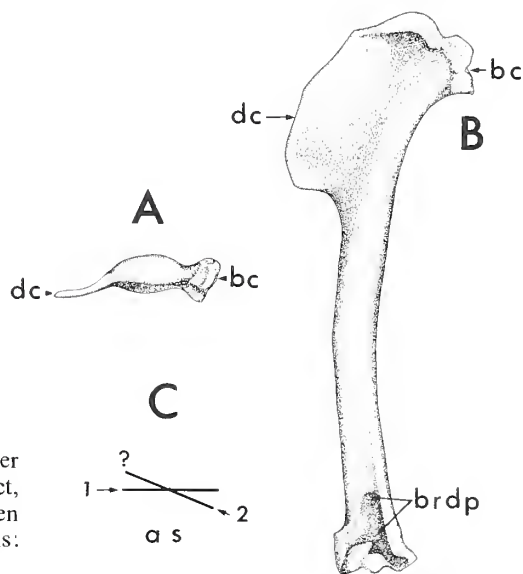
Archaeopteryx lithographica von Meyer. Comparison was made with the holotype (BMNH 37001; text-fig. 7) from the Upper Jurassic of Bavaria. Like *Wyleyia*, *Archaeopteryx* lacks most of the distinct prominences and ridges generally found in modern flying forms. The whole bone is slender and shows about the same amount of torsion in the shaft. The proximal end bears a simple head, slightly swollen and laterally elongated with a rounded articulation surface. The deltoid crest, however, diverges less abruptly from the shaft and is set almost at right angles to the palmar surface.



TEXT-FIG. 6. *Deimonychus antirrhopus*. Right humerus (AMNH 3015). A, proximal aspect; B, palmar aspect, $\times \frac{1}{2}$; C, diagram showing approximate angle between proximal (1) and distal (2) articulations. Abbreviations: see legend to text-fig. 2.



TEXT-FIG. 7. *Archaeopteryx lithographica*. Right humerus (BMNH 37001). A, proximal aspect; B, palmar aspect, $\times 1$; C, diagram showing approximate angle between proximal (1) and distal (2) articulations. Abbreviations: see legend to text-fig. 2.



TEXT-FIG. 8. *Ichthyornis dispar*. Right humerus (after Marsh, 1880). A, proximal aspect; B, palmar aspect, $\times 1\frac{1}{4}$; C, diagram showing approximate angle between proximal (1) and distal (2) articulations. Abbreviations: see legend to text-fig. 2.

Hesperornis Marsh and *Enaliornis* Seeley. These flightless birds had very reduced wings. The humerus of *Hesperornis*, from the Upper Cretaceous of Kansas, is long and slender with few prominent features; the humerus of *Enaliornis* (Lower Cretaceous of England) is unknown.

Ichthyornis Marsh. Plates in Marsh (1880; text-fig. 8) and a specimen in the BMNH A 905 were used for this comparison, although humeri of *I. victor* Marsh were distorted by crushing. The humeri of this Upper Cretaceous bird from Kansas resemble *Wyleyia* in the proportions of the various parts (including the length of the deltoid crest), the large deltoid crest projecting in approximately the same plane as the palmar surface, and the relatively flat nature of the proximal portion. They differ, however, in that (a) the bicapital crest does not project so far and is reduced in thickness, (b) the impression of the branchialis anticus muscle is shallow proximally and lies nearer the internal side of the shaft than the external.

CONCLUSIONS

Comparison with other Mesozoic material and Recent birds suggests that the new humerus is also that of a bird, showing the greatest resemblances to *Archaeopteryx* and *Ichthyornis*.

The fact that the humeri of *Archaeopteryx*, *Ichthyornis*, and *Wyleyia* are similar would not, however, seem sufficient reason to place *Wyleyia* in either the Archaeopterygiformes or Ichthyornithiformes, which would imply an affinity with the corresponding Jurassic or Cretaceous forms. It therefore seems advisable to consider the new genus *incertae sedis* until further evidence of affinity is forthcoming.

Acknowledgements. We wish to thank Mr. J. F. Wyley for making this specimen available for description; Dr. A. J. Charig (British Museum (Natural History)) for criticizing the manuscript; Miss M. L. Holloway for the line drawings; and Messrs. T. Parmenter and C. Keates for taking the photographs.

Abbreviations. BMNH—British Museum (Natural History); AMNH—American Museum of Natural History.

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A PROBLEMATICAL DINOFLAGELLATE FROM THE TERTIARY OF VIRGINIA AND MARYLAND

by DEWEY M. MCLEAN

ABSTRACT. *Inversidinium exilimurum*, gen. et sp. nov., a problematical dinoflagellate recovered from the Aquia Formation (Upper Paleocene) of the Virginia–Maryland Coastal Plain, displays an atypical peridinioid outline characterized by a truncated antapex which ruptures to form a hitherto unreported type of antapical excystment apparatus; antapical archeopyles are exceedingly rare among the dinoflagellates.

IN the Cretaceous and Tertiary dinoflagellate and acritarch assemblages of the Virginia–Maryland Coastal Plain are problematical palynomorphs of which the morphological interpretation and taxonomic treatment cannot be unequivocally assessed. A cyst recovered from the marine Aquia Formation (Upper Paleocene), displays characteristics which suggest affinities with the Pyrrhophyta; however, interpretation of these characters is subjective. Its outline compares most closely with that of a peridinioid but is atypical by having a truncated antapex which lacks antapical horns; the excystment apparatus (= archeopyle?) does not conform in shape or position with any thecal plate, or combination of plates, known to the author; and features of the periphragm which seemingly correspond in position to a cingulum and sulcus are reflected not by indentations, but by convex-outward folds. Orientation of the cyst is subjective. By comparison with a general peridinioid outline, the pointed tip of the periblast is considered apical and the truncated end showing the excystment feature, antapical. In addition, convex-outward folds of the periphragm which correspond in position to a cingulum and sulcus seemingly reflect dorsal and ventral surfaces, respectively. Following this orientation, the cyst is interpreted to have a hitherto unreported type of antapical excystment apparatus. Antapical archeopyles are exceedingly rare among dinoflagellates.

All samples are from the Aquia Formation (Upper Paleocene) of the Virginia–Maryland Coastal Plain from outcrop localities along the Potomac River south of Washington, D.C. They are:

Locality 1. Prince Georges County, Maryland. Reference: U.S. Geol. Svy. Anacostia, Md.–D.C. quad., 7.5 minute series; geog. coords. $38^{\circ} 45' 10''$ N. Lat., $76^{\circ} 59' 15''$ W. Long. Approx. 45 feet (14 m) of lowermost Aquia glauconitic quartz sands are exposed about 0.5 mile (0.80 km) west of Friendly, Maryland, along the stream occurring immediately south of, and paralleling, the Old Fort Road.

Locality 2. Stafford County, Virginia. Reference: U.S. Geol. Svy. Passapatanzy, Va.–Md., quad., 7.5 minute series; geog. coords. $38^{\circ} 22' 15''$ N. Lat., $77^{\circ} 17' 50''$ W. Long. This is the type locality of the Aquia Formation. Approximately 70 feet (21 m) of Aquia glauconitic quartz sands are exposed in the bluffs along the south bank of Aquia Creek, about 0.5 mile south-east of the Maryland–Virginia Monument No. 37.

Locality 3. Stafford County, Virginia. Reference: U.S. Geol. Svy. Passapatanzy, Va.–Md., quad., 7.5 minute series; geog. coords. $38^{\circ} 20' 35''$ N. Lat., Long. $77^{\circ} 17' 17''$ W. Long. Approximately 35 feet (10 m) of Aquia glauconitic quartz sands are exposed in the bluffs along the south bank of Potomac Creek, from 0.5 and 0.15 mile west of the Maryland–Virginia Monument No. 35.

Standard acid maceration techniques were utilized for all samples. Palynomorphs were concentrated by use of ZnBr (sp. gr. = 2.0), and were darkened for study and photomicrography by acetolysis. Slides are stored at Stanford University and are assigned Stanford University Paleontological Type Collection (= SUPTC) numbers. Coordinates are measurements in millimetres to the right (R) or left (L) and toward the top (+) or bottom (−) of the slide from an index cross engraved on the coverslip near its lower left corner.

SYSTEMATIC PALAEOONTOLOGY

Division PYRRHOPHYTA Pascher

Class DINOPHYCEAE Pascher

Genus INVERSIDINIUM nov.

Derivation of name. Latin, *inversus*, inverted, with reference to the antapically oriented archeopyle.

Type species. *Inversidinium exilimurum* sp. nov.

Diagnosis. Bi-layered cyst; periblast outline peridinioid with pointed apex and truncated antapex; lacks indications of tabulation; endoblast outline variable. Convex-outward folds of the periblast reflect cingulum and sulcus. Excystment apparatus (= archeopyle?) antapical; forms by rupture of antapical tips of periblast and endoblast. Periphragm and endophragm externally smooth to granulose.

Remarks. *Inversidinium exilimurum*, gen. et sp. nov., is assigned to the Pyrrhophyta on the basis of its generalized peridinioid shape, excystment apparatus, and features of the periphragm that seemingly reflect a cingulum and sulcus.

Inversidinium exilimurum sp. nov.

Plate 90

Derivation of name. Latin, *exilis*, thin or meagre; *murus*, wall-in reference to the thin, transparent nature of the periphragm and endophragm.

Holotype. Pl. 90, figs. 1–2. Loc. 2, sample 3384, SUPTC 10079 (R26.0, +12.5).

EXPLANATION OF PLATE 90

Inversidinium exilimurum, gen. et sp. nov.; all specimens are from the Aquia Formation (Upper Paleocene) of the Virginia–Maryland Coastal Plain.

Figs. 1–2. Holotype, $\times 920$. 1, Shows details of ventral longitudinal ridge; dorsal transverse ridge is shown in optical section on left side of specimen. 2, Shows general peridinioid outline of periblast and triangular outline of endoblast; note truncated antapex of periblast and complete absence of antapical horns. Dimensions: $L \times W = 50 \times 40 \mu\text{m}$. Loc. 2, sample 3384, SUPTC 10079 (R26.0, +12.5).

Figs. 3, 6. Two focus levels of one specimen oriented with antapex facing the observer and ventral surface facing up. 3, Transverse optical section at level of dorsal transverse ridge, $\times 1340$. The bulge facing up in the photograph shows in cross section the ventral longitudinal ridge. 6, Antapical tip of periblast, $\times 1710$. Maximum width of specimen $35 \mu\text{m}$. Loc. 1, sample 3370, SUPTC 10080 (R14.2, +4.3).

Figs. 4–5. Two views of one specimen, $\times 925$. 4, Shows optical section of triangular endoblast; note ruptured antapex of both periblast and endoblast. 5, Phase contrast, shows details of ruptured antapex of both periblast and endoblast. Dimensions: $L \times W = 54 \times 45 \mu\text{m}$. Loc. 2, sample 3390, SUPTC 10081 (R19.0, +12.0).

Figs. 7–9. Several focus levels of one specimen oriented with antapex facing observer and ventral surface facing up, $\times 2000$. 7, Transverse optical section at level of dorsal transverse ridge showing optical section of ventral longitudinal ridge. 8, Focused on extreme antapical tip of periblast. 9, Antapical view of periblast focused slightly deeper into specimen than in fig. 8, showing what is interpreted to be a circular excystment aperture (= archeopyle?). Maximum width of specimen $40 \mu\text{m}$. Loc. 2, sample 3392, SUPTC 10082 (R24.3, +1.5).



1



2



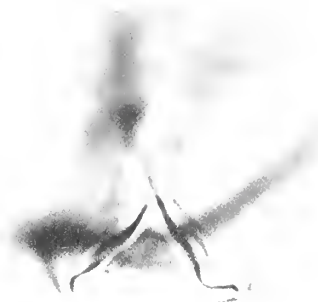
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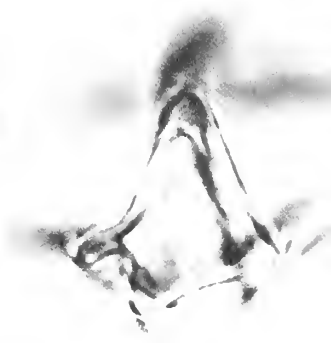
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8



9

Diagnosis. As for genus.

Description. Periphragm transverse section elliptical at widest part and triangular at antapex. Endoblast dorso-ventral outline roundly triangular with elliptical transverse section at widest part and triangular cross section at antapex; endoblast occupies hypotractal portion of periblast. A narrow convex-outward fold 1–3 μm wide traverses periblast dorsal surface at its widest part; a similar fold extends longitudinally along the periblast ventral midline from the antapex to about midway between the widest part of the periblast and the apex. Excystment apparatus (= archeopyle?) forms by posterior tip of endophragm breaking away and posterior tip of periphragm rupturing irregularly. Periphragm and endophragm less than 1 μm thick, transparent, and externally smooth to granulose.

Dimensions. Holotype $L \times W = 50 \times 40 \mu\text{m}$. Observed range (eleven specimens measured): length 45–60 μm (mean 51 μm); width 32–52 μm (mean 41 μm).

Remarks. The narrow convex-outward folds on the dorsal and ventral surfaces of the periblast are commonly folded secondarily such that the resultant deformed folds have the appearance of furrows. Rotation of such specimens into both lateral and polar views, so that the features could be examined in cross section, confirmed that they are convex-outward folds that had been folded secondarily and are not furrows. Rupture of the periphragm along the crests of the folds has not been observed.

Comparison with similar species. *Inversidinium exilimurum*, gen. et sp. nov., is unique among the Pyrrhophyta with the possible exception of *Wetzelietta* (*Rhombodinium*?) *minuscula* Alberti, 1961, which resembles the new species in appearance. They differ in details concerning the antapex and shape of the endoblast. According to Alberti's description, *W. (R?) minuscula* exhibits two antapical protrusions separated from one another by means of a longitudinal split; *I. exilimurum*, on the other hand, has a sharply truncated antapex that lacks any vestige of protrusions (horns) and has an outward-convex fold along its ventral midline instead of a split. The endoblast of *W. (R?) minuscula* is rhombohedral in outline and nearly fills the periblast whereas that of *I. exilimurum* is triangular in dorso-ventral outline and occupies the hypotractal portion of the periblast.

W. (Rhombodinium?) minuscula lacks the intercalary type archeopyle typical of *Wetzelietta*, thereby raising questions concerning its assignment to *Wetzelietta*. Should later investigations show it to have an antapical excystment apparatus, it should then be transferred to *Inversidinium*.

Occurrence. Loc. 1, less than 1% of the phytoplankton content through all but the upper 20 feet of the section; Loc. 2, less than 1% of the phytoplankton content throughout the section; Loc. 3, less than 1% of the phytoplankton content of one sample taken 20 feet above the base of the section.

Acknowledgements. It is a pleasure to express my thanks to Dr. W. R. Evitt of Stanford University who offered many helpful suggestions during this study which was made possible by National Science Foundation Grants GB 4702 and GB 4711 (to Evitt).

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THE APPLICATION OF ELECTRON MICROSCOPY TO PALAEOONTOLOGY

by M. D. MUIR *and* W. L. DIVER

THE Palaeontological Association and British Micropalaeontological Group were joint sponsors of the Symposium 'The Application of Electron Microscopy to Palaeontology' held on 11 September 1972, as a part of the 5th European Electron Microscope Congress, EMCON 72. The following four papers form part of the proceedings of the Symposium and illustrate how both the transmission electron microscope (TEM) and the scanning electron microscope (SEM) can be used in a wide range of palaeontological applications to give information on a variety of specimens that would be unobtainable by any other means. Most speakers emphasized that the reliable interpretation of electron micrographs requires supporting evidence from a thorough light optical microscope investigation.

In the general discussion that followed the meeting, it became clear that combined studies using all available techniques on a limited amount of material offered much greater returns in terms of understanding than large numbers of 'pretty pictures' produced using only one technique. Several novel preparation techniques were presented, all of them giving significantly better results than conventional methods. The short discussions printed here illustrate some of the interesting points raised at the meeting.

It was evident at the meeting that applications of electron microscopy (both TEM and SEM) will increase rapidly in all branches of palaeontology as access to equipment becomes possible for more and more palaeontologists. It is to be hoped that all new palaeontological electron microscopists will show such care in specimen preparation, instrument operation, and interpretation of results as was evident in the papers presented by the contributors to the EMCON 72 Symposium.

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MORPHOLOGY AND EVOLUTION OF THE EYE IN UPPER CAMBRIAN OLENIDAE (TRILOBITA)

by E. N. K. CLARKSON

ABSTRACT. The eyes of selected olenid species from Scandinavian concretionary shales were examined with the scanning electron microscope. Though these eyes are small, many previously unknown details were visible, including the 'peripheral zone' of *Olenus wahlenbergi* and other genera. Reconstructions, prepared by camera-lucida techniques, show the eye and the whole cephalon of certain species.

In early olenids the visual surface was dehiscent in the adults and is preserved only in meraspids; in later genera the ocular suture became fused and the visual surface was retained. Details of lens distribution and manner of emplacement are described in *Peltura minor*, *P. scarabaeoides*, and *Ctenopyge* (*Mesoctenopyge*) *similis*. Evolutionary changes in the structure and shape of the eye are clear in different lines of descent. Some of the observed modifications are thought to be due to paedomorphosis.

Some comments on the mode of life of olenids are also given.

THE EYES OF CAMBRIAN TRILOBITES

AT the end of the Cambrian there was a major crisis in the history of the trilobites. Most of the rather undifferentiated Upper Cambrian stocks became extinct and were replaced, first by a number of short-lived Tremadoc groups, and then soon afterwards by several very distinct suborders which came to dominate the Ordovician trilobite fauna (Whittington 1966).

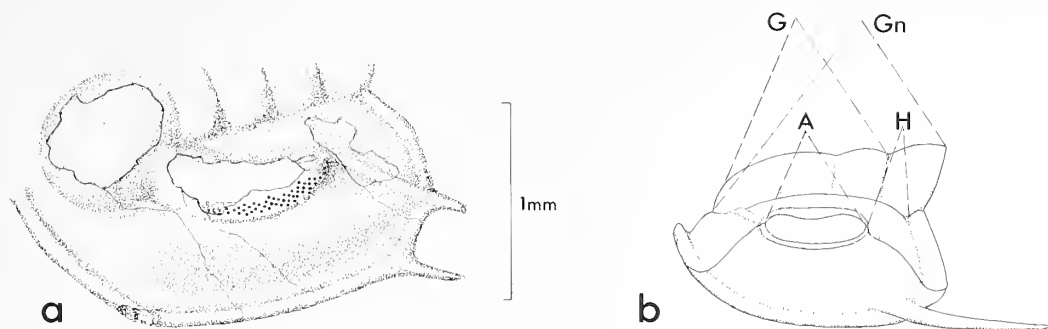
This late Cambrian crisis had far-reaching effects on the evolution of trilobites. Certain morphological features which had remained rather conservative during Cambrian times became much more diversified and novel kinds of functional organization came into being. Amongst the characters affected was the visual system, and the new trilobite stocks of the early Ordovician evolved eyes exhibiting greater variety than those possessed by their Cambrian forebears. Not only did the primitive holochroal organization, which was already established in the earliest Cambrian trilobites, become modified in many different ways, but there first appeared an entirely new kind of visual organ, the schizochroal eye (which may have been derived from a holochroal ancestral pattern by paedomorphosis according to Clarkson (1971). This kind of eye is probably confined to the suborder Phacopina, which persisted from Arenig to Famennian times.

Though some of the many different kinds of eye in Ordovician and later trilobites have been quite extensively studied there is at present so little information on the eyes of Cambrian genera that we do not have a comprehensive picture of the evolution of the eye in trilobites. One good reason for this is that the eyes in adult specimens of Cambrian trilobites are not very often preserved, though in a few cases intact lenticular surfaces have been reported. Thus Walcott (1910) noted lenses in the eyes of meraspids of the Lower Cambrian *Olenellus gilberti* Meek and Öpik (1961, p. 57) and later Jell (1970, p. 306) and Jago (1972, p. 230) discussed the presence of lenticular surfaces in Cambrian pagetiids, where the eye has a 'schizochroal' appearance.

I am not aware that any visual surfaces are known to be preserved in Middle Cambrian trilobites, but amongst the Upper Cambrian fauna certain genera with intact eyes occur sporadically, and different kinds of eyes may be preserved within particular groups such as the family Olenidae, which are the subject of the present study. Lindström (1901, p. 29, pl. III) in his monograph on trilobite eyes figured the visual surfaces of the olenid genera *Peltura*, *Sphaerophthalmus*, and *Ctenopyge*, illustrating highly magnified lenses, thin sections, and the librigenae in position on the cranidium. As a matter of historical interest, he regarded the olenids as the oldest known 'oculate genera', and did not think that earlier trilobites had functional eyes. Upper Cambrian trilobite eyes were also described by Öpik (1967) in his monograph of the Mindyallan fauna of Queensland, where, amongst others, the large and well-preserved eyes of *Blountia mindycrusta* Öpik were illustrated.

Öpik (1967, p. 54) discussed the question of the preservation of the eye in Cambrian trilobites very thoroughly. Noting that the visual surface is rarely preserved, he suggested that in life the visual surface had been bounded by a peripheral *circumocular suture*, and that during ecdysis or after death the whole lentiferous area would fall out and not be preserved. This suture comprised the *palpebral suture* and the *ocular suture* (text-fig. 2a), which ran along the upper and lower borders of the visual surface respectively, meeting at the front and rear. He pointed out that in post-Cambrian trilobites, the lower part of the circumocular suture or *ocular suture* became fused, so that during ecdysis, the visual surface separated only along its contact with the palpebral lobe. The visual surface adhered to the librigena and thus stood a much higher chance of preservation. Some of the Upper Cambrian trilobites also had non-functional ocular sutures and, as Öpik pointed out, fusion of the visual surface with the librigena became reasonably common in Upper Cambrian times in unrelated groups, and is not a character of phylogenetic significance. The only alternative possibility is that in many Cambrian trilobites the visual surface was so delicate that its preservation in any case would be unlikely; but then one would expect there to be a ragged edge to the eye-socket, to which the visual surface was attached, and this is not so. I therefore agree entirely with Öpik's suggestions, adding that there is some evidence of the ocular suture having been functional only in adult trilobites. The meraspids of *O. gilberti* Meek described by Walcott (text-fig. 1a) and sometimes very small holaspids of Ordovician *Flexicalymene* species from the Waynesville formation, Ohio, have intact visual surfaces with visible lenses. Adult individuals of these species, however, never have visual surfaces preserved, although in mature *Flexicalymene* the lower surface of the palpebral lobe, along the line of the palpebral suture, may be denticulate as if elongate prisms or 'lenses' had originally rested there.

In the course of the present study, I found some small but complete visual surfaces in meraspids of *Olenus wahlenbergi* Westergård. The retention of the visual surface in *Parabolina* and other derivatives of *Olenus* may be seen as an example of paedomorphic development, in which the ocular suture, which had been functional only in the adult, was even there dispensed with. The role of paedomorphosis in the evolution of olenid and other eyes is discussed later.



TEXT-FIG. 1. *a. Olenellus gilberti* Meek. Meraspid figured by Walcott (1910, pl. 36, fig. 4c; pl. 43, fig. 5, 6) in oblique lateral view with the individual lenses visible. Where the visual surface has been broken away at x, impressions of the lenses are left on the underlying matrix. Lower Cambrian, Ptarmigan Pass, Alberta. Smithsonian Institution Catalogue number 56828f.

b. Olenus wahlenbergi. Lateral view of cephalon reconstructed, showing the 'eye-indices' of Struve (1958). A = length of visual surface. H = Distance from posterior edge of eye to posterior border furrow. G = prelabellar to occipital furrow. Cn = prelabellar furrow to rear edge of occipital ring.

THE OLENIDS

Because so many Cambrian trilobites had functional ocular sutures, it is unlikely that we shall ever obtain a good record of the evolution of the most ancient trilobite eyes. Studies of the detailed morphology of the eyes of single species can, however, contribute towards this end, and when the phylogeny of Cambrian trilobites becomes better known these may be seen more clearly in an evolutionary perspective. In addition, it is fortunate that there is one family at least, the Olenidae, where the phylogeny is well known and in which material for study is so well preserved and abundant that at least some features of the evolutionary history of the visual system within this family can be elucidated.

The Olenidae are a geographically widespread family, which arose early in Upper Cambrian times and abounded to the end of the Tremadoc. A few genera persisted into the Ordovician, and *Triarthrus* until the close of the Middle Ordovician. Olenid faunas are best known in Scandinavia where they have been the subject of many studies culminating in the major monographs of Westergård (1922) and Henningsmoen (1957); they are common throughout the Acado-Baltic province and in the Tremadoc of South America (Harrington and Leanza 1957), and there are isolated occurrences elsewhere.

In the alum shales of the Oslo region and the old quarries of Andrarum, in Scania, there occur stinkstone concretions with vast numbers of disarticulated olenid fragments, frequently with very fine structure preserved, and in full relief with no trace of flattening. In the early genera, *Olenus*, *Leptoplastus*, *Eurycare*, and others, the lenses are preserved only in small meraspids. The visual surface in adults is unknown, but even so there remains, at least in the best-preserved adults of *Olenus*, a wealth of interesting detail on the palpebral lobe and the lower rim or eye-socket, which suggests that the whole region peripheral to the visual surface may have been a highly sensory zone. Later genera, which include *Sphaerophthalmus*, *Ctenopyge* s.l., *Peltura*,

and *Parabolina*, retained the visual surface, often with excellent details of the lenses and peripheral zones. Though no details of subsurface layers in the eye are preserved, but only the lenses, it is hoped that the present study will be a useful contribution to olenid morphology in general, and to the understanding of the evolution of trilobite visual systems. Because the olenid faunas of Scandinavia are so well known I have made extensive reference to Westergård (1922) and Henningsmoen (1957) in which full accounts of morphology and complete synonymies are given. Following Henningsmoen both proposed international and local Norwegian zones are given, e.g. *Olenus wahlenbergi* occurs in Zone II (2a β).

METHODS AND TECHNIQUES

Since all the material available to me consisted of disarticulated fragments the work on olenid eyes fell naturally into two parts. The first task was to reconstruct the cephalon with the cranidium and librigenae fitting together as they were originally assembled in the living animal. This was to show the visual surface (where present) in its original relationship to the palpebral lobe, and the eye in its true relationship to the cephalon. The second phase of the work was the detailed study of the visual surface and the bordering regions (palpebral lobe and eye-socle) with the scanning electron microscope (SEM). With this information, certain inferences could be made about the evolution of the eye in the family, though it was not possible to study all the genera.

Technique of reconstruction. The reconstructions were made from cranidia and librigenae, accurately drawn with a Wild-Heerbrugg microscope with an M5 drawing tube or 'camera-lucida'. For each species several undamaged or nearly complete cranidia were drawn in dorsal, lateral, and frontal views; the plane of the palpebral lobe being normally taken as horizontal. High magnification drawings were also made in oblique lateral view. Where the specimen was slightly damaged appropriate details could be filled in with reference to other cranidia.

Librigenae of equivalent size were also selected. Each was drawn in an orientation where its camera-lucida image fitted the drawing of the reconstructed cranidium, with the slope of the cheek region, and the edges of the librigena and fixigena matching all the way along the suture. In the final drawing the dimensions of the parts of the reconstructed cephalon were the same in all the different views.

Scanning electron microscopy. Both gold-palladium and aluminium coatings were used; the latter were found to be equal to the former in conducting properties. Visual surfaces, palpebral lobes, and eye-socles were all examined in different orientations, to build up a complete picture of the eye. Where the lenses had become detached from the eye in some areas, their total thickness was apparent. Unexpected features visible with the SEM were the remarkable peripheral zones in the eye of *Olenus wahlenbergi*, which are recorded in detail below.

Deposition of specimens. All olenid specimens used in this study are in the collections of the following institutes: Palaeontologisk Museum, Oslo (P.M.O.); Geology Department, University of Lund (LO); British Museum (Natural History), London (BMNH); Grant Institute of Geology, Edinburgh (Gr. I.).

OLENID EYE MORPHOLOGY

Subfamily OLENINAE

Olenus s.s. is the earliest olenid genus and seems to have been the rootstock of the whole family. The eye of *O. wahlenbergi*, described below from exceptionally well-preserved material, is representative of early olenids as a whole and eyes of this kind were retained by various later genera which include *Leptoplastus* and *Eurycare*. Later leptoplastines, however, had eyes of modified form.

In adults of *Olenus* the visual surface has not been found, but small meraspids have been found with the visual surfaces still intact, so that some details of their structure can be determined. In the adults, fine details of the palpebral lobes and eye-socles remain, and these can be reconstructed in their original relationship.

Only two genera of the Oleninae, *Olenus* and *Parabolina*, have been studied. *Parabolina* is probably a derivative of *Olenus* (see p. 744) in which the adult has a visual surface of similar kind to that in the meraspids of *Olenus*. The palpebral lobe, moreover, though inflated and of peculiar form, is confluent with the ocular ridge, again as in immature specimens of *Olenus*. These two factors amongst others are suggestive of a pedomorphic origin for the eye of *Parabolina*, a situation paralleled by *Peltura* and more distantly by other olenids.

Olenus wahlenbergi Westergård, 1922

1922 *Olenus Wahlenbergi* n. sp; Westergård, p. 128, pl. IV, figs. 5–14.

1957 *Olenus wahlenbergi* Westergård 1922; Henningsmoen, p. 110, pl. 3 (with complete synonymy).

Plates 91, figs. 1–6; 92, figs. 1–4; text-fig. 2 *a–j*

Material. Twenty-two blocks of topotype material from Andrarum, Zone II (2a β). Gr I 5514–5536.

Remarks. The gross morphology described by Westergård is supplemented by my reconstruction which shows the librigenae in place (text-fig. 2, *c–e*). Both lateral and frontal views show how the genal spines were in life directed horizontally and may be interpreted as props for supporting the cephalon on the sea floor. The anterior arch (Clarkson 1966*b*) is well developed, though it might have been partially blocked by the hypostome.

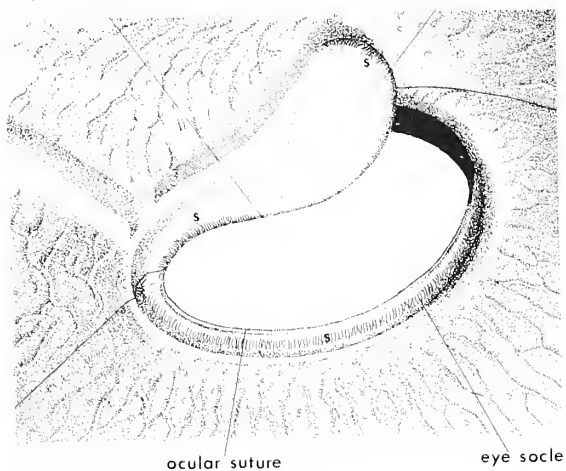
Development. Though the ontogenetic development of *O. wahlenbergi* has not been documented in detail, Strand's (1927) description of ontogeny in *O. gibbosus* show a broadly comparable mode of development. Many larval stages of *O. wahlenbergi* are present in the material which I studied, those figured in text-fig. 1 *g, h*, and *j* being close in morphology to Strand's stages 8 or 9 (length 0.70. – 0.71 mm) and 11 (length 1 mm). Strand remarks upon the presence of continuous eye-ridges from the earliest stages, though the severance of these from the palpebral lobe in later development was not noted. The equivalent stages to Strand's stages 8 and 9 are here referred to as meraspids, following Whitworth (1970).

Structure of the cuticle. At high magnifications (over $\times 1000$), the external surface of the palpebral lobe, eye-socle, and other parts of the exoskeleton can be resolved into raised polygons, all of the same general size and of semi-regular form (Pl. 91, fig. 3). Such polygons also underlie the ridges of the alimentary prosopon. They are found only on the external surface and have no internal expression. They seem to be similar to the 'cell polygons' of modern arthropod cuticles (Dalingwater, in press); each of the underlying cells which secretes the cuticle contributes a single 'tile' to the mosaic which forms the whole cuticle, and its form is retained on the outside of the cuticle. Though cell-polygons are present in other olenids they have not been found so clearly preserved as in *O. wahlenbergi*. Fractured cuticular surfaces show radial structures though these have not been investigated further.

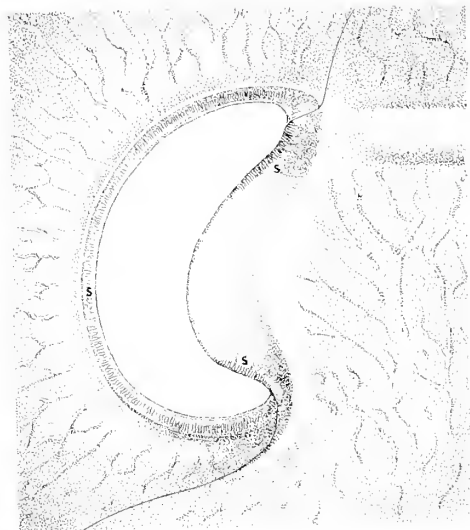
Eye-morphology: Meraspid eyes. The visual surface is present in meraspids where the length of the eye

palpebral suture

palpebral lobe

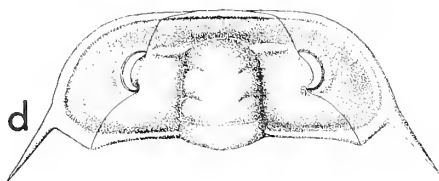


a



b

1 mm
(a,b,c,g,h,j)



d



c

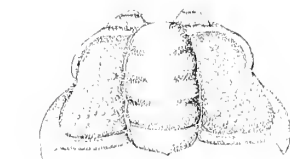


e

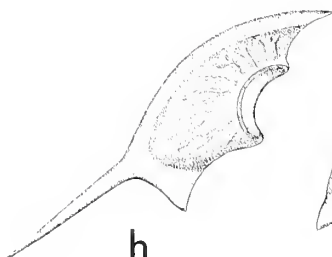
10 mm
(d,e,f)



f



g



h



j

does not exceed 0.45 mm. In these the external surface of the lentiferous area is smooth, though examination of internal surfaces shows the undersides of the lenses, which are small and weakly convex. Preservation of these small structures is not particularly good, and therefore details of their structure and arrangement are indeterminate. The eye-socle is distinct from the visual surface, though at this stage in development does not exhibit the vertical ridges of the adult (Plate 91, fig. 2).

In meraspids the palpebral lobe is at first very narrow, and is connected to the ocular ridge (text-fig. 1g). Later it widens and eventually, when the eye has attained a length of more than 0.75 mm, it becomes separate from the ocular ridge. The specimen illustrated in text-fig. 2j, in which the ornament of the fixigena is still pustulose, shows the beginnings of separation of the palpebral lobe from the ocular ridge. In adult specimens, the pustulose ornament is replaced by the ridges of the prosopon (Öpik, 1961), and the ocular ridge does not connect with the palpebral lobe, but is separated from it by a pronounced channel. It is noteworthy that the visual surface in juveniles is first of all directed more anteriorly, and only later commands a more lateral field of view.

Adult eyes. Sometime after the meraspid stages illustrated in text-fig. 2 h, j, the ocular suture must have been effective, for there is never any trace of the visual surface thereafter. The visual surface must have been reniform and of moderate height, though not spherical or globular. It was set opposite S2 with its posterior edge set slightly further from the mid-line so that the long axis of the eye (line joining the anterior and posterior edges) made an angle of about 10° with the exsagittal plane. This contrasts with the situation in meraspids where the equivalent angle may be up to 45° . Eye-indices (Struve 1958): A/G 37%, A/Gn 30%, H/A 108% (text-fig. 1b). The palpebral lobe is reniform, separated from the fixigena by a distinct palpebral furrow, depressed centrally, and rising anteriorly and posteriorly to low elevations (the rear elevation is the more prominent). From these elevations the surface plunges very steeply and the palpebral lobe narrows as it joins the eye-socle. The surface of the palpebral lobe is rather smooth but becomes highly ornamented in the outer region near the facial suture. Two separate elements can be distinguished. The first kind of structure (Pl. 92, figs. 1-4) consists of thin elongated ridges, nearly normal to the outer edge of the palpebral lobe and especially prominent on its anterior and posterior elevations. On these raised areas the ridges resemble alimentary prosopon and bifurcate as they approach the edge. In the outer central part of the lobe, which lies between the two elevations, the ridges are less prominent and anastomose, forming an area of irregular polygons (Pl. 92, fig. 2), again confined to the outer part of the lobe.

Secondly, there are a number of peculiar swellings, usually elongate, situated along, or sometimes between, some of the ridges. They sometimes show a well-developed crystalline structure (Pl. 92, fig. 2), but are otherwise of indeterminate morphology. These alone have some similarity of appearance to the much more highly developed corrugated surface of the eye-socle, and might have had a similar function. They might have been the sites of glands or sensory organs. In addition, the surface of the palpebral lobe, like that of the rest of the cuticle, has many round pits, possibly the openings of perpendicular canals in the cuticle (Dalingwater, in press).

The eye-socle is a prominent band, which could on superficial inspection be taken for the visual surface itself. The true shape of the eye-socle was determined by excavating inverted librigenae, which retained their upper edges within the rock matrix and were more likely to possess intact anterior and posterior edges than specimens with the dorsal surface uppermost. From librigenae such as that figured in text-fig. 2c, it was

TEXT-FIG. 2. *Olenus wahlenbergi* (Westergård 1922). Zone II, Andrarum, Scania.

a, b. Reconstructions of the eye region of a medium-sized adult in antero-lateral and dorsal views showing the visual surface missing because of the functional ocular-suture. 's' marks the position of peripheral (possibly sensory) zones on the palpebral lobe and eye-socle. Mainly from Gr. I. 5521.

c. Part of specimen showing undamaged anterior horn of the eye-socle, lying ventral side uppermost and excavated from above. Gr. I. 5526.

d, e, f. Reconstructions of complete cephalon in dorsal, frontal, and lateral views from Gr. I. 5521 and 5522.

g. Early meraspid, slightly damaged anteriorly, approximating Strand's (1927) stages 8 or 9. Gr. I. 5523.

h. Librigena of meraspid still retaining the visual surface. Gr. I. 5524.

j. Cranidium of meraspid of about the same size, approximating Strand's stage II. Gr. I. 5525.

seen that these edges curved upwards sharply to meet the descending edges of the palpebral lobe, which are slightly recessed where they meet the eye-socle. Text-fig. 2 (*a, b*), showing the reconstructed eye, was constructed from camera-lucida drawings of a perfectly preserved palpebral lobe, and a nearly perfect librigena of a similar-sized specimen.

The vertical ridges on the eye-socle are confined to a median horizontal band, above which the socle thins abruptly (Pl. 91, figs. 4–6). These ridges are more or less vertical and parallel, but sometimes lie obliquely and anastomose with neighbours. The ridges of the palpebral lobe and eye-socle, though not really similar in appearance, form a continuous zone peripheral to the visual surface and may have been the sites of accessory sensory organs; a concept discussed in more detail later on. Since their function is not proved, it is convenient to refer to the whole complex of ridges and grooves as the 'peripheral zone', and this term is used hereafter. Many other trilobites have a similar peripheral zone, sometimes in the form of ridges and grooves, sometimes as tubercles, and sometimes as funnel-shaped pits. The existence of such a zone in *Olenus* is the earliest recorded occurrence, and it is of interest that it should apparently be much less well developed, at least in external expression, in later olenid derivatives.

Parabolina spinulosa (Wahlenberg 1821)

- 1821 *Entomostracites spinulosus*; Wahlenberg, p. 38, pl. 1, fig. 3.
 1854 *Parabolina spinulosa* Wahl.; Angelin, p. 46, pl. XXV, fig. 9; pl. XXVII, fig. 3.
 1922 *Parabolina spinulosa* (Wahlenberg); Westergård, p. 134, pl. VI, figs. 14–20.
 1957 *Parabolina spinulosa* (Wahlenberg); Henningsmoen, p. 126, pl. 1, fig. 2; pl. 3, fig. 12 (with complete synonymy).

Plate 92, figs. 5, 6; text-fig. 3 *a, b*

Material. Five blocks from Westergård's collection, University of Lund, Andrarum. Zone III (2*b*). LO 4527–31.

Remarks. The morphology of this species is very well known and I have not attempted complete restorations, but only antero-lateral views primarily to show the eye and the alimentary prosopon, drawn with a camera-lucida.

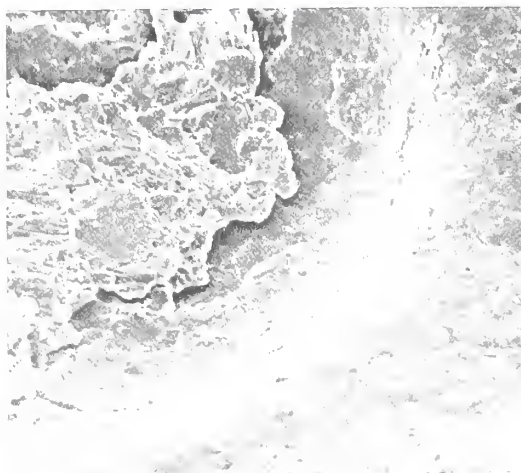
Eye-morphology. As no juveniles were available for examination this description is based upon adults. The eye is small, and set relatively close to the anterior border. It lies obliquely, and the long axis (line connecting the anterior and posterior edges) makes an angle of some 20° to the exsagittal plane. Eye-indices: A/G 25%, A/Gn 19%, H/A 270%. By contrast with an adult *Olenus*, the ocular ridge contacts the glabella and runs laterally and slightly backwards, expanding to become confluent with the swollen palpebral lobe. The palpebral lobe which is defined by a shallow palpebral furrow, is smooth with no evidence of a peripheral zone, nor is there any indication of such a zone on the (very narrow) eye-socle. The visual surface is reniform and not strongly curved, so that it subtends a rather restricted field of view directed antero-laterally. The external corneal surface is smooth and structureless (Pl. 92, figs. 5, 6), and the lenses below, which seem to be welded to the lower corneal surface, are poorly preserved, but their lower surfaces are weakly convex as in the case of meraspids of *Olenus*. Ridges of the alimentary prosopon radiate from near the base of the eye, branching towards the cephalic border and anastomosing towards the rear of the librigena.

EXPLANATION OF PLATE 91

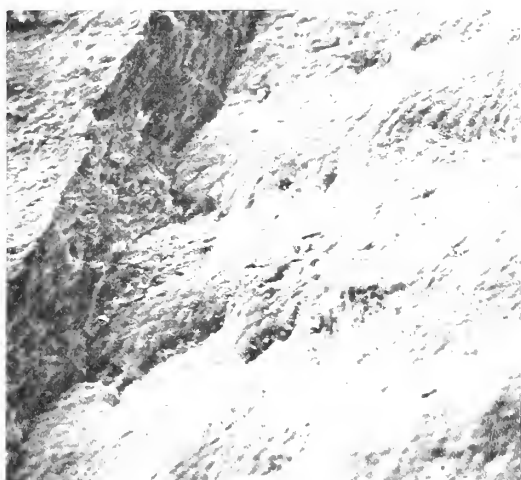
Figs. 1–6. *Olenus wahlenbergi* (Westergård 1922). Zone II. Andrarum, Scania. 1, Meraspid cephalon showing confluence of palpebral lobe and ocular ridge. Gr. I. 5514, $\times 90$. 2, Meraspid. External mould of visual surface with some parts of the cornea and underlying lenses still adherent. Gr. I. 5515, $\times 175$. 3, External mould of the surface of an adult cephalon, with cell-polygons and tubercles. The full thickness of the cuticle is seen on the left. Gr. I. 5516, $\times 220$. 4, External mould of eye-socle (inverted) showing faint striations of the sensory zone and undamaged upper rim. Gr. I. 5517, $\times 65$. 5, Outer surface of eye-socle, with prominent striations. Upper rim damaged. Gr. I. 5518, $\times 120$. 6, Same, showing striations highly magnified, $\times 2400$. Bar = 5 μm .



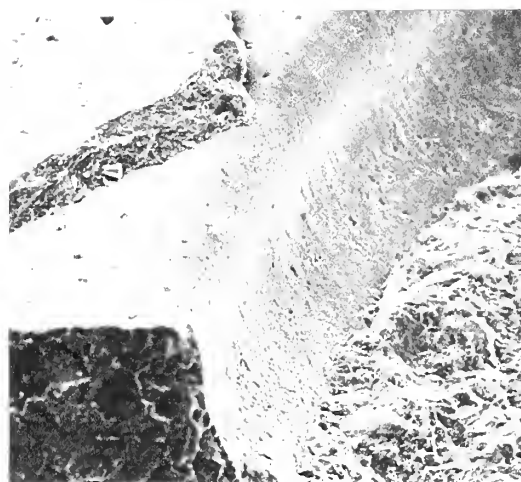
1



2



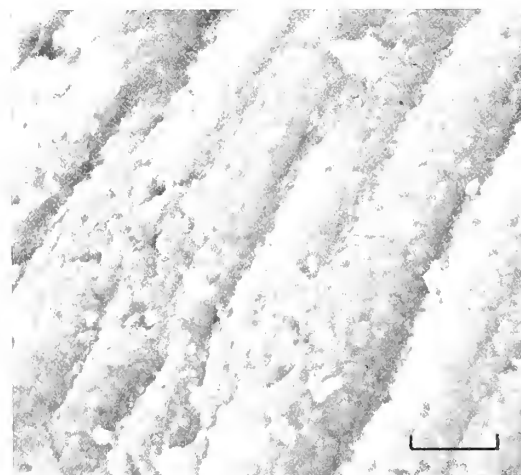
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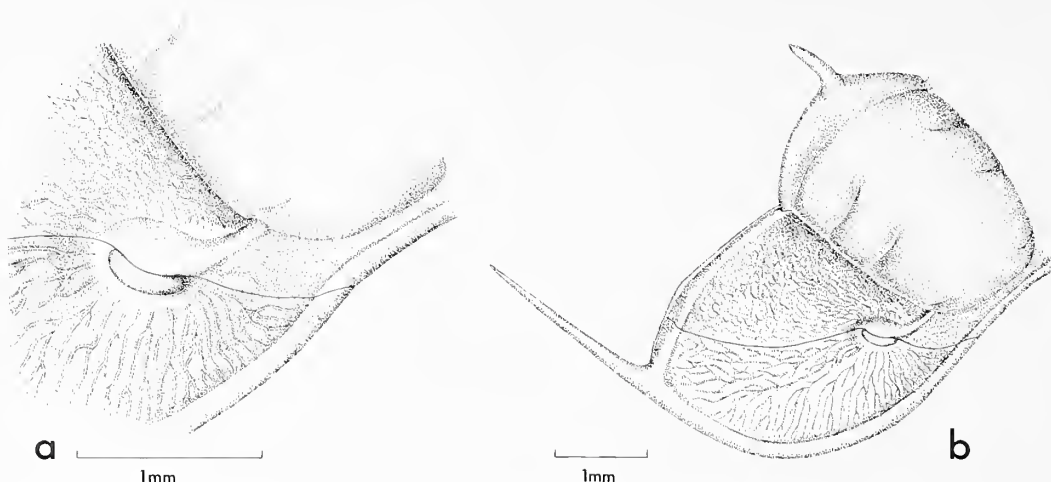
4



5



6



TEXT-FIG. 3. *Parabolina spinulosa* (Wahlenberg 1821). Zone III, Andrarum, Scania.

a. Eye region reconstructed from cranium and librigena with a near-perfect visual surface. b. Whole cephalon restored. From LO 4259, 60.

Features of the eye of *Parabolina* which bear resemblance to the eyes of meraspid of *Olenus* suggest that the *Parabolina* eye was derived from the eye of *Olenus* by pedomorphosis. These include: (i) The retention of the visual surface and obsolescence of the ocular suture; (ii) Confluence of the palpebral lobe with the ocular ridge; (iii) The anterior position of the eye and its high inclination to the exsagittal plane, and possibly (iv) the absence of surface features of the peripheral zone. Other features, such as the inflation of the palpebral lobe, are not pedomorphic and have a separate origin.

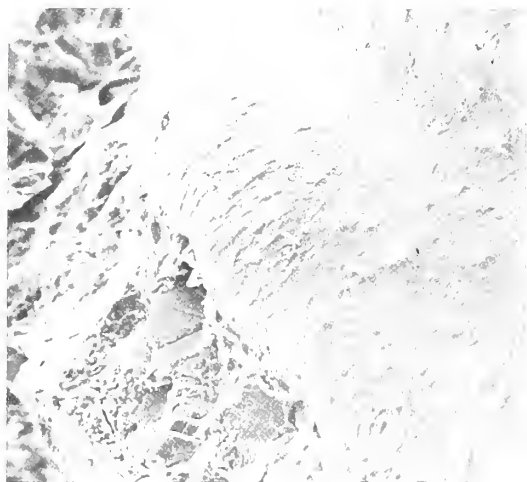
Subfamily PELTURINAE

As far as is known, all Pelturinae have eyes of the same general kind. They are small, placed far forward, shaped so as to cover only the anterior hemisphere of vision, and are normally preserved with the visual surface intact. The palpebral lobe is swollen and connected to the glabella by an unbroken ocular ridge, though this may become indistinct near the glabella. In such material of *Protopeltura* as was available for study, the eye was not well preserved, and there is less certainty about ocular morphology. Some of Westergård's figures of various species of *Protopeltura* (1922, Taf. XIV, figs. 4, 27), suggest that the visual surface is absent whereas others (Taf. XIV, fig. 20; Taf. XV, fig. 1) seem to indicate its presence; but as he also figured species of *Peltura* both with and without the visual surface, its absence in some

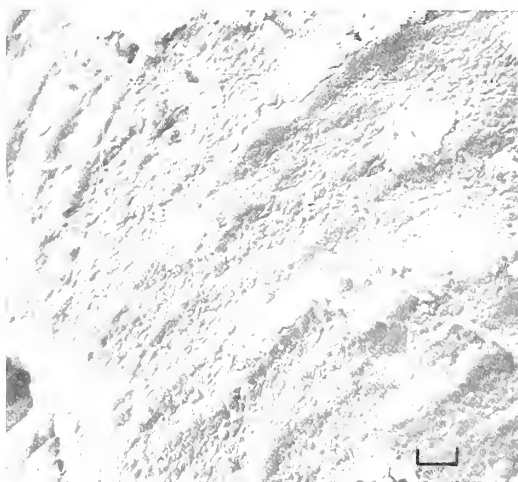
EXPLANATION OF PLATE 92

Figs. 1-4. *Olenus wahlenbergi* (Westergård 1922). Zone II. Andrarum, Scania. 1, Palpebral lobe, anterior region with structures of sensory zone. Gr. I. 5519, $\times 190$. 2, The same showing 'prosopon' and 'sensory nodes', $\times 935$. Bar = 5 μm . 3, Palpebral lobe of another specimen, anterior region with structures of 'sensory' zone. Gr. I. 5520, $\times 130$. 4, The same, magnified $\times 500$.

Figs. 5, 6. *Parabolina spinulosa* (Wahlenberg 1821). Zone III. Andrarum, Scania. 5, Librigena with eye. LO 4527, $\times 46$. 6, The same, magnified $\times 125$.



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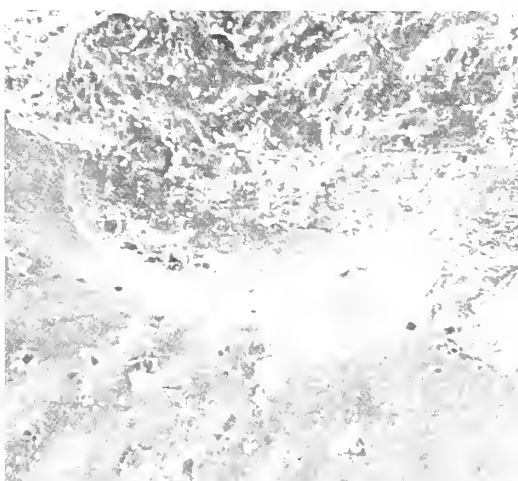
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specimens of both genera suggest breakage rather than the presence of an ocular suture. Indeed, it seems fairly certain that *Protopeltura* had an eye similar to that of *Peltura*.

Certain morphological characters of the eyes of Pelturinae can be interpreted, as with *Parabolina*, as being pedomorphic in origin. Into this category fall the small size, forward position and inclination of the long axis of the eye, the unbroken ocular ridge, the retention of the visual surface in the adult, and the over-all similarity of structure to the eyes of meraspid of *Olenus*. Henningsmoen (1957, p. 114) pointed out the resemblance between the earliest *Parabolina* species, *P. brevispina* and *Protopeltura*, suggesting that the two are closely related descendants of *Olenus*. The similarity of eye structure in *Peltura* and *Parabolina* accords with this relationship; presumably this kind of eye arose once only.

The two species discussed below were selected as having eyes representative of Pelturinae, and both of them displayed excellent structural details showing the arrangement of lenses on the visual surface.

Peltura scarabaeoides scarabaeoides (Wahlenberg 1821)

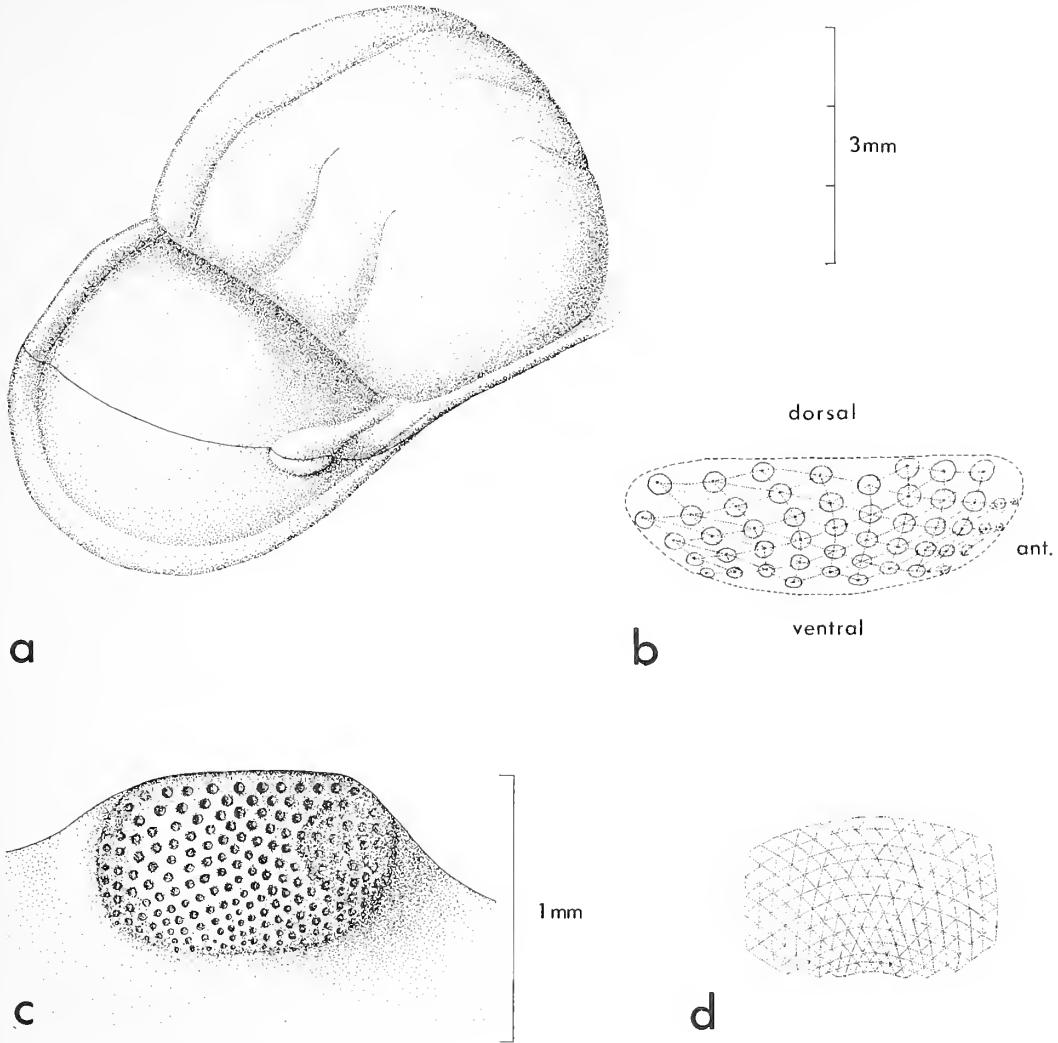
- 1821 *Entomostracites scarabaeoides*; Wahlenberg, p. 41, pl. 1, fig. 2.
- 1854 *Peltura scarabaeoides* Wahl.; Angelin, p. 45, pl. XXV, fig. 8.
- 1922 *Peltura scarabaeoides* (Wahlenberg); Westergård, p. 173, pl. XV, figs. 12, 13, 18.
- 1957 *Peltura scarabaeoides scarabaeoides* (Wahlenberg 1821); Henningsmoen, p. 237, pl. 2, fig. 1; pl. 6; pl. 25, figs. 6, 13, 14; pl. 26, figs. 1, 2.
- 1958 *Peltura scarabaeoides* (Wahlenberg 1821); Whittington, p. 200, pl. 38, figs. 1-18.

Text-fig. 4 a, c

Material. Three blocks from Slemmestad, Norway Zone Vc (2d γ) P.M.O. 29268, 29270, 29272. Also ontogenetic series BM It. 5516-9. One block from Andrarum, Scania associated with *Ctenopyge linnaarsoni*, and *Sphaerophthalmus humilis*. Zone Vc Gr. 1. 20803.

Remarks. Of all the cephalic reconstructions made to show the true position of the eye that presented here for *P. scarabaeoides* is the most tentative. Though the restoration of the cranidium posed no problems, it is very much more difficult to be certain as to how the cranidium and librigena fit together. Several camera-lucida drawings were made of the cranidium in different orientations. Various librigenae were then successively examined under the camera lucida microscope so that the image of the librigena could be seen adjacent to the previously drawn cranidium. Each librigena in turn was then manœuvred into an orientation such that the image of the whole cheek region showed a smooth unbroken curve; this was then taken as the most lifelike construction. Such a reconstruction shows that the librigenae slope down quite steeply at about 45° and that there is a moderately well-developed anterior arch, though this was probably partially blocked by the hypostoma.

Eye-morphology. The eye is small, placed far forward on the cephalon and quite near the glabella. Its long axis is inclined at 45° to the exsagittal plane. Eye-indices: A/G 20%, A/Gn 15%, H/A 350%. Whittington (1958) showed that the palpebral lobe is poorly defined, though present early in ontogeny. Thereafter it becomes more distinct and the visual surface is present in the smallest known librigenae (ibid., Pl. 38, figs. 12, 13). The material of *P. scarabaeoides* is not particularly good, and did not photograph well, hence the drawing (text-fig. 4c); lens arrangement in the early stages is better shown in *P. minor*. The palpebral lobe of adult specimens is entirely smooth, swollen near the facial suture, and confluent with the short ocular ridge which connects with the glabella, though in some specimens the ocular ridge becomes faint and ill defined towards the glabella. The lenses themselves are not preserved, and the material is found as internal and external moulds. External moulds show that the cornea must have been entirely smooth and without any distinct structure, whereas impressions of the lower surfaces of the lenses appear distinctly on internal moulds. Lindström (1901, p. 29, Pl. III, figs. 35-42) illustrated the fine structure of the eye of



TEXT-FIG. 4. *a*, *Peltura scarabaeoides scarabaeoides*. (Wahlenberg 1821.) Zone Vc, Slemmestad, Norway. Cephalon in oblique lateral view, restored from Gr. I. 20803.

b, *Peltura minor* (Brøgger 1882). Diagram exhibiting the spatial relationships of the lenses. From P.M.O. 87558 (vide Pl. 93, fig. 1). *c*, *Peltura scarabaeoides scarabaeoides* (Wahlenberg 1821). Right eye of a large specimen drawn from photographs and camera-lucida. From BM It. 5519. *d*, Idealized hexagonal close-packing system showing geometrical relationships between lens centres typical of pelturines. Based on 4c.

P. scarabaeoides from material with the lenses preserved. He showed that the lenses are plano-convex with a smooth upper surface. As Lindström saw no trace of an organic junction between the lenses and the cornea, he regarded them, not as 'free lenses', but as inwardly bulging extensions of the cornea like those of *Limulus*. My present study has given no evidence for or against this suggestion, neither in *Peltura* nor in the similar *Olenus meraspidis*, where the lenses and cornea apparently can only be detached together. It seems more likely, considering that the olenids are a close-knit group, that the lenses are in fact free structures of plano-convex form, closely welded to the lower surface of a very thin cornea, which did not show in Lindström's

sections because of recrystallization. Nevertheless, the extraordinarily wide spacing of the upper lenses in *P. minor*, and their curious distribution could accord with either hypothesis, and Lindström's suggestion should not be discounted.

Peltura minor (Brögger 1882)

- 1882 *Cyclognathus costatus* n. sp. var *minor*; Brögger, p. 110, pl. II, figs. 10–11.
 1922 *Peltura minor* (Brögger); Westergård, p. 175, pl. XV, figs. 3–11.
 1957 *Peltura minor* (Brögger, 1882); Henningsmoen, p. 235, pl. 6, pl. 25, figs. 2–5.

Plate 93, figs. 1, 2; text-fig. 4b

Material. One specimen from Gamlebyen, Oslo, associated with *Sphaerophthalmus alatus*, Zone Vb (2d β). P.M.O. 87558.

Eye-morphology. Only the visual surface is present, preserved as an internal mould. There appears to be little difference in eye structure between this species and *P. scarabaeoides*. The lenses are represented by the impressions of their lower surfaces. There is considerable variation in the spacing of these lenses; those near the facial suture being very widely spaced, and almost certainly disjunct, whereas those near the lower margin are somewhat smaller and much closer together, probably being contiguous.

Development of the eye in pelturines. In young pelturines the lenses have an unusual pattern of arrangement, unlike that of leptoplastines or indeed of other Cambrian trilobites. There may have been a similar system in the Oleninae, but the preservation is not good enough to determine this. This basic pattern is retained, though modified by the addition of many more lenses in fully grown pelturines. The beautifully preserved eye of *P. minor*, figured in Pl. 93, figs. 1, 2, serves as a model showing an early stage of development; young *P. scarabaeoides* eyes are very similar though less well preserved.

Here the pattern is a form of hexagonal close packing, but the dorso-ventral files radiate dorsally, diverging in a fan-like manner. The uppermost lenses are the most widely spaced; they are also somewhat larger than the others. By analogy with other trilobites these were presumably the first-formed lenses. This odd pattern, with the files converging as they plunge downwards seems to be adapted to accommodate more lenses in the lower central part of the visual field, whilst giving wide-ranging though less intensive coverage elsewhere. The approximate maximum visual range for this eye, which has fifty lenses, is 0° to 90° (long.) and –20° to 50° (lat.). Vision is thus entirely confined to the anterior hemisphere, with the main clustering of lens

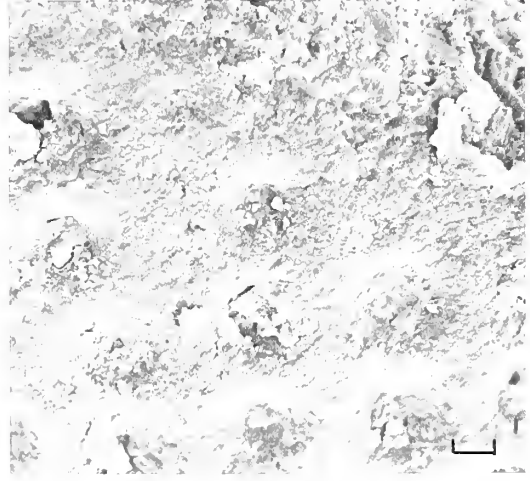
EXPLANATION OF PLATE 93

Figs. 1, 2. *Peltura minor* (Brögger, 1882). Gamlebyen. Oslo. Zone Vb. (2d β). 1, Internal mould of visual surface (right edge = anterior). P.M.O. 87558, $\times 135$ (vide text-fig. 4b). 2, Same, upper part of visual surface, $\times 500$. Bar = 10 μ m.

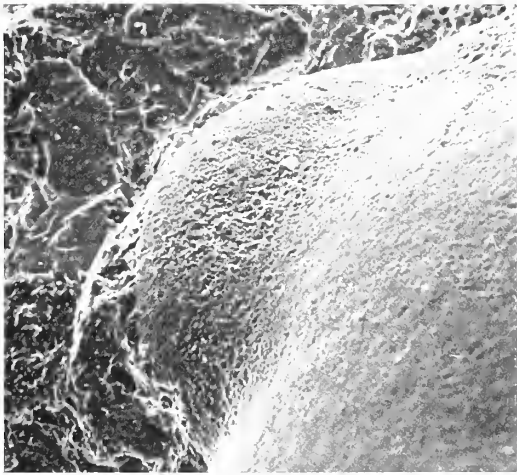
Figs. 3–6. *Ctenopyge* (*Mesoctenopyge*) *similis* Henningsmoen 1957. Sars Gate. Oslo. Zone Vb (2d β sim.). 3, Palpebral lobe showing nearly structureless surface (top right = anterior). P.M.O. 87567, $\times 120$. 4, Adult visual surface in lateral view showing dorso-ventral files and eye-socle with faint vertical striations. P.M.O. 87566, $\times 85$. 5, Oblique dorsal view of adult visual surface. P.M.O. 87565, $\times 65$. 6, Oblique dorsal view of visual surface of a young specimen (right edge = anterior), (see also text-fig. 5e), (enlargement of left-hand specimen in Pl. 94, fig. 5). P.M.O. 87564, $\times 120$. (Figs. 5 and 6 are illuminated from the south).



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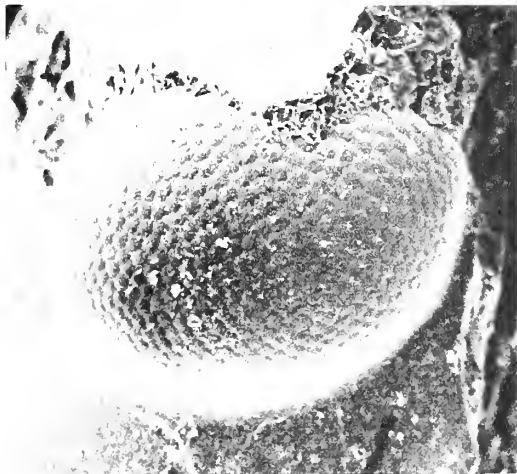
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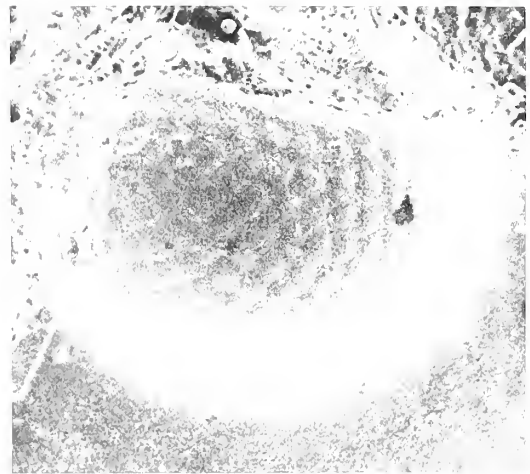
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axes centred on an axis 45° from the sagittal plane, and directed downwards at $10\text{--}20^\circ$ below the 'equator', towards the sea floor.

Though no large adults of *P. minor* were available for study, the fully developed pelturine system of lens arrangement was seen in mature specimens of *P. scarabaeoides scarabaeoides*. Here there are some 180 lenses, arranged in a pattern like that of *P. minor*, though modified through growth. Most specimens have some fortuitous irregularities, like those figured in text-fig. 4c, but apart from these the lens centres are arranged in a regular geometric sequence, idealized in text-fig. 4d. This is clearly a hexagonal close-packing scheme, but one in which the distances between lens-centres decrease arithmetically towards the base of the eye. Three intersecting component rows are evident, as follows: (a) arching latitudinal rows, becoming closer together ventrally, (b) a set of files converging ventrally towards the anterior ventral edge of the eye, vertical near the anterior edge and curving more and more obliquely towards the posterior edge, (c) an identical set, vertical near the posterior edge and curving towards the anterior.

The lenses are largest at the top and decrease in size ventrally and it is probable that their growth is inhibited by the proximity of neighbouring lens-centres, as suggested in my analysis of the eye of *Ormathops* (Clarkson 1971). One advantage of having lenses graduated in size is that irregularities in distribution are avoided. When the lenses are all the same size, as in *Ormathops* or *Ctenopyge*, irregularities are inevitable. The eyes of *Ctenopyge* are similar to those of the pelturines in that the dominant files, which are diagonal near the top of the eye, swing into a more nearly vertical position towards the base but these do not converge in *Ctenopyge*, and identical-sized lenses with inevitable irregularities in distribution result (see p. 737). A full analysis of different systems of lens-packing in trilobites is beyond the scope of this paper, but it is worth noting that the system exhibited by pelturines is found also in certain post-Cambrian trilobite groups and is especially distinct in cyclopygids, though here the decrease in spacing may be logarithmic.

Subfamily LEPTOPLASTINAE

The eye of *Leptoplastus stenotus* Angelin was less well preserved than that of *O. wahlenbergi* in the material studied. Basically, it is of the same general type, though relatively smaller. The visual surface is absent, and none of the small meraspids were preserved showing the visual surface. No detailed structure was visible on the palpebral lobe or the eye-socle, due to poorer preservation. *Eurycare* again has an eye of similar type, with the visual surface missing.

Though the similarities between the eyes of early Leptoplastinae are clear, there was a great change with the incoming of *Ctenopyge* and *Sphaerophthamus*. Not only was the visual surface retained but there were substantial modifications in the palpebral lobe and associated regions. The visual surface furthermore departed from the primeval reniform shape and became larger, and elliptical or nearly spherical, often projecting laterally from the head. Though the peripheral zone is less clearly marked than in *Olenus*, ridges and grooves are still detectable in some cases on the palpebral lobe and the eye-socle. Preservation of the eyes in the later Leptoplastinae was good, though less perfect than in *O. wahlenbergi*. The granular structure seen at high magnification implies at least some diagenetic alteration.

Ctenopyge (Eoctenopyge) modesta Henningsmoen 1957

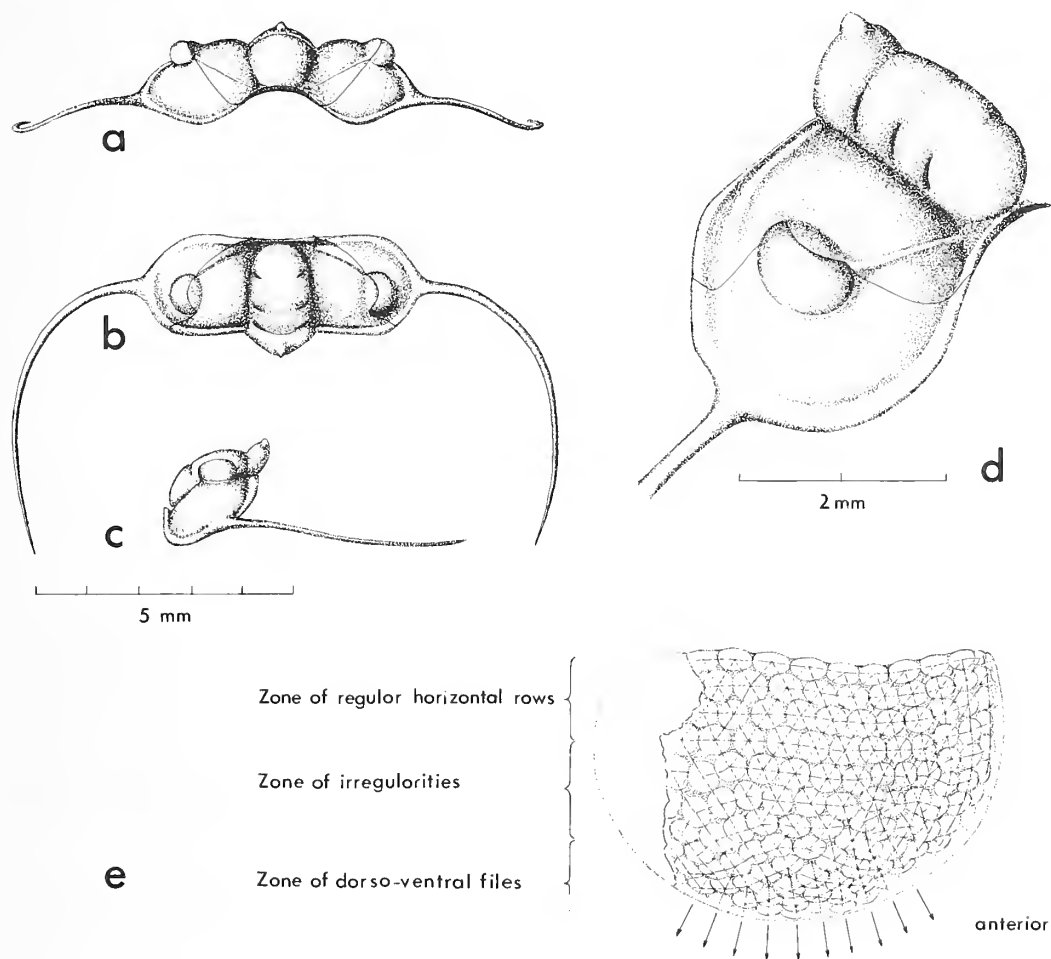
1922 *Ctenopyge flagellifera angusta* n. var. (partim); Westergård, p. 185, pl. XI, fig. 6-7.

1957 *Ctenopyge (Eoctenopyge) modesta*; Henningsmoen, p. 191, pl. 5; pl. 19, figs. 1-10.

Plate 94, fig. 5; text-fig. 5 a-d

Material. Four blocks from Sars Gate, Oslo, associated with *Ct. similis*, *Protopeltura bidentata*, *Parabolina mobergi*. Zone Vb (2d β sim.) P.M.O. nos. 87564-7.

Remarks. The reconstructions, made from camera-lucida drawings, show how the slender genal spines emerge on the librigenae opposite the eye, and thence springing away at right angles to the cephalon curve



TEXT-FIG. 5. a-d. *Ctenopyge (Eoctenopyge) modesta*. Henningsmoen 1957.

a, b, c. Restoration of the cephalon in frontal, dorsal and lateral views, from P.M.O. 87564-7. d. Same, enlarged, in antero-lateral view.

e. *Ctenopyge (Mesoctenopyge) similis* eye drawn from stereoscan photograph (vide Pl. 93, fig. 6) showing relationships of the lenses, the different zones, and the development of the dorso-ventral files. Arrows represent the directions of the emergent dorso-ventral files. P.M.O. 87564.

backwards and downwards coming to lie in the same plane as the antero-lateral border of the cephalon. Such a cephalon could be given support to rest upon the sea floor by these spines, and as with many other trilobites (Clarkson 1966b) the base of the eye would then be horizontal.

Eye-morphology. The eye is one-third the total length (sag) of the cephalon, and set opposite S1, high on the cheek towards the rear. Eye-indices are A/G 44%, A/Gn 34%, H/A 36%. The palpebral lobe, relatively large and defined by a pronounced palpebral furrow, rises outwards and in some specimens carries prominent radial ridges, all the way round, and normal with the facial suture. A thin ocular ridge connects the palpebral lobe to the anterior region of the glabella. The visual surface, of elliptical form, is set upon a vertical eye-socket, about one-fifth the height of the whole eye. In the material to hand there are no vertical ridges on the socket. Some specimens have an eye of symmetrical form: a regular oblate spheroid truncated below by the upper edge of the eye-socket, in others the anterior part of the spheroid is depressed, and the highest curvature is posterior. This may, however, be a preservational feature. The visual field commanded by such an eye is panoramic, and the visual fields of the two eyes meet, though hardly overlap, in front, above and behind. Laterally, the limit of vision is directed a few degrees below the equatorial or horizontal plane.

Ctenopyge (Mesoctenopyge) similis Henningsmoen 1957

1922 *Ctenopyge erecta* n. sp. (partim); Westergård, p. 156, pl. XI, figs. 26–27.

1957 *Ctenopyge (Mesoctenopyge) similis* n. sp.; Henningsmoen, p. 195, pl. 5; pl. 20, figs. 10–14.

Plate 93, figs. 3–6; text-figs. 5e, 6 a–c, e

Material. Four blocks from Sars Gate, Oslo, associated with *E. modesta*, *Protopeltura bidentata*, and *Parabolina mobergi*. Zone Vb (2dβ sim.) P.M.O. nos. 87564–7.

Remarks. The most striking feature of the reconstructed cephalon is the pair of large genal spines, which project forwards and curve round to the rear, terminating behind the body. Though such long spines have sometimes been used in inferring a planktonic mode of life through frictional retardation of sinking, their orientation, as the front and side views show, is much more suggestive of an adaptation for supporting not just the cephalon, but also the whole body upon the sea floor. The flattening of these massive spines suggests their functioning as a gigantic snowshoe giving support to the body when resting on a muddy sea-floor.

Eye-morphology. The eye is one-fifth the total length (sag.) of the cephalon, and set high on the cheek opposite S2 with its anterior edge about midway between the anterior and posterior borders. Eye-indices: A/G 33%, A/Gn 38%, H/A 125%. The palpebral lobe is relatively small and narrow, with distinct ridges, though these are not so deeply impressed as in *O. wahlenbergi* or *E. modesta*. The visual surface is very similar to that of *E. modesta* though the lenses are relatively smaller, and it commands a similar visual field. Some specimens have faint vertical ridges on the eye-socket.

Ctenopyge (Mesoctenopyge) tumida Westergård 1922

1922 *Ctenopyge tumida* n. sp. (partim.); Westergård, p. 155, pl. XI, figs. 15–18.

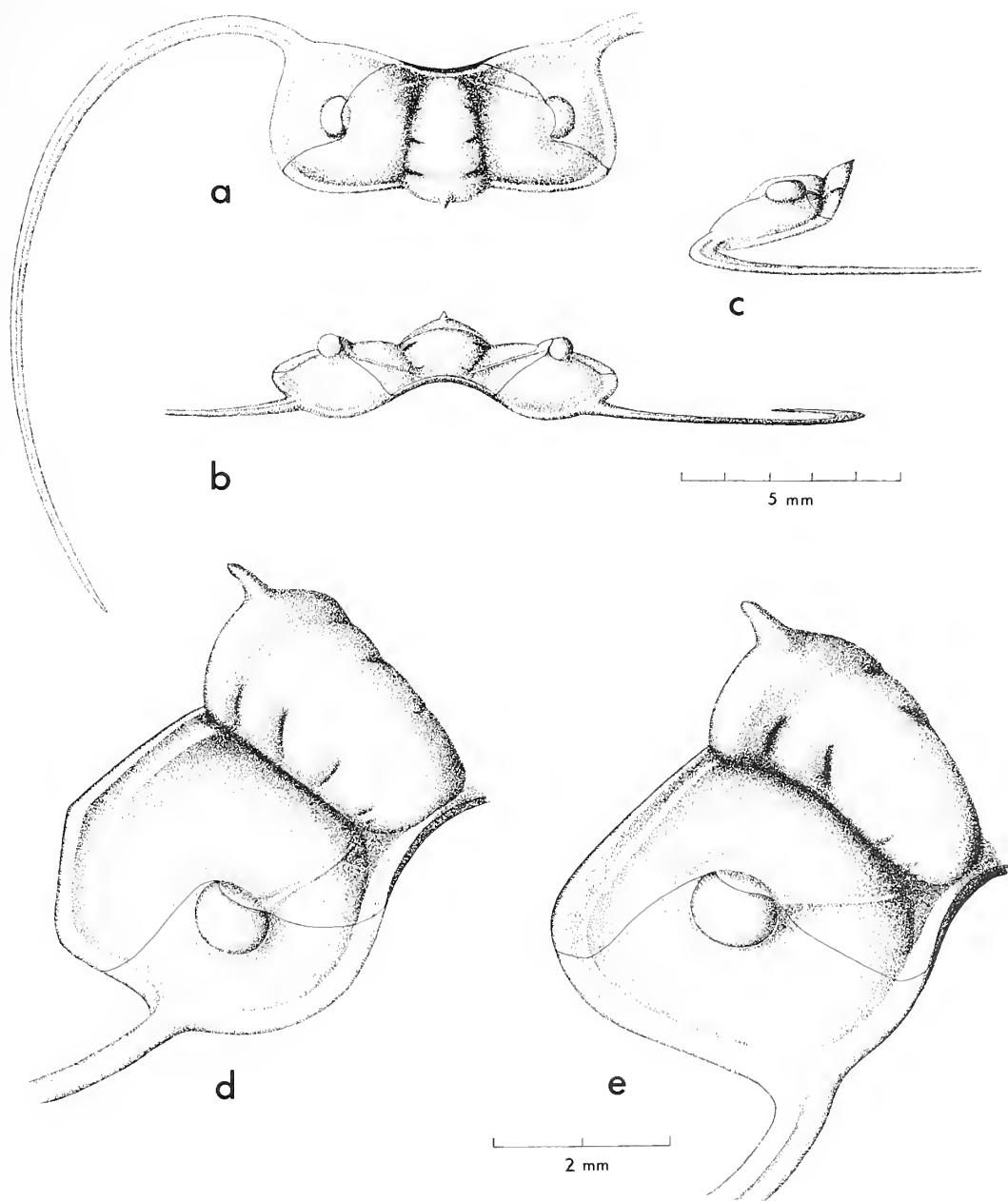
1957 *Ctenopyge (Mesoctenopyge) tumida* Westergård 1922; Henningsmoen, p. 198, pl. 5; pl. 20, fig. 16.

Plate 94, figs. 1–4; text-fig. 6d

Material. Five blocks from Naersnes, Røyken, associated with *Peltura acutidens*. P.M.O. no. 87551–5. Also two blocks from Sars Gate, Oslo of *C. cf. tumida* associated with *C. angusta*, Zone Vb (2dβ). P.M.O. nos. 29751, 29757.

Remarks. Though the genal spines are less massive, less flattened, and jut out laterally rather than first being directed anteriorly, they could still have been used for the support of the cephalon and body on the sea floor. The morphology of this species does, however, seem to be less ideally adapted for that purpose than does that of *M. similis*.

Eye-morphology. The eye is of almost identical morphology to that of *M. similis*, except in position. It is set further forward and lower down, so that the posterior edge of the eye lies about midway between the anterior and posterior borders of the cephalon, and the orientation of the ocular ridge and other structures is correspondingly altered. Palpebral lobes lie opposite S2. Eye-indices: A/G 28%, A/Gn 35%, H/A 150%.



TEXT-FIG. 6a-c, e. *Ctenopyge (Mesoctenopyge) similis* Henningsmoen 1957. Zone Vb. Sars Gate, Oslo. Restoration of the cephalon in dorsal, frontal, and lateral aspects, and (c) in enlarged antero-lateral view from P.M.O. 87564-87567.

d. *Ctenopyge (Mesoctenopyge) tumida*. Westergard 1922. Zone Vb. Royken. Cephalon in antero-lateral view restored from P.M.O. 87551-87555.

Sphaerophthalmus alatus (Boeck 1838)

- 1838 *Trilobites alatus* mh.; Boeck, p. 143.
 1857 *Sphaerophthalmus alatus* Boeck; Kjerulf, p. 92.
 1922 *Sphaerophthalmus major* Lake; Westergård, p. 163, pl. XIII, figs. 9–19.
 1957 *Sphaerophthalmus alatus* (Boeck); Henningsmoen, p. 212, pl. 2, fig. 15; pl. 5; pl. 22, figs. 18–26.
 1968 *Sphaerophthalmus alatus* (Boeck): Rushton, p. 414.

Plate 95, figs. 1, 2; text-fig. 7a–d

Material. Three blocks from Gamlebyen, Oslo, labelled *S. major*, and associated with *Peltura minor*. Zone Vb (2d β). P.M.O. 87556–8. Also two blocks from Andrarum (old collection) associated with *Peltura? acutidens*. Zone Vb (2d β) Gr. I. 20775–6.

Remarks. Three-dimensional material shows that the genal spines of *S. alatus* (in standard orientation) spring out laterally from the librigenae and are not bent downwards below the cephalon as in *S. humilis*. Even in the best specimens studied, the tip of the genal spine was always broken, but can be restored from the illustrations of previous authors, especially Henningsmoen and Rushton. The anterior arch is of moderate height, and the postero-lateral border rises from the genal spine obliquely. Thus the cephalon could rest upon the sea floor upon the antero-lateral border and the genal spines; a position impossible for the related *S. humilis*.

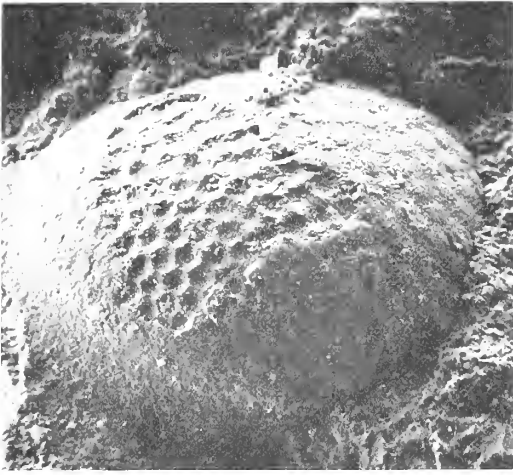
Eye-morphology. Eye one-quarter the total length of the cephalon, and set high on the cheek, opposite S1. Eye-indices: A/G 35%, A/Gn 27%, H/A 108%. The palpebral lobe is relatively narrow with a curving outer edge, and is confluent with the long narrow and backwardly curving ocular ridge. In side view it forms a nearly semi-circular arch, with a slightly flattened top, where it is widest. The upper surface of the palpebral lobe flares outwards and upwards from the deeply incised palpebral furrow at about 45°. There is little trace of surface ornament apart from scattered indistinct tubercles, but the granular surface seen at high magnifications implies that some recrystallization has taken place. The visual surface is closely similar to that of typical representatives of *Ctenopyge*, and is a nearly perfect oblate spheroid in form with irregularities in lens distribution typical of all later leptoplastines. The eye-socket is extremely narrow, more so than in any species previously discussed, though faint vertical striations are visible.

Sphaerophthalmus humilis (Phillips 1848)

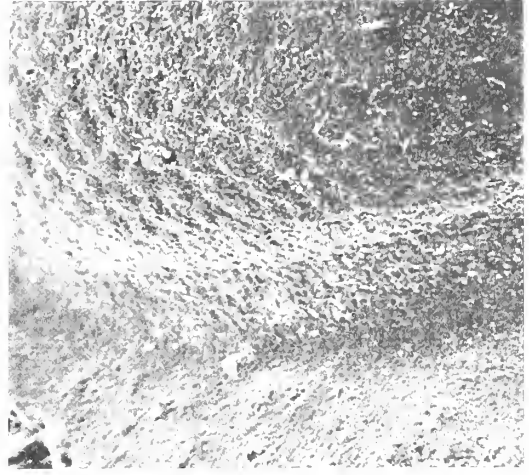
- 1848 *Olenus humilis* n.s.; Phillips, p. 55, figs. 4–5, p. 347.
 1901 *Sphaerophthalmus alatus* Angelin (*sic*); Lindström, p. 29, pl. III, figs. 31–34.
 1913 *Sphaerophthalmus alatus* (Boeck sp.); Lake, p. 74, pl. VIII, fig. 1–5.
 1957 *Sphaerophthalmus humilis* (Phillips 1848); Henningsmoen, p. 215, pl. 5; pl. 22, figs. 7, 11–15.
 1968 *Sphaerophthalmus humilis* (Phillips); Rushton, p. 415, text-fig. 2, 3a, pl. 78, figs. 11–15.

EXPLANATION OF PLATE 94

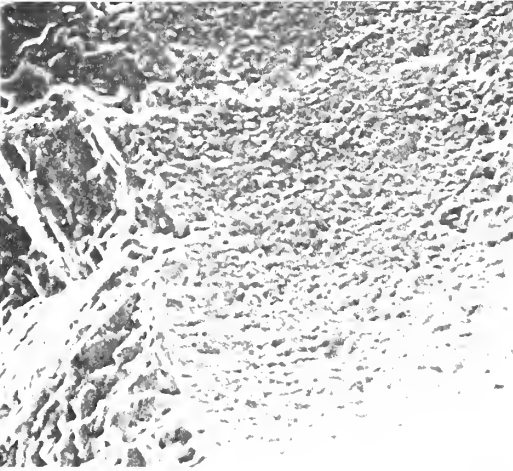
- Figs. 1–4. *Ctenopyge* (*Mesoctenopyge*) *tumida* Westergård 1922. Naersnes, Royken. Zone Vb (2d β).
 1, Anterior region of small adult eye with some lenses missing. P.M.O. 87552, $\times 105$. 2, Lowermost lenses and eye-socket of large adult eye; faint vertical striations visible on eye-socket. P.M.O. 87554, $\times 135$.
 3, Palpebral lobe, outer central region with striations nearly normal to the outer edge. P.M.O. 87552, $\times 250$. 4, Adult eye in lateral view showing eye-socket. Visual surface damaged. P.M.O. 87553, $\times 75$.
 Fig. 5. Block with librigenae and eyes of *Ctenopyge* (*Mesoctenopyge*) *similis* Henningsmoen 1957 (left), and *Ctenopyge* (*Eoctenopyge*) *modesta* Henningsmoen 1957 (centre and right). Sars Gate, Oslo. Zone Vb (2d sim.). P.M.O. 87564, $\times 26$.
 Fig. 6. *Sphaerophthalmus humilis* Phillips 1848. Andrarum, Scania. Zone Vc. Lower central part of eye; external surface of cornea and internal moulds of lenses. Gr. I. 20706, $\times 180$.



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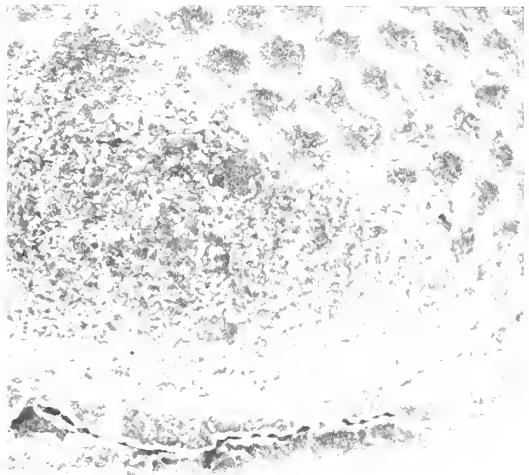
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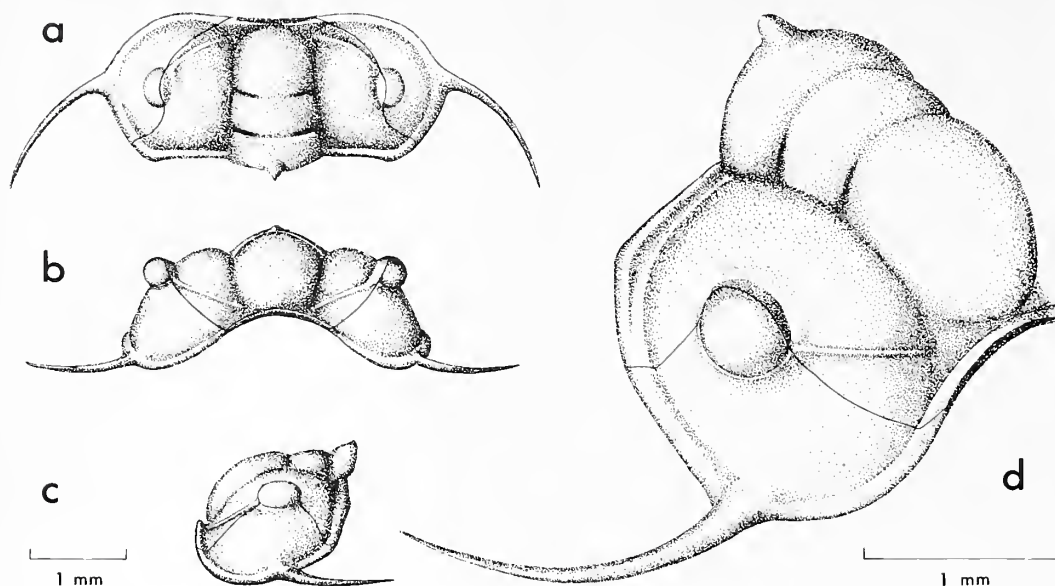
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TEXT-FIG. 7. *a-d*. *Sphaerophthalmus alatus* (Boeck 1838). Zone Vb. Gamlebyen, Oslo. Restoration of the cephalon in dorsal, frontal, and lateral aspects and (*d*) enlarged in antero-lateral view from P.M.O. 87556-87558.

Plate 94, fig. 6; Plate 95, figs. 3-6; text-fig. 8*a-d*

Material. Three blocks from Andrarum, associated with *P. scarabaeoides scarabaeoides*, *Ct. linnaerossi*, and *Ct. teretifrons*. Zone Vc (2d γ). Old collection, Gr. I. 20706, 20803, 5537.

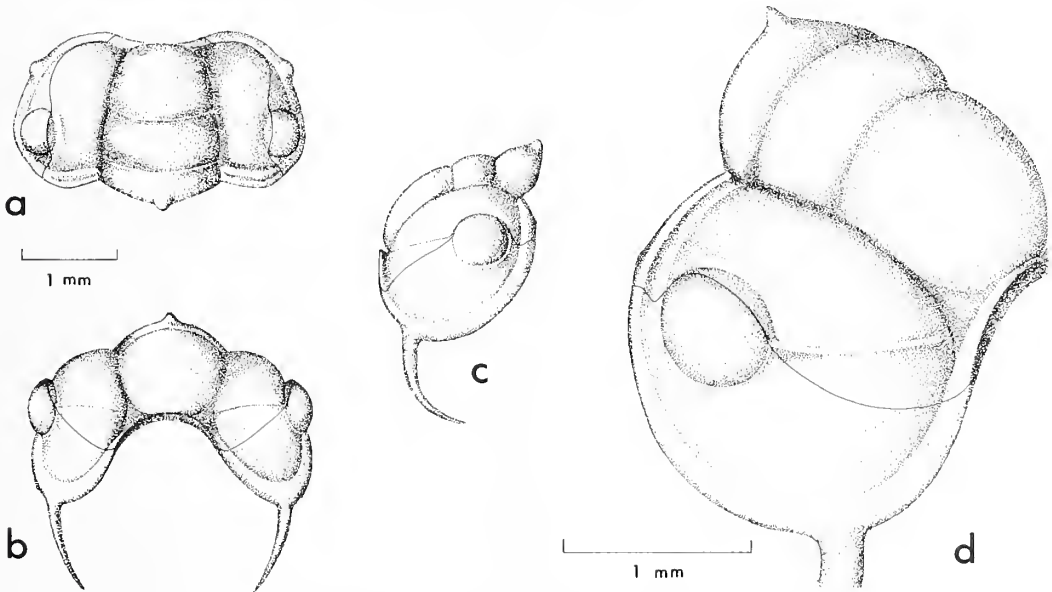
Remarks. *S. humilis* is an extremely convex trilobite with a very pronounced anterior arch and almost vertical librigenae. The peculiar attitude of the genal spines in this species was first noted by Rushton (1968, p. 415). He reconstructed the cephalon with steeply sloping librigenae, and ventrally projecting genal spines, curving in under the cephalon. I have been able to confirm that the genal spines do plunge downwards as Rushton described, so that the cephalon could not rest upon the sea floor. In my restoration, these spines do not curve inwards quite so strikingly, but in all other respects I agree with Rushton.

Eye-morphology. This species is unusual because of the relatively enormous size of the eye, and its very far posterior position. It is one-third the total length of the cephalon, with its anterior edge opposite S1. Eye-indices: A/G 38%, A/Gn 30%, H/A 335%. The palpebral lobe, which is jointed to the ocular ridge, is similar in form to that of *S. alatus*, though narrower. No surface ornament has been detected in the material examined. Since the palpebral lobe is placed slightly behind the widest part of the cranidium, the anterior edge of the visual surface appears to be slightly recessed. The visual surface forms about a third to a half of a slightly oblate spheroid, with the long axis horizontal. Its edge lies in an exsagittal plane, inclined at some 10° from the vertical. In side view the eye appears nearly globular. Each eye subtended a visual field whose lower limits are 70° to 80° below the equator, and which just overlap at the front, rear, and above so as to give an almost entirely panoramic range not found in other olenids, and, indeed, in few other trilobites. Juvenile eyes are of similar form, but have fewer lenses (c. 70 as compared with c. 200). Both in juvenile and adult eyes the eye-socket is very narrow and shows no definite structure.

In the material to hand the thin biconvex lenses are easily detached. Where they are partially removed from the matrix each is preserved as a single calcite crystal with a very slightly convex upper surface and a more strongly convex inner face. Distinct cleavages are visible, from which it can be deduced that the c-axis of each crystal is normal to the surface. Sometimes the finer detail has been destroyed by recrystallization, but the impressions left by the lower surfaces of the lenses show their arrangement very clearly (Pl. 95, figs. 3-4).

Development of the eye in later leptoplastines. In most trilobites the first-formed lenses are emplaced in an initial horizontal row parallel with the facial suture. New lenses are added below these, in parallel horizontal rows. The new lenses are offset relative to those above so that there develops an array of lenses arranged in a regular system of hexagonal close packing. This pattern is most clearly shown in the phacopids, where the lenses are large and separate; dorso-ventral files can be seen intersecting with ascending and descending diagonal files (Clarkson 1966a). In some phacopid eyes new small lenses may actually develop in an accessory row above the initial horizontal row, but this seems to be confined to certain genera only (Beckmann 1951; Clarkson 1966b). The eyes of *Ct. (E.) modesta*, *Ct. (M.) similis*, and *Ct. (M.) tumida* are closely similar to one another, and though there are differences in size and position the resemblance in detailed structure is such that though most of the comments given here are based upon *Ct. (M.) similis* (Pl. 94, fig. 2, text-fig. 5e) they are appropriate also to the others. In most respects they apply also to *Sphaerophthalmus* eyes, though the latter have more lenses.

All these olenid eyes begin their development in much the same way as phacopids, though being holochroal the lenses are contiguous and they are all much the same size. The first-formed lenses lie in a horizontal row following the curve of the facial suture. When seen from above this row and subsequent rows appear to be concentric and curving outwards like parallel strings of beads. In the upper (i.e. the oldest) part of the eye the close-packing system is regular and arranged with respect to the dominant elements—the horizontal rows. But some distance below the facial suture, usually after the first half-dozen rows, irregularities are encountered which break up this clearly defined pattern. Why do these develop?



TEXT-FIG. 8. *a-d. Sphaerophthalmus humilis* (Phillips 1848). Zone Vc. Andrarum, Scania. Restoration of the cephalon in (a) dorsal, (b) frontal, and (c) lateral aspects and (d) enlarged in antero-lateral view, from Gr. I. 20706.

It has long been established that in trilobites generally new lenses are usually added only along the lower margin of the visual surface, and that each normally arises below and directly between two existing lenses of the preceding horizontal row. Irregularities come into being when extra lenses are intercalated into this system, in other words when at a few loci two new lenses are emplaced instead of one. If, as I discussed previously in the phacopid *Ormathops* (Clarkson 1971), the developmental system is 'programmed' to produce new lenses when a particular spatial threshold has been reached, then such new intercalated lenses will necessarily be emplaced to fill the 'extra space' as the visual surface expands in circumference. Each of the new intercalated lenses will in turn act as a focus for lens-initiation in successive horizontal rows, and the effects of these small, though inevitable irregularities are clearly visible. Had these olenids possessed lenses graduated in size such irregularities would never have arisen, but since they are all much the same size, disruptions of the regular packing system are, as in *Ormathops*, a geometrical requirement.

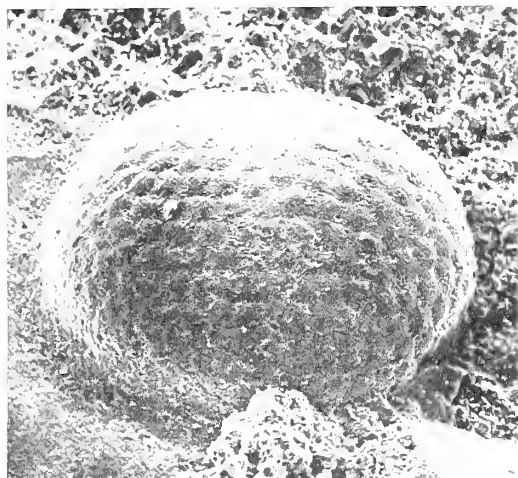
The lower third of the eye lies below the ambitus (this term used as in an echinoid) where the eye has reached its greatest horizontal circumference and thereafter decreases slightly in diameter. Since the visual surface is no longer increasing no new lenses are added by intercalation and it is hardly surprising to find another change in the manner of lens emplacement. What usually happens is that one of the two original sets of diagonal rows swings into a vertical orientation, these becoming the vertical files characteristic of the lower part of the eye, though they are not homologous with the dorso-ventral files of the phacopids. The lenses in this region are slightly smaller than the upper ones, accommodating the slight decrease in the diameter of the eye.

Thus the eyes of olenids of this type have three horizontal zones, an upper regular zone where the horizontal rows are the dominant elements, a zone of intercalation, where the horizontal rows are still dominant though there are notable irregularities, and a lower zone of dorso-ventral files where the system of hexagonal close packing is based upon one set of diagonal rows which has now become vertical in response to packing requirements. This system resembles that of the pelturines only in so far as the diagonal rows change direction and become more vertical. But the pelturine system is based upon arithmetical change in distances between lens-centres, whereas in later leptoplastines, distances between lens-centres remain constant, except where the increasing girth of the eye promotes hiatuses.

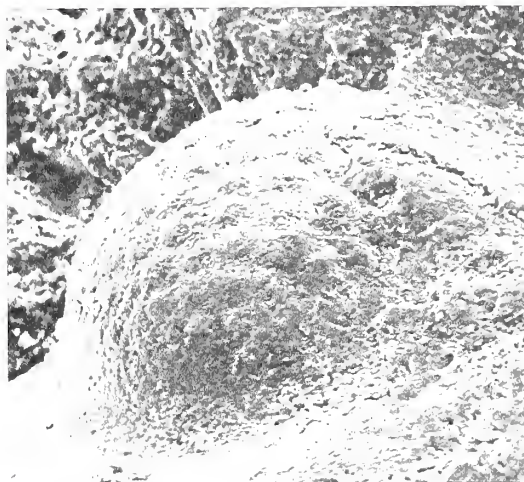
EXPLANATION OF PLATE 95

Figs. 1, 2. *Sphaerophthalmus alatus* (Boeck 1838). Andrarum, Scania. Zone Vb (2d β). 1, Dorso-lateral and 2, anterior view of young eye. Gr. I. 20775, $\times 140$. In 1 right edge is anterior.

Figs. 3-6. *Sphaerophthalmus humilis* (Phillips 1848). Andrarum, Scania. Zone Vc. 3, Single lens, partially detached from matrix, and internal moulds of missing lenses. Gr. I. 20803, $\times 1200$. Bar = 10 μm . 4, Internal mould of adult eye with a few lenses still adherent. Left edge anterior. Gr. I. 20803, $\times 60$. 5, Very young eye; outer surface Gr. I. 5537, $\times 200$. 6, Internal mould of lenses near base of eye. Gr. I. 20803, $\times 500$. Bar = 10 μm .



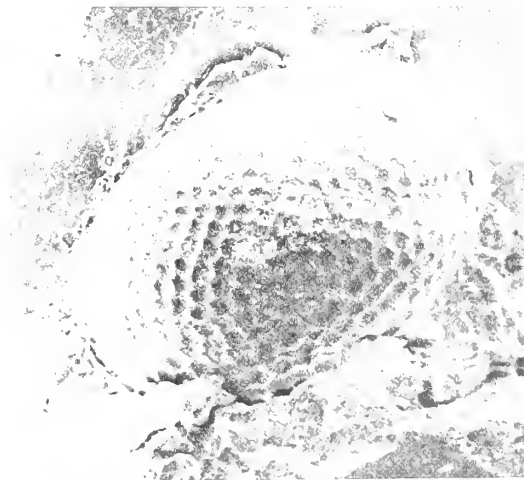
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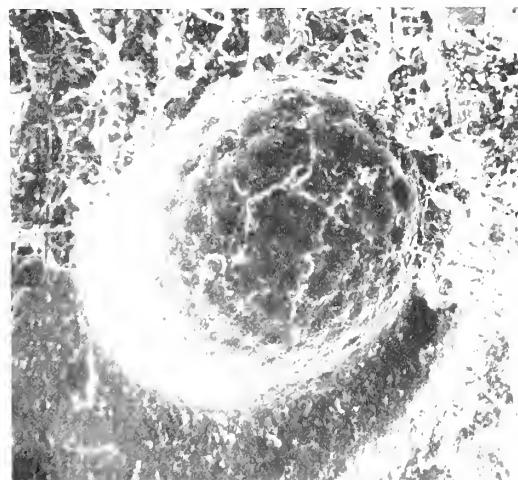
2



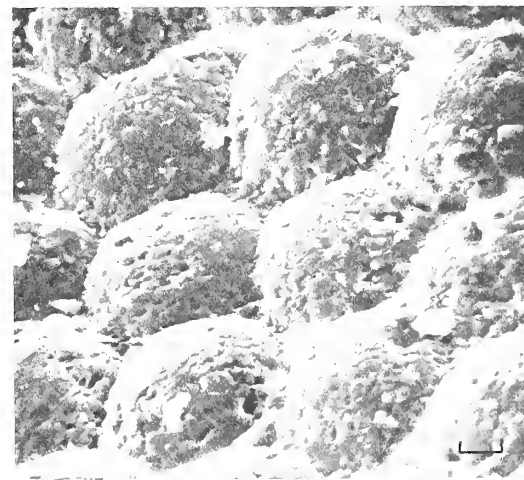
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SUMMARY AND CONCLUSIONS

Evolution of the eye in the Olenidae. In this summary of observations I have largely followed the phylogenetic scheme of Henningsmoen (1957, Chart 6), and though this will certainly need to be modified in the light of recent and future observations, it still forms a useful provisional basis for discussion of phylogeny.

According to Henningsmoen, *Olenus*, which was the earliest Upper Cambrian genus, persisting through Zones I and II only, gave rise to three lines of descent. The most conservative line led to *Parabolina* (Zone III to Lower Tremadoc), and to other Olenidae. At about the same time (Zone III), the first pelturine genus *Protopeltura* appeared, and was followed later (Zone Vb), by *Peltura* and other Pelturinae. From *Olenus* also descended a third group, the Leptoplastinae, which began with *Leptoplastus* in Zone IV, a genus which gave rise to the elaborate leptoplastines *Ctenopyge* and *Sphaerophthalmus* which flourished in the time of Zone V.

Though the Triarthrinae and various other genera of the established families appeared and evolved in Tremadoc and later times, none of these have been studied in detail in my present work: in most of them the eye is small and rarely well preserved, though some of the Argentinian olenid species, e.g. *Parabolina argentina*, *Saltaspis steinmanni*, have relatively large eyes (Harrington and Leanza 1957, pp. 83, 95).

Öpik (1963) included the monogeneric Australian subfamily Rhodonaspidinae Öpik in the Olenidae. Because of the marked similarity of the pygidium of *Rhodonaspis* to that of *Parabolina*, he suggested a close relationship between these two genera, and noted that *Parabolina* may not have been derived from *Olenus*, but was part of another complex (including *Rhodonaspis*), which had persisted from the early Upper Cambrian. The evidence for this rests on the pygidial resemblance alone.

Study of the eye-morphology of Scandinavian genera, however, supports the other criteria used by Henningsmoen in erecting his phylogenetic scheme; the similarity of the eyes of *Olenus* meraspids and adult *Parabolina* has already been pointed out. *Rhodonaspis* has very large eyes of unusual form, having the palpebral lobe and probably the ocular ridge also as double structures, divided by an ocular striga. The ocular ridge is separated from the glabella, as in adult *Olenus*.

Further descriptions and discussions of new olenid material may help to resolve conflicting suggestions as to olenid phylogeny, and it is to be hoped that the rich Cambrian successions of Queensland may furnish yet more material of olenids and related trilobite families. For the moment, however, I have preferred to take a conservative view of olenid phylogeny.

The principal conclusions which have emerged from the present studies are as follows:

(a) The 'primeval' olenid eye from which all other kinds ultimately derived is exhibited by *Olenus*. Here the ocular suture is functional in the adult, so that the visual surface is found only in meraspids. Large adults have a highly structured and possibly sensory zone surrounding the visual surface, well supplied with alimentary prosopon. This peripheral zone is, however, weakly developed in meraspids. In the latter the lenses are plano-convex, and are probably welded to the inner surface of the cornea, sometimes being quite widely spaced.

(b) In both the later Oleninae and in all the Pelturinae, the eyes have many features

very similar to those of meraspids of *Olenus*. These include their small size and forward position, the inclination of the long axis to the exsagittal plane, the non-functional ocular suture, structure of the visual surface, poorly developed peripheral zone, and the confluence of the palpebral lobe with the ocular ridge. All these are suggestive of a paedomorphic origin for these adult eyes. Pelturine eyes have lenses decreasing in size ventrally, arranged in a geometrically regular system with logarithmic diminution of distances between lens-centres. It is probable that the eyes of most Tremadoc and later olenids are also of this type.

(c) Early Leptoplastinae had eyes like those of *Olenus*, though their generally poorer preservation precludes very detailed comparison. The later leptoplastines *Ctenopyge* and *Sphaerophthalmus* retained the visual surface in the adult, and the eye is often strikingly well developed, though the peripheral zone is not greatly in evidence. Some features of these eyes may likewise be regarded as paedomorphic. Eyes of this kind are usually spheroidal, and have thin biconvex lenses underlying a very thin cornea. They are variable in size, position, and in the shape of the palpebral lobe and the range of the visual field (the most extreme form being *S. humilis*). The visual surface has a peculiar pattern of development, which is very clear in *Ct. (M.) similis*, but seems to be constant throughout the group. In this the lenses are all of the same size, and have a distinct zone of irregularities. Following the extinction of the last species of *Ctenopyge* and *Sphaerophthalmus* before the close of the Upper Cambrian, no other olenids evolved such remarkably developed visual organs.

Adaptations of the olenid cephalon. Henningsmoen (1957, pp. 70–82) has written extensively about the mode of life and environment of the olenids. He suggested that although most olenids were capable of swimming above the sea floor, they could also sojourn for certain periods on the floor of the stagnant Olenid Sea, and were probably adapted for life in waters with a restricted oxygen content. Further evidence of bottom-dwelling habits in some olenids is provided by recent trace-fossil analysis (Orlowski, Radwański, and Roniewicz 1970; Birkenmajer and Bruton 1971).

The cephalic reconstructions presented here, which were made to show the eye in its correct relationship to the rest of the cephalon, also seem to indicate, in some cases, functional adaptations for a benthonic mode of life. Most olenid cephalons (with the notable exception of *S. humilis*), seem to be well adapted for resting upon the sea floor. The short genal spines of most species of *Olenus*, *Parabolina*, and *Leptoplastus*, together with *S. alatus*, project horizontally from the cephalon, so that the trilobite could lie on the sea floor, with its cephalon propped in a stable position and having its anterior arch open. Such support is even more evident in genera with long genal spines. Thus the genal spines of *E. modesta* are long and elegantly curved, in such a manner that the cephalon could be supported on four points; the lowest parts of the two antero-lateral borders, and the lower surfaces of the genal spines just in front of their tips. *Ct. similis* and *Ct. tumida* have very long flattened and horizontal genal spines, which would give support over their whole length. In these the height of the occipital ring above the base level, and the oblique appearance of the postero-lateral border, when seen from the side suggest that the body was carried high above the sea floor, a habit which no doubt carried real functional implications. I have elsewhere contended (Clarkson 1969) that long spines in the odontopleurid trilobites are

support structures rather than being used to prevent sinking through frictional retardation. Judging by the structure of the cephalon in the long-spined olenids, the same principle seems to apply, but it will be necessary to prepare complete lateral reconstructions with the thorax and pygidium in place before these suggestions can be fully worked out. The immensely long thoracic spines of *Ctenopyge*, and their relationship to the rest of the body still pose intriguing problems.

Clearly *S. humilis* was very differently modified, as witness the nearly vertical genal spines and the very large eye with its greatly expanded visual field. Though the purpose of such adaptations is far from certain, it is evident that even within the confines of the organization of such a close-knit family as the Olenidae, there was still a substantial degree of evolutionary plasticity, and the possibility of individual functional differentiation.

Acknowledgements. I am very grateful to Dr. D. L. Bruton (Paleontologisk Museum, Oslo), Mr. S. F. Morris (British Museum, Natural History), and Mr. F. J. Collier (Smithsonian Institution, Washington), for the loan of specimens. I am also glad to record the assistance of Dr. Jan Bergström of the University of Lund for loan of specimens and for much helpful discussion in the early stages of the work. I particularly appreciate the generosity of the Trustees of the Moray Fund of the University of Edinburgh, who contributed towards the cost of a Wild-Heerbrugg camera-lucida microscope.

All the SEM photographs were taken using a Cambridge 'Stereoscan' by Mr. J. Goodall of the Department of Engineering, Edinburgh University, to whom I am greatly indebted for his continued skill and patience. I gratefully acknowledge a grant towards plate cost from the Carnegie Trust for the Scottish Universities.

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Discussion on Dr. Clarkson's paper:

Chaloner: Did you clean the surface in any way prior to examination?

Clarkson: Yes. I used a Directional Ultrasonic Cleaner, which is a gun device manufactured by the Simms Group R. & D. Ltd. The specimen is placed under water and 'blasted' for two or three seconds by a stream of high-velocity bubbles from the gun. This suffices to remove all the loose dirt and dust; but if the gun is operated for longer than a few seconds the surface of the specimen may be damaged by abrasion.

COMBINED TRANSMISSION AND SCANNING ELECTRON MICROSCOPY OF *IN SITU* PALAEOZOIC SPORES

by T. N. TAYLOR

ABSTRACT. This paper discusses pollen and spores isolated from Carboniferous reproductive organs, including fructifications belonging to lycopods, cordaites, and seed ferns. Microspores of the monosaccate genus *Endosporites* were macerated from sporangia of a single cone. Morphological variability ranges from grains still within the tetrahedral arrangement to solitary spores. Information is provided concerning saccus-corporum organization and exine ultrastructure, ornamentation, and stages of saccus ontogeny. Pollen grains included within the genus *Florinites* were examined in cordaitalean pollen sacs from different localities and stratigraphic levels. Both proximal and distal attachments between saccus and corpus are demonstrated. Spores of a new Pennsylvanian reproductive structure are described as consisting of a complex tectate exine supporting a verrucate ornamentation. Prepollen grains of the *Schopfipollinites*-type were isolated from a number of medullosan pteridosperm reproductive structures including the genera *Dolerotheca*, *Rhetinotheca*, *Aulacotheca*, *Whittleseyia*, and *Halletheca*. Comparative studies of the spore exines suggest the occurrence of fundamental ultrastructural differences among the grains. Information is presented concerning the possible site of gamete emission from *Schopfipollinites* prepollen grains.

THE successful application of transmission electron microscopy to the study of fossil pollen exines by Ehrlich and Hall (1959) initiated a new era of palaeobotanical inquiry. With the subsequent availability of the scanning electron microscope and its ease of application in palaeontological research problems, researchers today are examining evidences of biological activity extending from the Precambrian to Recent, and including all levels of biological organization.

While dispersed spores and pollen grains found in rocks of Palaeozoic age have received a great deal of attention both for palaeontological and geological purposes, spores and pollen found in fructifications of known biological affinities have received little attention. It is the intent of the present paper to discuss the application of combined transmission and scanning electron microscopy to the study of *in situ* pollen, prepollen, and spores of Carboniferous (Pennsylvanian) age, and to demonstrate some of the types of information which have been made available utilizing these methods.

Studies of *in situ* pollen grains and spores are of particular importance because in most instances grains are present in sufficient numbers that ontogenetic differences may be separated from those which are truly taxonomic. This developmental approach may be undertaken with certain types of reproductive structures which mature in a sequential manner. The opportunity of sampling almost pure populations of spores, differing developmentally, from varying positions within a single cone provides an ideal means of studying spore wall ontogeny.

Because of the nature of this symposium the number of light photomicrographs used has been greatly reduced. It must be pointed out, however, that the use of light microscopy constitutes a valuable and indispensable aspect of any study in which the maximum number of pollen grain or spore features are to be elucidated.

Technique. Pollen grains and spores were macerated from sporangia using dilute hydrochloric acid (2%), soaked in 12% hydrofluoric acid for 12 hours, and subsequently divided into three fractions. Grains to be examined by transmission electron microscopy were dehydrated to propylene oxide and embedded in Spurr low viscosity media. Sections cut at approximately 20 nm were poststained in a 5% aqueous solution of uranyl acetate for 20 minutes, followed by lead citrate. Grains to be examined with the scanning electron microscope were washed in two changes of distilled water, spread on standard SEM specimen stubs coated, while in suspension, with a thin film of dried silver conductive paint, and allowed to dry in air. The grains were then vapour coated with a thin film of gold and examined with a Cambridge Mark IIA instrument. Grains of the final sample were dehydrated to xylene and embedded in Harleco Synthetic Resin for examination by light microscopy.

In the case of very large grains, several hundred microns in diameter, such as specimens of *Schopfipollinites*, very satisfactory results have been obtained using the transmission-scanning operational mode (Swift and Brown, 1970). This technique enables entire sections to be examined in a single field of view. It consequently eliminates the necessity of constructing elaborate montages which are otherwise necessary for large grains because the minimum magnifications available with the transmission electron microscope are too high to record cell and wall component interrelationships. Sections ranging from 50 nm–1 μ m were cut and mounted on single-hole slot grids covered with a thin collodion/carbon support film. Grids were subsequently stained with aqueous uranyl acetate followed by lead citrate and fitted into a special device mounted in the instrument stub holder.

The following is a discussion of four different spore types and the kind of information which has been assembled on their organization, morphology, and ultrastructure.

ENDOSPORITES

Endosporites Wilson and Coe 1940 is a monosaccate, trilete, microspore now known to be biologically related to some heterosporous members of the Lycopytina. The source of *Endosporites* specimens in previous studies has been from compressed, structureless cones, or from *spora dispersae* assemblages. The material presented here comes from calcium carbonate petrifications collected from probable lower Pennsylvanian sediments in eastern Kentucky (Good and Taylor 1970). Of particular

EXPLANATION OF PLATE 96

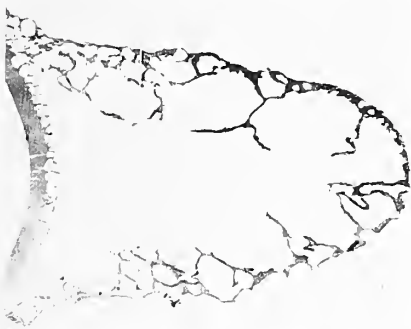
- Fig. 1. Transmission electron micrograph. Composite reconstruction of three spores of *Endosporites* tetrad. Arrows indicate positions of apical papillae. $\times 510$.
Fig. 2. Partial lateral view of monosaccate spore showing thickened corpus wall (left) with external ornamentation, and internal saccus reticulations. $\times 2700$.
Fig. 3. Three spores of *Endosporites* tetrad showing relationship between corpus and saccus wall. $\times 2100$.
Fig. 4. Scanning electron micrograph of *Endosporites* tetrad showing three spores, with the fourth represented by the corpus and a remnant of the saccus. $\times 500$.
Fig. 5. Lateral view of *Florinites* grain showing proximal and distal saccus attachment, and internal saccus reticulations. $\times 1000$.
Fig. 6. Limbus and proximal surface of *Endosporites* spore. $\times 4750$.
Fig. 7. Immature *Endosporites* spore prior to saccus enlargement. $\times 3300$.



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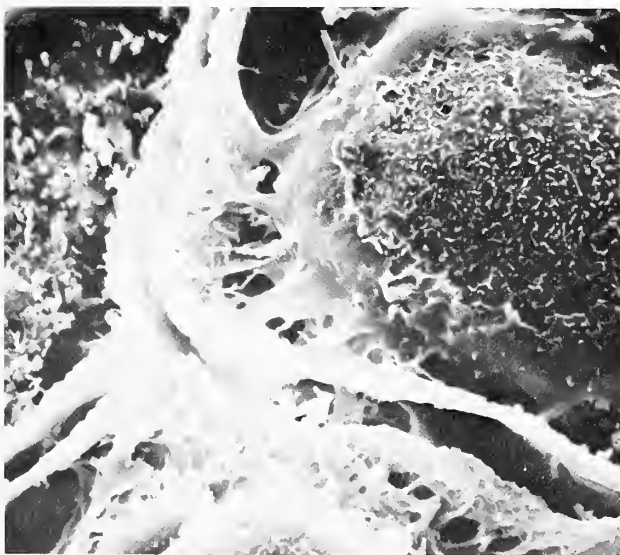
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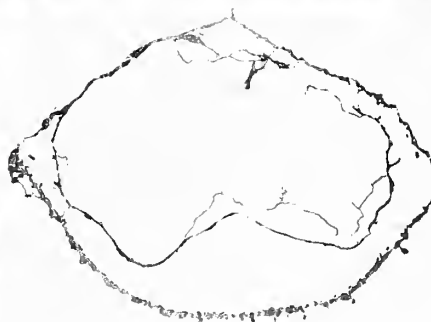
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importance with this material is the fact that within certain sporangia various stages of spore ontogeny are represented, including spores still within the tetrahedral arrangement (Pl. 96, fig. 1).

One of the most obvious advantages of transmission and scanning electron microscopy in the study of pollen grains and spores lies in the ability to discern more accurately and interpret correctly, complex ornamentation patterns which may be present on both the internal and external exine surfaces. Pl. 96, fig. 6 shows the distal surface of a spore ornamented by closely spaced, blunt-tipped spinules which are basally fused to form a reticulum. Along the equatorial rim of the spore, where the proximal and distal faces of the saccus become continuous, the spinous projections are fused, and together with the loosely arranged exinous strands, provide a thickness to the limbus. The proximal surface of *Endosporites* is uniformly smooth, interrupted only by irregularly shaped and randomly disposed pits (Pl. 96, fig. 6). Such features are too small to be resolvable with light microscopy, and are extremely difficult to characterize by transmission electron microscopy.

Pl. 96, fig. 4 shows three complete spores of a tetrad and the fourth represented by the corpus and a small remnant of the saccus wall. Spores with the saccus fragmented and torn allow observations to be made of the internal saccus surface and show irregular reticulations of the wall, as well as ornamentation of the corpus.

One of the conspicuous features of *Endosporites* microspores from the Kentucky locality when examined by light microscopy is the occurrence of three apical papillae (= interrarial papillae) that appear as small dark crescent-shaped objects close to the spore centre; one between each of the laesurae. Transmission and scanning electron microscopy define the nature and relationship of these structures to the saccus and corpus walls. The lowest spore in Pl. 96, fig. 1 shows two of the apical papillae separated by a shallow depression and occurring on the inner surface of the corpus wall; but not arising from the outer saccus wall as has been previously thought.

Ultrastructure and exine stratification of *Endosporites* are best illustrated in Pl. 96, fig. 1 where the relationship between the wall of the corpus and saccus is apparent. The exine is constructed of two layers, with units comparable to the topographic equivalents 'nexine' and 'sexine'. In *Endosporites*, corpus-saccus attachment occurs only at the proximal pole (Pl. 96, figs. 1, 7). In the region where the corpus and saccus are fused on the proximal surface the wall is quite thick (3 μm) and consists of a series of anastomosing exinous strands. Pl. 96, figs. 1, 3 illustrates the proximal continuity provided between saccus and corpus by these delicate strands as viewed in both the transmission and scanning modes.

The spores macerated from the sporangia range from 73 to 121 μm in diameter; however, some of the microspores are appreciably smaller (21 μm). A large number of these smaller spores lack trilete scars and it has been suggested that these may represent isolated central bodies. Other small spores of a similar diameter, but possessing a well-defined trilete mark and in some instances apical papillae, are further distinguished from the more typical *Endosporites* grains by a more highly ornamented distal surface and the absence of a clearly defined saccus (Pl. 96, fig. 7). Transmission micrographs of this latter spore type show apical papillae and a reduced saccus surrounding the central body. These two features suggest a level of spore ontogeny in which the saccus is just beginning to differentiate through the

separation of the two wall layers. A fully developed saccus in *Endosporites* appears like the configuration of the spores in Pl. 96, fig. 1.

FLORINITES AND FLORINITES-TYPE POLLEN

The genus *Florinites* Schopf, Wilson, and Bentall 1944 was instituted for dispersed monosaccate pollen grains of presumed cordaitalean affinity. The generic diagnosis has been difficult to apply, principally because of the confusion regarding grain morphology and structural organization. With the improved techniques now available, new information has been obtained on the morphology of this type of grain. Specimens used were macerated from *Cordaianthus* pollen sacs found in coal balls collected near West Mineral, Kansas (middle Pennsylvanian), and in eastern Kentucky.

Florinites grains are monosaccate, and consist of a spherical central body (= corpus) surrounded laterally by a large, internally reticulate, air bladder (= saccus). In polar view the saccus appears circular-elliptical, with the corpus typically circular in outline. In several morphological studies of cordaita pollen the grains are described as consisting of a large air sac which completely encircles the internal corpus. In these studies body-bladder attachment has been described as occurring only at the distal pole. Combined transmission and scanning electron microscopy demonstrate that the attachment between the body and the bladder occurs at both the proximal and distal poles (Pl. 96, fig. 5). On the proximal surface body-bladder attachment is approximately equal to the maximum body diameter, whereas distally this attachment is typically less than body diameter. Distally the body-bladder attachment may assume a variety of configurations, varying from small and irregular to large and highly angular. In some instances attachment may approach a configuration which superficially resembles a sulcus. On the proximal surface of the grain attachment appears to be more regular and conforms to the symmetry of the central body. Thus in the case of the monosaccate grain *Florinites* the structure consists of a central body totally enclosed by a bladder and fused to it on both the proximal and distal surface.

External bladder ornamentation is best described as laevigate when viewed with the light microscope. When examined with the SEM, the bladder appears as a series of irregular depressions corresponding to the outlines of the internal bladder reticulations (Pl. 96, fig. 5). The ability to examine a fractured internal or enclosed grain component, in this instance the external surface of the corpus, provides information which would be impossible to discern with light microscopy (Pl. 97, fig. 5).

Florinites grains demonstrate the same apparent bladder ontogeny characteristic of extant saccate pollen in which the bladder arises by a separation between the sexine and nexine. Small ridges which characterize the external surface of the central body on the lateral walls represent former regions of exine attachment prior to saccus inflation (Pl. 96, fig. 5). The nexine, which is typically lamellated in extant saccate pollen, shows no observable ultrastructural layering in the *Florinites* specimens.

Another monosaccate pollen grain resembling *Florinites* in many morphological features was also recovered from *Cordaianthus* pollen sacs collected at the eastern Kentucky locality. The grains are larger than the *Florinites* specimens, ranging in size from 115 to 180 μm . Both radially symmetrical and bilaterally symmetrical specimens were found. Grains which show a radial organization are exclusively

trilete, while the bilateral specimens have a suture organization of the monolete type. Most grains show varying degrees of suture expression between these two types. In this grain saccus-corpus attachment also occurs at both the proximal and distal poles.

Externally the saccus is psilate except in the region of the proximal pole. Pl. 97, fig. 6 indicates that the region of the trilete mark is complex, consisting of a series of uneven muri which are most prominent closest to the suture, decreasing in size away from the laesurae. The trilete mark consists of a narrow Y-shaped depression supporting a median, elevated ridge. The central ridge appears to arise from the base of the depression, and is supported by delicate ribs which are uniformly situated at right angles to the long axis of the laesura.

Internally, the saccus of this grain is ornamented by a network of inwardly projecting wall thickenings which form a reticulate pattern, and appear similar to the ornamentation of *Florinites*. The external corpus wall is ornamented by a delicate reticulum (Pl. 96, fig. 2). In section view the projections of the reticulum appear as finely spaced, uniformly developed processes which at some levels appear to bifurcate at their tips (Pl. 96, fig. 2). These processes appear continuous with the saccus reticulum and constitute an ontogenetic feature resulting from the separation of the sexine early in the formation of the saccus. The corpus wall is quite thick, measuring approximately 2 μm (Pl. 96, fig. 2). Ultrastructurally, this layer is composed of a series of irregularly thickened lamellations which may be up to 0.2 μm thick (Pl. 97, fig. 4).

TECTATE GRAIN

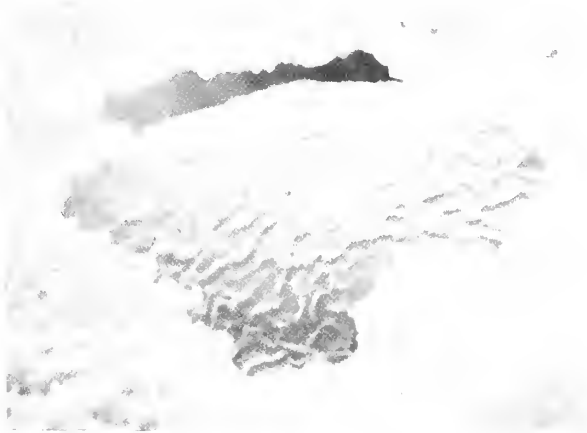
The grain illustrated in Pl. 97, fig. 1 was extracted from a reproductive organ consisting of numerous thick-walled sporangia which are attached to vascularized bract-like structures by elongate pedicels (Taylor 1972). The spores are trilete and circular—subcircular in outline. They range from 38 to 55 μm in diameter and are characterized by trilete rays which extend approximately three-quarters of the spore radius. The spore illustrated in Pl. 97, fig. 1 shows the elevated and prominent nature of the trilete mark. Ornamentation consists of a series of irregular verrucae which extend up to 1.4 μm high (Pl. 97, figs. 1, 2). When examined by light microscopy the surface of the verrucae appear to bear slight depressions. Ultrathin sections of the spores indicate, however, that this pattern is the result of

EXPLANATION OF PLATE 97

- Fig. 1. Proximal surface of Pennsylvanian spore showing verrucate ornamentation and trilete mark. $\times 1200$.
Fig. 2. Fractured surface of spore in Fig. 1 showing level of exine organization and relationship of wall layer components. $\times 6000$.
Fig. 3. Transmission electron micrograph of Fig. 1 spore exine. $\times 8500$.
Fig. 4. Transmission electron micrograph of corpus wall of monosaccate spore in Pl. 96, fig. 2, showing nexine lamellations. $\times 15000$.
Fig. 5. Scanning electron micrograph of *Florinites* grain showing ruptured saccus and ornamentation of corpus. $\times 5900$.
Fig. 6. Proximal region of monosaccate grain showing complex organization of trilete mark. $\times 900$.
Fig. 7. Transmission electron micrograph of spore in Fig. 1 showing wall stratification. Interruptions in the nexine indicate the position of two laesurae of the trilete mark. $\times 1400$.



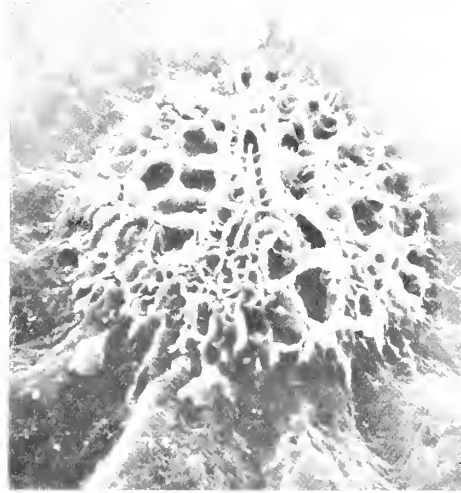
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exine organization rather than surface features of the verrucae (Pl. 97, figs. 3, 7). The section of the spore illustrated in Pl. 97, fig. 7 is slightly oblique in the proximal-distal plane so that two of the laesurae appear as interruptions in the inner component of the wall.

The exine of the grain consists of four easily delimited layers. Using the terms commonly applied in pollen exine organization, these may be called tectum, columellae, pedium; and some level of nexine development (Pl. 97, figs. 3, 7). The columellae extend from the foot layer or pedium, but are not in contact with the tectum at their distal ends. The tectum appears to be attached along the sides of the columellae, rather than at the distal end of each structure (Pl. 97, fig. 7). The broken surface of the spore wall illustrated in Pl. 97, fig. 2 clearly shows the relationships of the exine components, and further clarifies that the tectum is not fused with the pedium between the columellae. The nexine, or inner preserved layer of the spore wall, is uniform in thickness except in the region of the trilete mark where some thickening is present (Pl. 97, fig. 7).

SCHOPFIPOLLINITES

The genus *Schopfipollinites* Potonié and Kremp 1954 (= *Monoletes*) has been used for large (100–500 μm) bilaterally symmetrical pollen grains of the prepollen type, thought to be produced by medullosan pteridosperms. The grains are typically characterized by a single proximal suture having a slight angular deflection (Pl. 98, fig. 2). On the distal surface two longitudinal grooves separated by a median ridge (umbo) are occasionally present; however, the occurrence of this ridge does not appear to be a constant feature of the taxon. Exine ornamentation as examined by transmitted light is typically described as minutely granulose-reticulate, or smooth. Pl. 98, fig. 6 is a light photomicrograph of what appears to be the external ornamentation pattern of a grain extracted from the microsporangiate organ *Halletheca* (Taylor 1971). The scanning electron micrograph of a *Halletheca* grain (Pl. 98, fig. 3) shows that the surface is highly variable in ornament, and that the apparent reticulate appearance of the wall in Pl. 98, fig. 6 is a feature of the internal organization of the wall rather than of surface topography. In some grains, especially in the region of the suture, exine deposition was not complete at the time of fossilization

EXPLANATION OF PLATE 98

Figs. 1–8. *Schopfipollinites* grains.

Fig. 1. Distal view of grain macerated from *Dolerotheca* fructification. $\times 204$.

Fig. 2. Proximal view showing suture with median deflection. $\times 216$.

Fig. 3. Portion of *Halletheca* grain showing internal lumina. Compare with organization illustrated in Fig. 6 obtained with light microscopy. $\times 4950$.

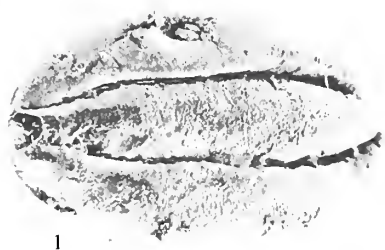
Fig. 4. Internal organization of exine of grain macerated from *Schopfitheca* reproductive organ. $\times 5600$.

Fig. 5. Transmission scanning micrograph of grain showing region of proximal suture and distal umbo. Note thickened wall in proximal suture region. $\times 4000$.

Fig. 6. Light photomicrograph of grain macerated from *Halletheca* sporangium. $\times 2500$.

Fig. 7. Proximal surface of grain showing incomplete deposition of exine. $\times 965$.

Fig. 8. Electron micrograph of grain macerated from *Schopfitheca* reproductive structure showing internal exine organization. Compare with organization of grain in Fig. 5. $\times 5500$.



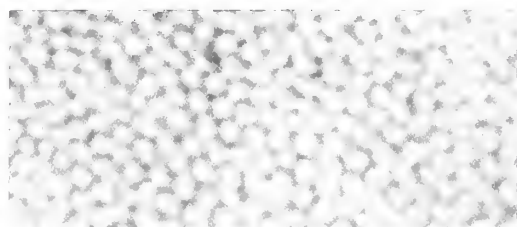
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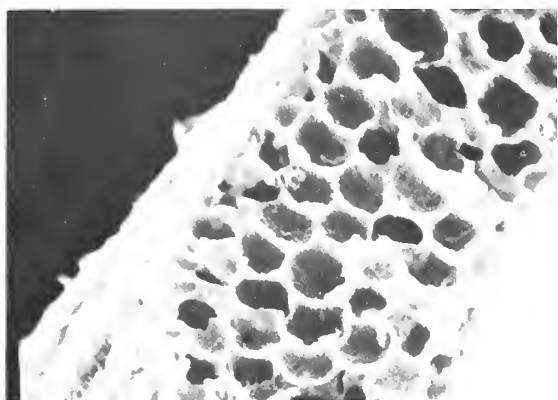
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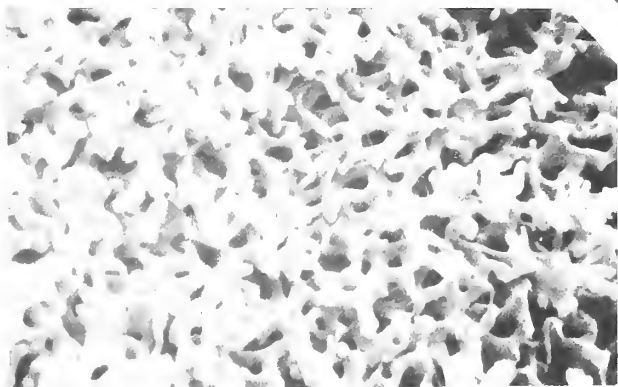
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so that internal exine organization is easily visible without fracturing or sectioning the spore wall (Pl. 98, fig. 7). Grains of this type further point out the necessity of a combined approach to the elucidation of spore wall features.

To determine the constancy of this form of exine organization and its potential use as a taxonomic feature in dispersed spores, specimens of *Schopfipollinites* were extracted from a number of medullosan pollen organs (*Dolerotheca*, *Rhetinotheca*, *Aulacotheca*, *Whittleseya*) and compared with the organization found in *Halletheca*. While a number of *Schopfipollinites*-containing reproductive organs have been described, only very few are known from structurally preserved specimens. Consequently, the opportunity accurately to delimit reproductive organs differing in preservational mode by the identification of their spores is of considerable importance to palaeobotanical systematics.

One such structureless reproductive organ containing *Schopfipollinites* grains is the genus *Schopfitheca* (Delevoryas 1964). The specimen consists of a stalked, clavate-pyriform microsporangiate structure approximately 20 mm long. Ultrastructurally, the wall of the prepollen grain consists of a thickened foot layer from which arise a series of anastomosing baculae (Pl. 98, fig. 8). At some levels these units are fused and demonstrate an organization similar to that in *Halletheca* or *Dolerotheca* grains (Pl. 98, fig. 5). The scanning electron micrograph of the fractured surface of one of these *Schopfitheca* grains (Pl. 98, fig. 4) indicates clearly a distinct difference in internal exine organization from the *Halletheca* grain.

One approach to the problem of identifying stages in exine development is the use of stereomicrography and photogrammetric analysis (Boyde 1970), which enables one to view and accurately measure structural components of the wall. The capability of making stereo pictures with the scanning electron microscope not only provides for an accurate three dimensional representation of the exine organization, but provides a means of making precise parallax measurements of these three dimensional structures. It has already been possible to correlate changes in exine thickness with distinct differences in structural configuration, and to correlate these in turn with grain maturity as determined by such additional features as level of sporangium ontogeny. Preliminary information on the internal wall organization of *Schopfipollinites* prepollen grains extracted from different reproductive organs, as well as on those of differing preservational modes, appears to show that structural differences in exine organization exist. Whether these differences represent stages in wall ontogeny or are solely taxonomic must await continued investigation.

The internal organization of fossil pollen and spores may also provide important information on other aspects of the plants that produced them; for instance, the mode of gamete emission in prepollen grains of the *Schopfipollinites*-type. Germinal exit in such grains has generally been regarded as occurring from the proximal suture (see Chaloner 1970 for an excellent review of this problem), although Renault (1896) suggested evidence of distal germination in grains produced by *Dolerotheca fertilis*. An examination of the proximal suture of a *Dolerotheca* grain (Pl. 98, fig. 5) indicates that although the total thickness of the grain wall is reduced by approximately one-third, the floor and wall adjacent to the suture are distinctly thickened. The suture would therefore seem an unlikely site for gamete emission. On the distal surface, however, the exine is appreciably thinner beneath each of the distal grooves, and super-

ficially appears a more probable exit site. Relative exine thickness, when compared in a large number of Palaeozoic prepollen and pollen types, may provide cumulative information on germination mode and evolutionary trends associated with the process of fertilization.

CONCLUSION

The examples included in this paper illustrate the value of combined transmission and scanning electron microscopy to the study of pollen grains and spores present in reproductive organs. The SEM thoroughly delineates features of the internal and external exine surfaces, and also provides a means whereby developmental features may be critically studied. Transmission electron microscopy provides information about the ultrastructural organization of the wall, as well as supplementing information obtained by the SEM. There is little doubt that basic structural and functional differences are present in the walls of spores and pollen grains produced by various types of Palaeozoic vascular plants. Such differences may be correlated to provide information on the evolutionary relationships between seemingly diverse taxa, as well as providing a means of determining the biological origin of various dispersed spores and pollen grains.

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Discussion on Dr. Taylor's paper:

Kempf: Dr. Taylor has extremely fine material from the Palaeozoic. In some of the spores it was quite obvious that two layers have been preserved, a thin inner layer and a thicker outer layer, which occasionally showed zonations. I would regard these layers as exine and perine. The saccus was always derived from the outer layer—it was not between the two layers, but within the outer layer—the perine. Did you also section *Equisetum*? What is the fine structure of the wall?

Taylor: The wall of *Equisetum* is very nondescript with really no fine structure at all.

Kempf: You know the work of Gullvåg, who is studying *Equisetum*. She has shown a tubular fine structure (which may be artefactual). Perhaps there is some fine structure of this kind?

Taylor: I don't know. I would like to comment on this perine problem. I'm not too concerned with what we call the layers of the walls, because in the Palaeozoic we have very little to compare the structures with. If we could compare with living plants, and show that the perine was present on the living form, then that would be a different matter. The other point is, the perine is the layer that is put on last. It is a developmental term really, and again, working with Palaeozoic material, we are not really in a position to put names to the different layers. If one is to make such distinctions, they must be made at the biochemical level, but at our present state of knowledge we are in no position to do this kind of work.

Kempf: At one time you were describing a wall with four layers; but there should be only two layers, and three of these layers are zonations of the outer layer. Also the perine is not formed last, it is a primary layer, and it is formed first, then the exine and then the intine. You can observe this optically, and sometimes you find spores with only the perine and the exine present and no intine.

Taylor: But how can you demonstrate that what you are calling the intine is not just another layer of the exine without doing biochemical tests? It seems to me rather a matter of semantics.

Skelton: Have you carried your research back to Silurian plants—prespore plants—to see if you can get any structure from them?

Taylor: No, I have restricted my work to the Upper Palaeozoic.

WALL STRUCTURE OF SOME AGGLUTINATED FORAMINIFERIDA

by J. W. MURRAY

ABSTRACT. Present knowledge of agglutinated wall structure and composition is briefly reviewed. Examination of 19 recent species shows the existence of three wall types: simple imperforate wall with an organic cement; complex alveolar imperforate wall with an organic cement; 'perforate' wall with a calcareous cement. It is concluded that more attention should be paid to wall structure and composition in descriptions of species and in taxonomy. Forms with a calcareous cement seem to be stenohaline marine or hypersaline and therefore useful indicators of environment.

WILLIAMSON (1858, p. xi) recognized and named the three main wall types seen in recent foraminiferids: agglutinated, porcellaneous, and hyaline. Then followed the classification by Carpenter, Parker, and Jones (1862) partly based on these characters, together with the presence or absence of pores. Since that time wall structure has held an important position in taxonomy.

Although there are many observations on agglutinated wall structure scattered through the literature, there have been no recent detailed studies (see Lindenberg 1967 for a review). Investigations using electron microscopy have been concentrated mainly on the porcellaneous and calcareous lamellar wall types. However, Jahn (1953) and Towe (1967) published micrographs taken with transmission electron microscopes and Murray (1971) has illustrated the surface texture of twenty-five species in seventeen plates of scanning electron micrographs.

The purpose of this paper is to present a brief review of the present state of knowledge of agglutinated wall structure and to compare with this the results obtained during the examination of nineteen recent species.

The present state of knowledge of agglutinated wall structure may be summarized as follows:

1. The wall consists of detrital particles held together by a cement secreted by the animal.
2. Many different kinds of detrital particles including organic debris (see Thalmann 1948) are used by different species. Some seem to show no selectivity (e.g. *Reophax curtus*, Smith and Kaesler 1970) while others are highly selective (see Hedley 1964). However, it is not uncommon for the grain size to vary from one part of the test to another or within the thickness of the wall (Lacroix 1931).
3. The cement may be entirely organic or it may be mineralized. Hedley (1963) found the organic material to be '... an acid mucopolysaccharide (protein linked with carbohydrate), with organically bound iron and, most probably, organically bound calcium'. Mineralization may involve calcareous or ferruginous deposits or both.
4. Cements mineralized with ferruginous material are known to contain the iron as ferric oxide (Hedley 1963; Towe 1967) in a fine-grained amorphous condition (Towe 1967).

5. Cements mineralized with calcareous material contain microgranular calcite 5 to 10 μm in diameter (Wood 1949).
6. Pores, tubes, and alveolae have been recognized in some walls and these are lined with a thin organic layer (Moebius 1880; Nørvang 1966). In most described examples the pore tubes do not penetrate to the outer surface of the wall. The pore tubes commonly branch (Lacroix 1939).
7. Thin organic membranes around the detrital particles have been recognized by Nørvang (1966).
8. The ratio of detrital particles to cement is highly variable (Cushman 1929).
9. Some walls contain inter-grain spaces due to incomplete cementation (Bartenstein 1952, p. 315).

METHODS

Well-preserved specimens from Recent sediment were selected for study. Some were examined whole, others broken to reveal internal structures and still others were sectioned using the following method:

The specimens were placed on a metal stub (for use in the scanning microscope) together with a small piece of 'Lakeside' thermoplastic cement. The stub was then gently heated in a Bunsen flame to melt the Lakeside and allow it to penetrate into and around the specimens. After cooling individual specimens were manipulated into the desired orientation using a hot needle. Then they were carefully ground away (under a stereoscopic microscope) using a finely ground glass slide lubricated with water. The sections were then etched in 5% EDTA for periods ranging from $\frac{1}{2}$ to 10 minutes.

All specimens were prepared for examination in the scanning electron microscope by coating them with a 40/60 mixture of gold/palladium in a vacuum coating unit.

The X-ray diffraction traces were made from bulk assemblages of each species.

The presence of ferric iron was inferred from the development of a prussian blue colour in specimens treated with a solution of potassium ferrocyanide in hydrochloric acid (2 gm in 100 mls of 1.75% HCl).

MATERIAL

<i>Species</i>	<i>Locality</i>
<i>Saccammina atlantica</i> (Cushman)	Shelf off Long Island, U.S.A.
<i>Miliammina fusca</i> (Brady)	Christchurch Harbour, England.
<i>Cribrostomoides columbiense</i> (Cushman)	Van Damme Beach, California.
<i>Cribrostomoides crassimargo</i> (Norman)	Shelf off Long Island, U.S.A.
<i>Cribrostomoides jeffreysii</i> (Williamson)	Western Approaches to English Channel.
<i>Cyclammina cancellata</i> (Brady)	Continental slope W. of English Channel.
<i>Ammoscalaria pseudospiralis</i> (Williamson)	Kattegat.
<i>Textularia earlandi</i> (Parker)	Celtic Sea.
<i>Textularia sagittula</i> (Defrance)	Western Approaches to English Channel.
<i>Textularia</i> sp.	Shelf off Trucial Coast, Persian Gulf.
<i>Siphotextularia flintii</i> (Cushman)	Celtic Sea.
<i>Trochammina inflata</i> (Montagu)	Christchurch Harbour, England.
<i>Trochammina lobata</i> (Cushman)	East coast, U.S.A.
<i>Jadammina macrescens</i> (Brady)	Christchurch Harbour, England.

Species	Locality
<i>Gaudryina rudis</i> (Wright)	Western Approaches to England Channel.
<i>Eggerella advena</i> (Cushman)	Shelf off Long Island, U.S.A.
<i>Eggerella scabra</i> (Williamson)	Western Approaches to English Channel.
<i>Clavulina pacifica</i> (Cushman)	Off Jeddah, Red Sea.
<i>Martinottiella communis</i> (D'Orbigny)	Western Approaches to English Channel.

RESULTS

Space limitations prevent a full description of each of the species studied so only a few species will be described in detail.

Forms having an organic cement. *Saccammina atlantica* has a unilocular test of variable form although it is commonly pyriform with an aperture at the narrow end. The wall is made up of a detrital quartz grains of variable size and shape (Pl. 99, fig. 1). Much of the wall is built of larger grains which span the entire thickness. These grains are closely fitted together with a separation of less than $1\ \mu\text{m}$ along most of their edges (Pl. 99, fig. 2). However, complete fitting is not possible and the spaces are filled with a mosaic of progressively smaller grains (Pl. 99, figs. 4, 5). In these areas the wall is several grains thick. The surface of the wall is rough both on the outside (Pl. 99, figs. 1, 6) and on the inside (Pl. 99, fig. 5). There are no wall pores. Specimens placed in 5% EDTA or 1.75% HCl showed no reaction and it is concluded that the cement contains no CaCO_3 .

Other species found to have a simple structure include *Eggerella advena*, *E. scabra*, *Cribrostomoides columbiense*, *C. crassimargo*, *C. jeffreysii*, *Textularia earlandi*, *Martinottiella communis*, *Trochammina lobata* and *Miliammina fusca*.

In *Ammoscalaria pseudospiralis* there is a clearly visible organic lining in the chambers (Pl. 99, fig. 7). This can also be seen in *Trochammina inflata*.

In many of these forms economy of cementation leads to small inter-grain spaces in the wall (first noted by Bartenstein, 1952) but no evidence has so far been seen to suggest that these are in any way pores.

Cyclammina cancellata has a complex labyrinthic wall structure (see Banner 1970, for the most recent description). The outer wall (epidermis) is imperforate and smoothly finished. The inner wall (hypodermis) is coarsely alveolar. It is known from previous studies that the cement is organic, with iron mineralization (Hedley 1963). In the present study it was found that the outer and inner wall surfaces and the linings of the alveolae are all completely bound with cement. Within the thickness of the wall the grains are only loosely cemented at their points of contact. No differences could be observed in specimens treated with acid so it is concluded that there is no calcite cement. However, some specimens have coccoliths among their detrital grains and the presence of such calcareous material may account for the calcium recorded in analyses by Brady (1884), Fauré-Fremiet (1911), and Vinogradov (1953). Hedley (1963) published an analysis of carefully cleaned specimens in which CaO was absent.

Forms having a calcareous cement. *Clavulina pacifica* starts with a triserial juvenile portion and then becomes uniserial (Pl. 100, fig. 1). The outer surface of the wall shows the presence of larger detrital grains, including quartz, amphibole, and sponge spicules, and smoother areas of cement and fine detrital grains (Pl. 100, fig. 2). There are no pores penetrating the outer surface. By contrast the inner surface is smoothly finished and shows many pores generally 2 to $3\ \mu\text{m}$ in diameter and closed with an organic membrane (Pl. 100, fig. 3). Broken sections reveal that the pores extend almost through the wall but end blindly just beneath the outer surface (Pl. 100, fig. 4). Specimens impregnated with 'Lakeside', sectioned and etched with 5% EDTA reveal the complexity of the pores. The latter, now filled with 'Lakeside', are seen to be cylindrical tubes through much of the wall but they branch just beneath the outer surface (Pl. 100, fig. 5). Moreover, they appear to be lined with an organic layer which also extends between the pores as vertical partitions (Pl. 100, fig. 6). Pores also extend into the septa but do not penetrate to the apertural side.

Apart from the organic material observed in the wall, the cement consists of calcite (confirmed by X-ray diffraction). It occurs as small units commonly less than $0.5\ \mu\text{m}$ in size (Pl. 100, fig. 7) and sometimes as elongate rods on the outer surface (Pl. 100, fig. 8). Much of the inner part of the wall seems to consist of calcite cement, the detrital grains being mainly in the outer part.

Brief etching with acid causes removal of some of the cement from the outer surface thus allowing the ends of the pore-tubes to be seen. A similar perforate appearance of the test results from gentle abrasion.

Textularia sagittula shows similarities with *Clavulina pacifica* particularly in having a calcite cement and blindly ending pore tubes. The detrital grains are mainly quartz and they are only loosely fitted together on the outer surface, the intervening spaces being occupied with calcite cement (confirmed by X-ray diffraction). Sections impregnated with 'Lakeside' and etched in acid reveal an anastomosing network of pore tubes which end blindly beneath the outer surface of the wall (Pl. 99, fig. 8). The calcite cement occurs as more or less equigranular grains 0.5 to 0.7 μm in size.

Gaudryina rudis likewise has an agglutinated wall with a calcareous cement. The outer surface is rough, due to detrital shell debris incorporated on the sides of the test, although the apertural face is smooth (see Murray, 1971, pl. 14). The inner surface of the chamber side wall is perforated by pores 7 to 8 μm in diameter. These tubular pores end blindly beneath the outer surface of the wall although etched and abraded specimens give the appearance of being perforate. The septa and apertural face lack pores and tubes.

Other species having this type of wall with blindly ending pores are *Textularia* sp. from the Persian Gulf and *Siphotextularia flintii*.

Ferric iron. With the exception of *Cribrostomoides columbiense*, *Cyclamina cancellata*, and *Ammoscalaria pseudospiralis*, all the species were tested for ferric iron and all reacted positively although with different intensities. In the case of the forms with calcareous cements the test was destroyed by the acid solution and the colouration was developed in the residual organic framework.

DISCUSSION

The results presented here agree, in general, with those of previous workers, but there are some differences.

The presence of pores in *Textularia* was first described by Carpenter, Parker, and Jones (1862, p. 191). A more complete description by Moebius (1880) recorded the presence of a 'chitinous' lining in the chambers and in the pore tubes. He also noted that the pores reached the surface only in the younger chambers. Lacroix (1931) studied the same species as Moebius, *T. agglutinans* d'Orbigny. He observed that the pore tubes bifurcate close to the outer surface and stated that they opened on to the surface through very small pores. He also noticed that the inner organic lining covered the pores as well as the chamber wall. Reyment (1969) recognized 'ultrapores' in *Textilina mexicana* (Cushman) but he gave no information about the passage of these pores through the wall.

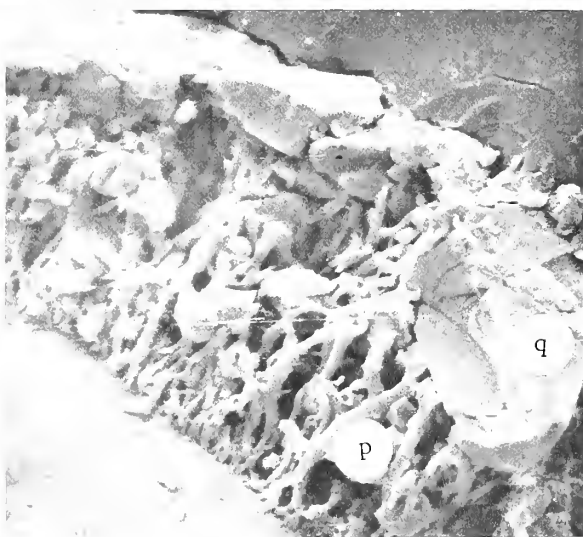
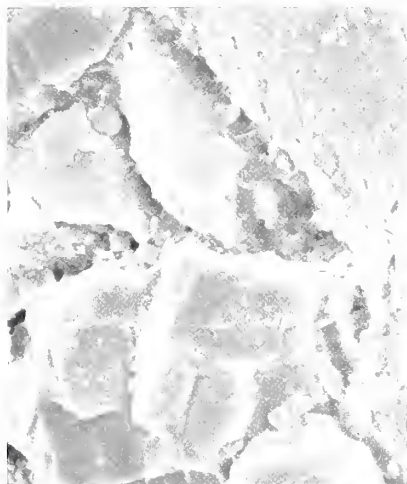
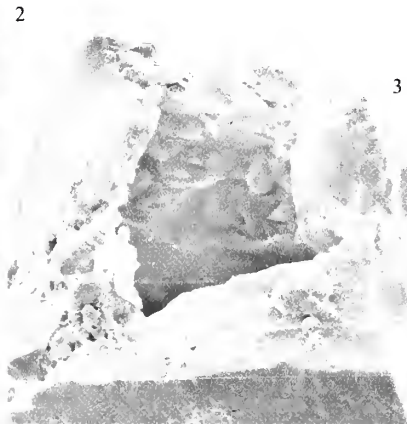
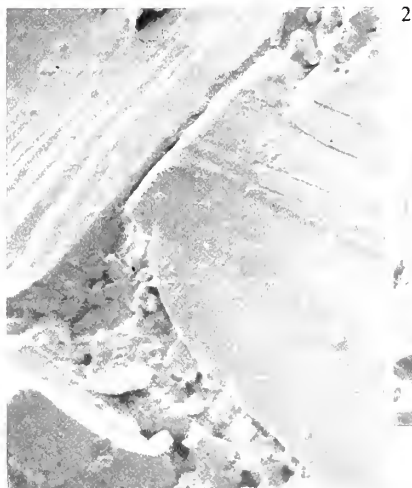
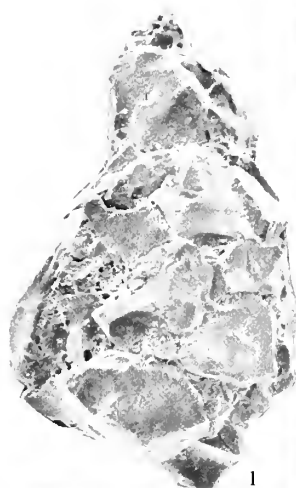
In the present study no evidence could be found of pore openings at the outer surface except where the test had clearly suffered abrasion or etching with acid. In *Clavulina pacifica* and *Gaudryina rudis* the pore-bifurcations beneath the wall surface have a diameter of approximately 1 μm and if they opened on the surface they should be clearly visible. It seems certain that they are closed either by an organic membrane or by calcite cement.

EXPLANATION OF PLATE 99

Figs. 1-6. *Saccammina atlantica* (Cushman) 1, General view, $\times 120$. 2, close fit of two quartz grains, $\times 1150$. 3, The aperture, showing large and small quartz grains, $\times 750$. 4, Close fit of small grains between large detrital grains, $\times 1500$. 5, Detail of inner side of wall showing small grains filling the gaps between the larger grains, $\times 650$. 6, Broken section of wall, $\times 1270$.

Fig. 7. *Ammoscalaria pseudospiralis* (Williamson) showing organic lining (o) on inside of wall, $\times 1300$.

Fig. 8. *Textularia sagittula* DeFrance. Impregnated and etched section of wall showing anastomosing pore tubes (p) and quartz grains (q) on the outer side, $\times 1400$.



MURRAY, agglutinated foraminifera

Nørvang (1966) studied *Textularia sagittula* DeFrance and found the walls to be imperforate. Lacroix (1931) studied what he called the same species and found the pores to be present but small ($1\text{ }\mu\text{m}$ in diameter).

The data on pores in agglutinated walls with a calcareous cement is summarized below:

1. They may be tubular with bifurcations near the outer wall surface or they may form an anastomosing network throughout the wall.
2. They end blindly just beneath the outer wall; no definite pore openings have been observed on the outer surface in the present study.
3. The pores are lined with a thin organic membrane.
4. They are closed with an organic membrane on the inside of the chamber and possibly also at the outer ends.
5. They are normally developed mainly in the chamber walls on the sides of the test. They are less well developed or are absent in the apertural face and in the septa.
6. In *Clavulina pacifica* the pores form 25% of the volume of the wall.

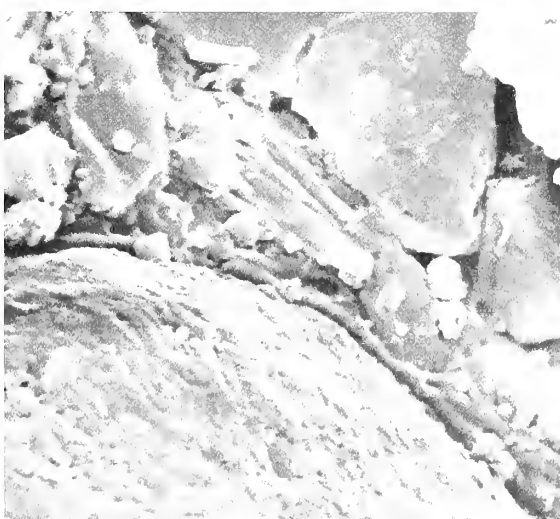
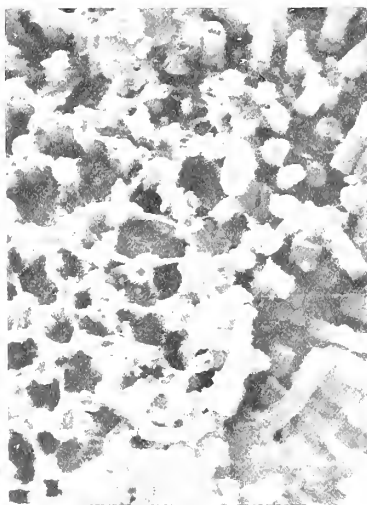
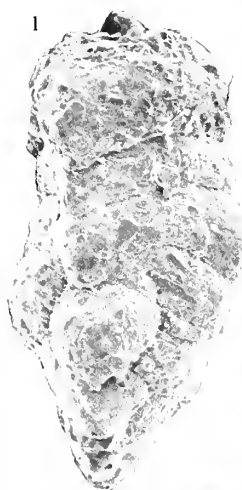
The pores of agglutinated walls were considered by Reiss (1963) to be different from those of calcareous lamellar foraminiferids because they are curved. Perhaps the most distinctive features are that they commonly branch and sometimes anastomose. In calcareous lamellar foraminiferids the pores are maintained even during the addition of further wall layers (see Hansen and Reiss 1971 for illustrations). By contrast, in agglutinated foraminiferids the wall is non-lamellar and each chamber wall is secreted as a single event.

All the forms with pores seem to be stenohaline marine or hypersaline species which are presumably in osmotic equilibrium with their environment. The forms with an organic cement not mineralized with calcareous material lack pores. Marszalek, Wright, and Hay (1969) have suggested such a test '... offers good refuge to the foraminifer under times of stress, and allows time for osmoregulatory adjustment to the new conditions'. This could account for the presence of such forms in hyposaline environments.

The wall of *Cyclammina cancellata* presents a special case. Although the hypodermis contains alveolae these are in complete communication with the chamber lumen and they are not crossed by an organic membrane at the inner ends. They do not therefore compare with the pores discussed above and the wall of *Cyclammina* must be regarded as imperforate.

EXPLANATION OF PLATE 100

Figs. 1-8. *Clavulina pacifica* Cushman. 1, General view, $\times 70$. 2, Detail of wall texture showing detrital grains (g), $\times 220$. 3, Inner side of wall with pores covered by an organic membrane, $\times 4000$. 4, Broken section of wall showing the pore tubes ending blindly at the outer side, $\times 1350$. 5, 6, Impregnated and etched section of wall showing the pore tubes bifurcating and ending blindly below the outer surface, $\times 1400$, in 5 and transverse sections of the pore tubes and associated organic membranes, $\times 670$, in 6. 7, Broken section of wall showing closely packed pore tubes built mainly of cement, $\times 3400$. 8, Detail of outer wall surface showing elongate cement crystals between detrital grains, $\times 3400$.



MURRAY, agglutinated foraminifera

WALL STRUCTURE AND CLASSIFICATION

In the classification adopted in the Treatise (Loeblich and Tappan 1964) nearly all agglutinated forms are placed in the suborder Textulariina. This includes the superfamily Ammodiscacea, in which the wall is said to be 'agglutinated, simple, or labyrinthic', and the superfamily Lituolacea, 'wall siliceous or agglutinated, with calcareous, siliceous, or ferruginous cement'.

At lower taxonomic levels the information is often lacking in detail or at variance with the present observations. For the Saccamminidae the wall is not mentioned. The family Lituolidae has 'wall agglutinated, with calcareous cement or microgranular calcite, interior simple to labyrinthic, epidermal layer imperforate'. Genera of this family which have been found in the present study not to have a calcareous cement include *Criboostomoides*, *Cyclammina*, and *Ammoscalaria*. The family Textulariidae has 'wall agglutinated'. For *Textularia* it is said to be 'simple'. The wall of *Siphonotextularia* is not described. The family Trochamminidae just has 'wall agglutinated'. The same is true of the Ataxophragmiidae. *Gaudryina* has no wall description, *Eggerella* has 'wall finely agglutinated on pseudochitinous base, may be of calcareous particles in calcareous cement'. This disagrees with the results presented here. *Clavulina* has 'wall agglutinated with much calcareous cement'. *Clavulina pacifica* agrees with this. *Martinottiella* has 'wall finely agglutinated'. Thus, of the four Ataxophragmiidae examined two have an organic cement and no pores (*Eggerella* and *Martinottiella*) and two have a calcareous cement and pores (*Gaudryina* and *Clavulina*).

This raises the question of the value of the wall structure and cement composition as taxonomic features. In a general sense the agglutinated wall structure is clearly useful. However, should more notice be taken of the detailed structure? Since the cement is secreted by the foraminiferid it must surely be of greater taxonomic value than the nature of the detrital particles gathered from the sediment. The kind of cement is a reflection of the physiology of the animal. This must be at least of equivalent importance to the nature of coiling or the arrangement of the chambers. Unfortunately, in the majority of descriptions of agglutinated species a full description of the wall structure and composition is omitted.

ECOLOGICAL SIGNIFICANCE

Foraminiferids with agglutinated walls are known to be particularly common in the deep sea, in cold shelf seas, and in shallow and intertidal hyposaline waters. There is now clear evidence that the nature of the cement is of ecological significance.

Pokorny (1958) suggested that forms with an organic cement characterize cold water. Lindenberg (1966) inferred that in the Dogger (Jurassic) of south west Germany the forms with a calcareous cement lived in more marine waters than those with an organic cement.

The results of the present study support Lindenberg's view. All the examined species having a calcareous cement come from normal marine or hypersaline environments (Western Approaches to the English Channel, Celtic Sea, Persian Gulf, Red Sea). Those with a simple wall and an organic cement are found in hyposaline marshes and lagoons (*Trochammina inflata*, *Jadammina macrescens*, *Miliammina fusca*),

hyposaline shelf seas (*Saccamina atlantica*, *Cribrostomoides crassimargo*, *Eggerella advena*), and normal marine shelf seas (*Martinottiella communis*, *Textularia earlandi*, *Eggerella scabra*). Thus they occur in many different environments. The only form with a complex alveolar wall studied here is characteristic of the continental slope with sigma-t values of 27.7 (see Banner 1970, p. 244).

The restriction of forms with a calcareous cement to normal marine and hypersaline shelf seas should prove useful in helping to interpret the palaeoecology of fossil assemblages.

CONCLUSIONS

The nineteen species discussed here are hardly representative of the hundreds of agglutinated species but the results nevertheless have some interest. Clearly there are more types of agglutinated wall structure to be discovered. At the taxonomic level many more species need to be investigated in detail and then it will be possible to emend generic and family descriptions and groupings. From the ecological point of view the nature of the cement appears to be important and controlled laboratory experiments should be carried out to gain further knowledge.

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Discussion on Dr. Murray's paper:

Green: Is there any organic membrane lining the pores?

Murray: Yes. This is something which I omitted to mention in the talk. I have some additional micrographs which show organic walls running between the pores perpendicular to the chamber surface, so the whole of the inside of the wall has a mesh-work of organic material, and this presumably replaces the calcitic cement.

Green: Filling the gaps in?

Murray: Or else the opposite; it is trying to reduce the density of the wall, because the density of calcite is great with respect to sea water.

Rood: Is the cement of such a nature that it could conduct an ion flow through the cement into the inner structures?

Murray: I do not think that any of the work I have done so far could prove this, but it seems strange if the animal felt the need to transport material through the cement, when it has tubular pores in the wall. The odd thing about these pores is that they only occur in the sideways facing parts of the test—they don't occur in the final face of the test, the one that is held down to the sea floor where the animal is living.

Daniels: Perhaps in life the grains over the ends of the pores are loose, and the animal can create some sort of exit.

Murray: I have taken many pictures of the outer surface, and the cement always comes round the grains holding them in place very firmly.

Sylvester Bradley: How do you think the cement got there?

Murray: When the animal secretes its skeleton, there would have to be places where the pseudopodia came out.

Sylvester Bradley: You don't think that these pores were where the pseudopods came out?

Murray: I must admit that that is a good point. But one has to ask why the pseudopods covered the ends of the pores with a membrane after withdrawing into the chamber.

TRANSMISSION ELECTRON MICROSCOPY OF FOSSIL SPORES

by E. K. KEMPF

ABSTRACT. Transmission electron microscopy of fossil spores presents special difficulties. A major problem in megaspores is obtaining low power pictures of whole spores; this is overcome by using single-hole discs instead of grids. Care is needed to avoid damaging sporoderm ultrastructure by oxidation during preparation. Results achieved since 1965 are reviewed, and the sporoderm fine structures of *Setosisporites* (Carboniferous) as well as *Salvinia* and *Alnus* (both Tertiary) are illustrated and interpreted.

SEVEN years ago, in May 1965, the Department of Geology at the University of Cologne was provided with a transmission electron microscope, and a program was started to investigate the stratification and fine structure of fossil sporoderms in ultra-thin sections.

At that time there were only two papers published on this subject. Ehrlich and Hall (1959) studied some Eocene pollen grains without knowing, however, to what genera the material belonged. Pettitt and Chaloner (1964) tried to elucidate the fine structure of Mesozoic microspores from pollen sacs of *Cheirolepidium muensteri*, which are of the *Classopollis* type. Both publications demonstrated that it is possible and worth while to study fossil material in this manner.

TECHNICAL PROBLEMS AND SOLUTIONS

Our investigations were carried out step by step. The first task was to ascertain that the fine structure of sporoderms had been preserved in the fossil state without any change during fossilization. For this, comparison was necessary between the fine structural details of Recent and fossil sporoderms of the same species, and selection of suitable material turned out to be quite difficult.

Most of the papers published since 1952 on transmission electron microscopy of Recent sporoderms dealt with microspores, and especially with pollen grains. In preparing the material for such investigations, anthers from living or herbarium plants were reduced to small pieces, fixed, dehydrated, embedded in epoxy resins, and ultra-thin sectioned. There are, in comparison, only a few cases where fossil anthers, or parts of them, are found that may be treated in this way; for example *Classopollis* (Pettitt and Chaloner 1964) or *Alnus* (this paper). Most fossil microspores, however, occur dispersed and because of their extremely small size are not easy to handle. While the latter problem can be mastered using a micromanipulator, the main difficulty still remains: to determine the plant species in which the single microspore originated. In consequence of this uncertainty and as fine structural details are not very numerous in sporoderms of microspores, we decided to turn towards megaspores.

Cenozoic megaspores, which had been collected for biostratigraphical reasons, as well as Recent megaspores to serve as comparative material, were at hand. For the task in question Recent and Pleistocene megaspores of *Salvinia natans* seemed to be

most suitable. They were subjected to the usual sample preparation techniques and ultra-thin sectioned. The transmission electron micrographs gave a positive answer to our question. Sporoderm fine structure was preserved, and apart from some differences in electron density there was no change observable which could have been caused by fossilization. Other megaspores from Cenozoic, Mesozoic, and Palaeozoic strata were subsequently studied and corroborated the result.

The illustration of the findings for publication posed new difficulties. Because of the formvar film coated copper grids, which were used to support the ultra-thin sections, up to 50% of the large megaspore sections (about 0.5 mm in diameter) were hidden. In many of the ultra-thin sections it was possible to reveal the stratification and fine structure of a megaspore sporoderm, but the photographs are not suitable for publication. The paper of Pettitt (1966), which had been published in the meantime, also suffered from this difficulty. Indeed in most papers that dealt with transmission electron microscopy of sporoderms very tiny areas were figured at large magnifications, while figures at low magnifications giving a general view were missing or presented only as non-equivalent photo micrographs.

To give the maximum amount of information, best presentation and interpretation of sporoderm stratification and fine structure it seemed absolutely necessary to cover the whole field from very low up to the highest magnifications with transmission electron micrographs. Therefore we changed from copper grids to copper discs with one single hole of 400, 800, or even 1000 μm in diameter. To support the large ultra-thin sections it is necessary to reinforce the thin formvar films with which the holes were covered. It is then possible due to this method to get transmission electron micrographs at a magnification of about $\times 90$ with moderate resolving power, at magnifications of about $\times 450$ and $\times 1700$ with better resolving power, and above $\times 6000$ with high resolving power. Thus micrographs of single megaspore specimens in transmission electron microscopy can be produced, which nowadays, of course, should be supplemented by scanning electron micrographs.

Another difficulty is to find the best embedding medium for fossil spores. Because of the hardness of fossil sporopollenin and the necessity of good impregnation we use traditional methacrylate, in the formulation given below.

A further question is whether to stain the specimens or not. Until now we have avoided staining apart from some trials in order not to complicate our studies. In the future it will be necessary perhaps to use different stains, especially in microspores. Unstained specimens, should, however, always be studied for comparison.

We consider the demonstration that fossil sporoderms are often preserved in an excellent state as a main result of our studies. If however, one follows standard micropalaeontological or palynological techniques in which oxidizing chemicals are used, a certain amount of damage may occur. A most careful separation of the fossils from the embedding sediments is therefore required. In order to clean the specimens selected for study by the transmission electron microscope cold hydrofluoric acid (40%) is used, followed by washing with hot hydrochloric acid (25%) and distilled water.

Recapitulating, one can say that transmission electron microscopy of fossil spores at least requires the following treatment:

1. Careful separation from the embedding sediments, if possible without making use of oxidizing chemicals, in order to prevent damage.

2. Cleaning of the selected specimens by using cold hydrofluoric acid (40%), followed by washing with hot hydrochloric acid (25%) and distilled water.
3. Dehydration in a graded ethanol series followed by embedding in a 1:9 mixture of butyl/methyl methacrylate, containing 1% benzoyl peroxide. If different resins are used as embedding media, another kind of dehydration might be necessary.
4. After polymerization, cutting of ultra-thin sections on an ultra-microtome using glass and diamond knives. For magnifications up to $\times 10\,000$ mounting of ultra-thin sections should be done on formvar-film coated single-hole copper discs; for larger magnifications copper grids with or without film coating may result in higher resolving power.

STRATIFICATION AND FINE STRUCTURE OF FOSSIL SPORODERMS

Most of the results have been obtained from fossil megaspores, but some characteristic features of microspores are also presented.

For the interpretation of sporoderm stratification and fine structure it is necessary to make comparative studies of Recent spores in ultra-thin sections. Until now the resulting transmission electron micrographs never revealed more than three layers, which in my papers are named intine, exine, and perine, from inside to outside. It should be mentioned here that my terms exine and perine do not correspond with such terms of some other authors.

Cenozoic filicopsid megaspores and microspores. Most of the megaspores which have been found in Cenozoic strata belong to genera of the heterosporous ferns. Many species have been studied in ultra-thin sections, such as *Azolla* (Kempf 1969 *a, b*) and *Salvinia* (Kempf 1971*b*).

In fossil *Azolla* megaspores, two layers are preserved. The inner one, the exine, is quite thick, electron dense, and restricted to the rounded distal half of the megaspore. The outer layer, the perine, surrounds the exine. At the proximal pole it forms a large gula, to which the floats adhere via threads. The number of floats differs from subgenus to subgenus.

When, at larger magnifications, megaspore sporoderms of different species are compared with each other, the exines look quite similar. The fine structure of the perine, however, is heterogeneous and changes from species to species. It is therefore very useful for identifications on the species level. Within one species, the perine fine structure changes according to a zonation. In Miocene *Azolla nana* the structure resembles the differentiation into foot layer, bacula, and tectum of certain pollen grains. Furthermore there are fine structural differences between the distal and the proximal part, so that around the gula, the perine is quite different from that in the distal part of the megaspore. In *Azolla*, the intine is not preserved in the fossil state because it consists mainly of cellulosic material.

Hitherto, fossil intine has only been found in the megaspores of some species of *Salvinia*, e.g. *Salvinia natans*. The electron density of this material suggests that its preservation was made possible by a certain content of sporopollenin. The exine fine structure, as in *Azolla*, does not vary very much from species to species. The perine is again characterized by its zonation and great variability of fine structure.

Sometimes even the remains of the sporangioderm, which enveloped the megaspore, are preserved.

From *Salvinia rhenana* megaspores, we learned that the sporoderms can be damaged where oxidizing chemicals are used in the laboratory. Where H_2O_2 had been used to disintegrate the sample, the intine had disappeared and the exine revealed initial signs of corrosion. New samples, treated without oxidizing chemicals, released megaspores in which the exine and intine were very well preserved.

The Miocene *Salvinia cerebrata* was preserved as complete sori, which, after breaking open, yielded megaspores and microsporangia. A longitudinal section of a megaspore shows the dense exine and the general arrangement of the perine fine structure, which is most complicated at the proximal pole (Pl. 101, fig. 3). There the delicate gula is hidden by three large germinal valves. The scanning electron micrograph gives a three-dimensional impression of this region (Pl. 101, fig. 4). The perine fine structure resembles that of *Halletheca* from the Carboniferous (Taylor 1971).

Ultra-thin sections of complete microsporangia disclosed the characteristics of the microspores. In *Salvinia* all microspore exines of a microsporangium share a common perine, which in its fine structure resembles that of the corresponding megaspore. Within the perine mass the exines are arranged in large cavities near the surface, each of which is provided with a triradiate germination mark. The exines are very homogeneous, electron dense and therefore poor in fine structure. With the exception of a slight thickening towards the germinal suture, there is no sculpture on the exine surface.

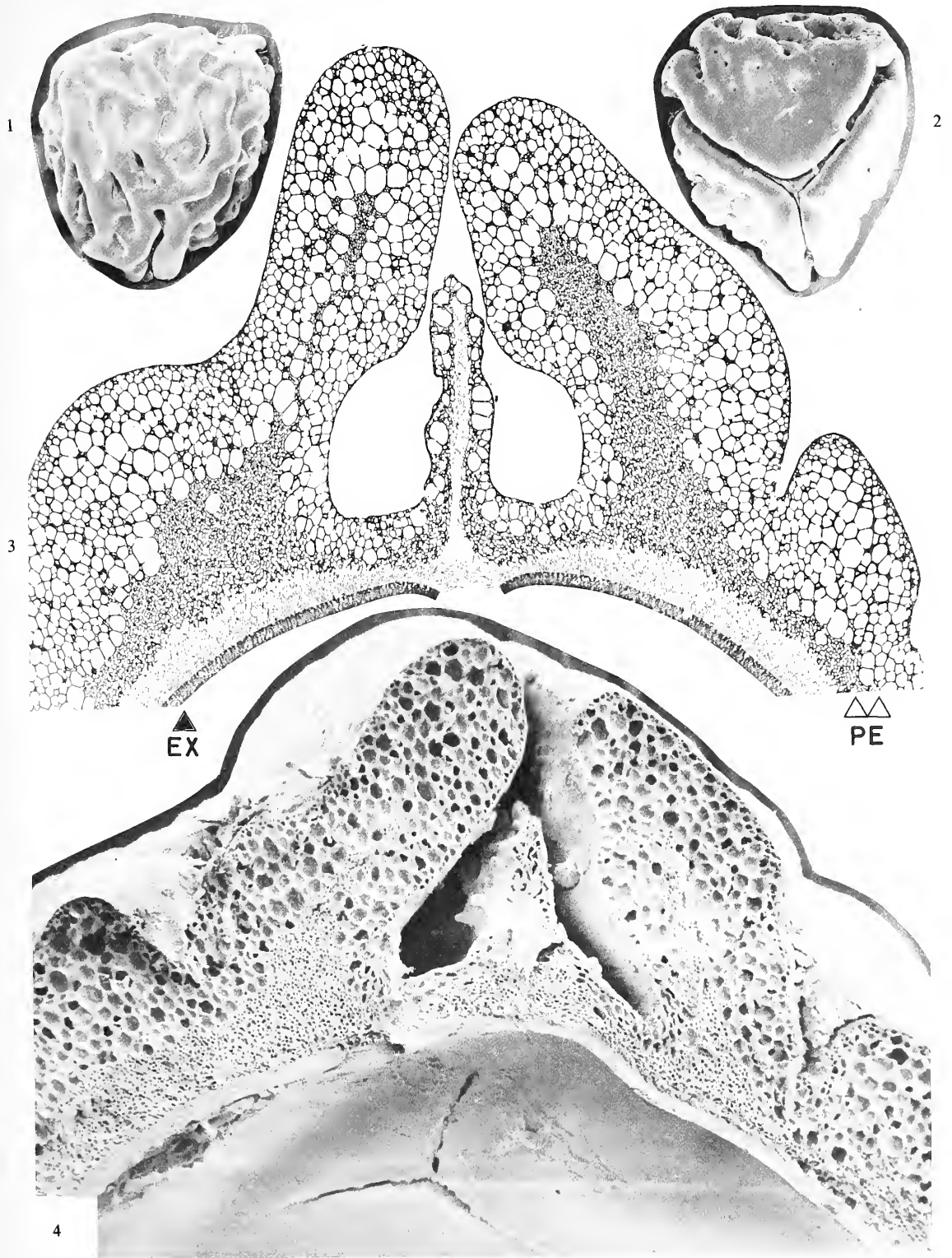
Cenozoic angiosperm pollen grains. As an example of fossil angiosperm pollen grains, pollen sacs of *Alnus* were embedded and ultra-thin sectioned. The material was collected from a clay lens within the lower-most part of the main seam of the Rhenish brown coal (Kempf 1971b), where it was found together with *Salvinia cerebrata*, amongst other plant fossils. The scanning electron micrograph of a piece of a pollen sac (Pl. 103, fig. 1) clearly demonstrates that these pollen grains represent the genus *Alnus*. As a dispersed spore, this type is known as *Alnipollenites metaplasmus* (Potonié 1931) Potonié 1960.

The transmission electron micrographs of ultra-thin sections (Pl. 103, figs. 2-4)

EXPLANATION OF PLATE 101

Megaspores of *Salvinia cerebrata*, Lower Miocene, W. Germany. Figs. 1, 2, 4: scanning electron micrographs; fig. 3: transmission electron micrograph.

1. Distal view; spore surface irregularly corrugated (cerebral sculpture), $\times 100$.
2. Proximal view; triradiate gula with germination mark largely hidden by the three germinal valves, $\times 100$.
3. Ultra-thin longitudinal section of proximal part showing two germinal valves and one ray of gula with germinal suture; exine (EX) relatively thin and quite dense; perine (PE) very thick and structurally subdivided in three zones (inner, middle, and outer zone); outer zone consisting of large, middle zone of small cavities; felt-like inner zone somewhat stretched because of laboratory treatment; $\times 675$ (E 10009-10012, B 661, S 36393-2).
4. Proximal part of longitudinal half seen from inside; thin, dense exine showing triradiate germination mark on inner side; perine presenting two germinal valves and one ray of gula; spongy fine structure zonally differentiated, $\times 675$.



KEMPF, Miocene megaspores

resemble those of Recent pollen grains of *Alnus* (Takeoka and Stix 1963). The sporoderm consists of two layers. The inner layer, the exine (= secondary exine, endexine, or nexine of other authors), is quite thin and electron dense. It is doubled in thickness over the arci, but looks like a porous membrane below the apertures. The perine (= primary exine, ektexine, or sexine of other authors) is formed by bacula and tectum. The bacula arise from the exine at irregular intervals, but are most numerous in the range of the arci. The coherent tectum is equatorially penetrated by the four large germinative pores and elsewhere by a great number of minute tubes (perpendicular bright lines). At each pore a vestibulum is formed by an arching upwards of the tectum. At the base of the bacula, exine and perine are fused together. There seems to be no foot layer; a condition recently described also for the Upper Cretaceous pollen grain *Wodehouseia spinata* (Leffingwell *et al.* 1970).

Mesozoic lycopsid megaspores and microspores. In Mesozoic nonmarine sediments, lycopsid megaspores are rather common microfossils. One of the first form species to be studied by us in ultra-thin sections was '*Horstisporites*' *semireticulatus* (Kempf 1971a). In this megaspore the sporoderm consists of a very heavy outer layer composed of ramifying sporopollenin threads—which was named perine, and a very thin laminated inner layer—which was named exine. Compared with the information at that time available about the sporoderm fine structure of Recent *Selaginella* megaspores (Martens 1960; Stainier 1965, 1967), this nomenclature seemed to be wrong.

It was necessary therefore to study some more Recent *Selaginella* megaspores (Kempf 1970), and this indicated that the naming of the layers in the fossil megaspore had been correct. In *Selaginella* the perine in fact is a very heavy layer with a variety of fine structure of different kinds, which mostly is arranged in concentric zones. The exine on the other hand is represented by a quite thin and laminated layer. The intine cannot be expected to be found in the fossil state since it is mainly composed of cellulosic substances.

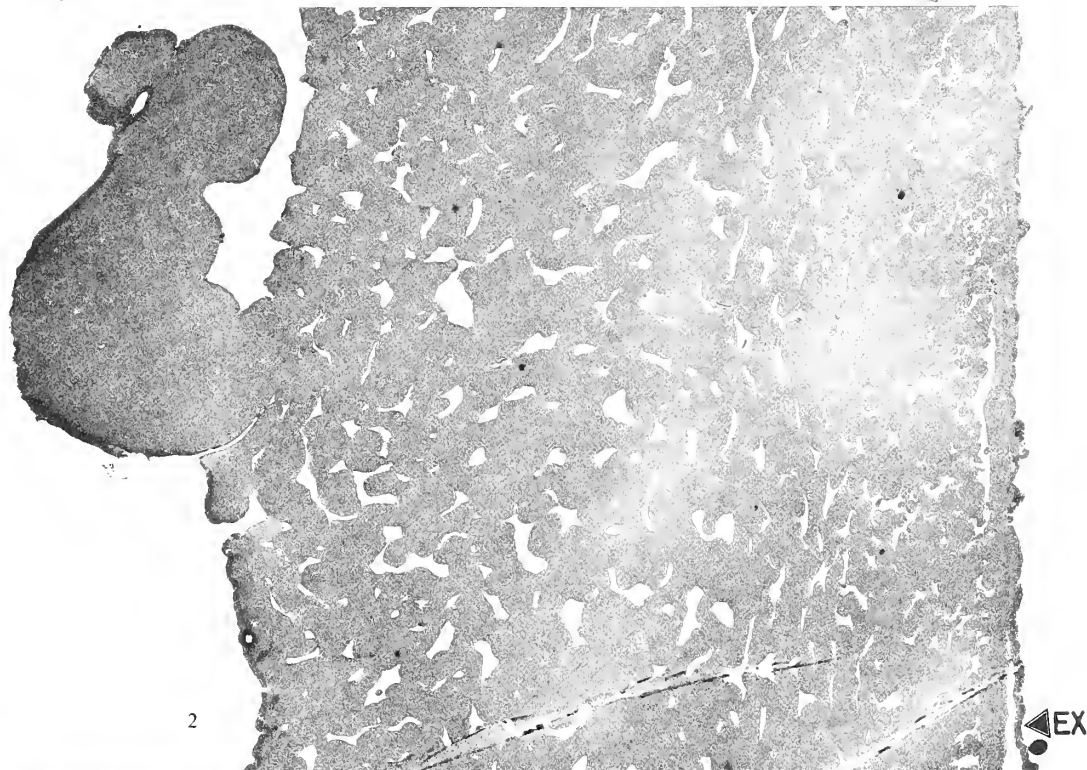
Subsequently other Mesozoic megaspore species were examined in ultra-thin sections (Kempf 1972). A very thin laminated exine and a quite heavy perine, with

EXPLANATION OF PLATE 102

Figs. 1, 2. Megaspore *Setosisporites brevispinosus*, Namurian, Poland.

Fig. 3. Megaspore *Setosisporites hirsutus*, Westphalian B, W. Germany. All transmission electron micrographs.

1. Ultra-thin longitudinal section of compressed specimen; proximal part with one ray of germinal suture (GS) and very thin exine which has loosened from inner side of perine; distal part with short spines rising from outer surface; inner third of perine more dense than outer two-thirds, indicating some kind of zonal differentiation in fine structure, $\times 340$ (E 9329, B 740, S 36398-P 5).
2. Distal part of sporoderm in ultra-thin section; exine very thin and dense; it is doubled in this place as the exine cavity has collapsed; perine very thick with a fine structure formed by sporopollenin threads; a certain zonation in fine structure caused by variations in diameter or in main orientation; the spine regularly arises from the outer zone, $\times 6300$ (E 9348, B 740, S 36398-Q 1).
3. Ultra-thin section of sporoderm; exine extremely thin; perine thicker by far with a zonal fine structure formed by sporopollenin threads; within inner and middle zone the threads are concentrically arranged but differing in diameter; within the large outer zone the threads form an irregular network the free space of which has partly been filled with an unknown substance during fossilization or laboratory treatment, $\times 5780$ (E 8857, B 621, S 36397-G 4).



KEMPF, Carboniferous megaspores

fine structure formed by ramifying sporo-pollenin threads, were found in nearly all of these sporoderms.

Microspores were adhering to the surface of some of these megaspores and thus were sectioned by chance. They also consist of two layers—exine and perine—but it is not possible to detect any relationships to the most likely corresponding megaspore. Pettitt (1966) made the same observation when he compared the fine structures of Recent *Selaginella pulcherrima* megaspores and microspores.

In one type of megaspore a single thick layer only was encountered (Jux and Kempf 1971). Because the fine structure, which consists of radial tubes, differs from that of all other previously known megaspore sporoderms, a new form genus was created. This type of megaspore may perhaps represent some kind of Calamitacean plant.

Palaeozoic megaspores. The number of megaspore forms known from Palaeozoic deposits is very large. At the moment, however, it is quite difficult to find megaspores which are in such a good state of preservation that they are really suitable for ultra-thin section studies. We have attempted this with megaspores of *Setosisporites hirsutus* (Pl. 102, fig. 3) and *Setosisporites brevispinosus* (Pl. 102, figs. 1, 2). In fine structure they are similar to some of the Mesozoic megaspores, but it is obvious that the exine is extremely thin, while the perine shows an enormous thickness.

GENERAL TRENDS AND FUTURE WORK

It can be demonstrated that transmission electron microscopy of fossil spores provides us with a large amount of new and valuable information. Details, previously unknown or misinterpreted because of the limitations of optical microscopy, are revealed.

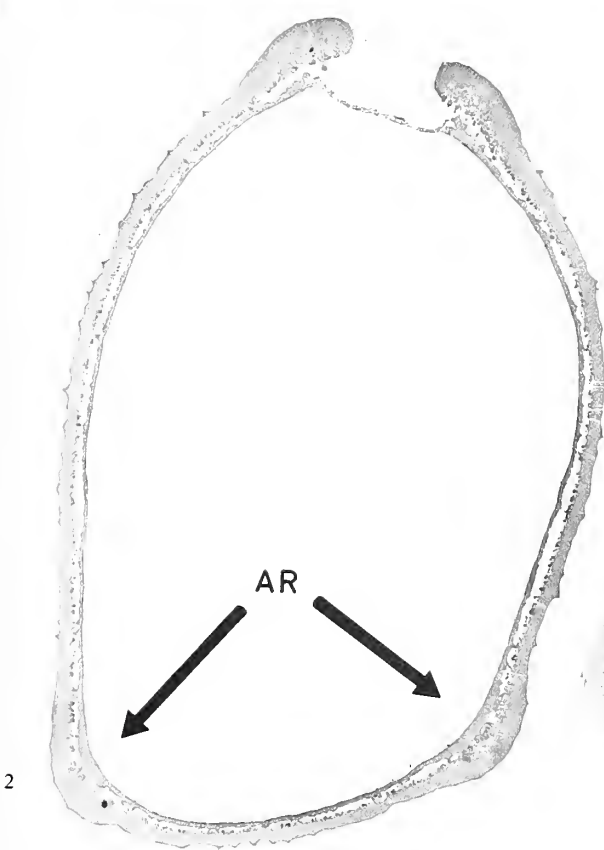
Of course most of the new information is relevant only to a single genus or species. There are, however, also general trends. One of these is the observation that in megaspores there is an obvious decrease in the ratio of perine to exine thickness, which is related to the state of evolutionary development of the megaspore (Kempf 1972).

EXPLANATION OF PLATE 103

Pollen grains of *Alnus* (*Alnipollenites metaplasmus*), Lower Miocene, W. Germany.

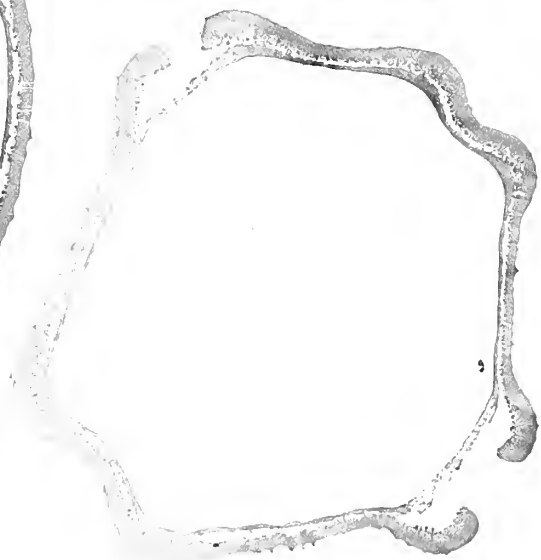
Fig. 1. scanning electron micrograph; figs. 2–4: transmission electron micrographs.

1. Part of pollen sac; all pollen grains with four equatorial apertures, which are connected with each other by two quite distinct arci; sporoderm surface provided with tiny spines, $\times 2000$.
2. Ultra-thin section of pollen grain; sporoderm consists of exine and perine; exine very thin, dense and doubled in thickness in the area of the arci (AR), but like a porous membrane below the apertures; perine is formed by bacula and tectum; bacula rising from the exine at irregular intervals, most numerous in the range of the arci; the otherwise coherent tectum is penetrated only by the four large pores and by a great number of minute tubes (perpendicular bright lines); at each major pore a vestibulum is formed by arching upwards of the tectum, $\times 5500$ (E 9899, B 771, S 62381–J 5).
3. Ultra-thin section of pollen grain, in which two pores and four arci were met with; $\times 3360$ (E 9871, B 771, S 62381–J 2).
4. Ultra-thin section of pollen grain; sporoderm consists of exine and perine which at the base of the baculae are fused together; foot layer seems to be missing; perine is penetrated by minute tubes (perpendicular bright lines); $\times 28\,000$ (E 9897, B 771, S 62381–J 5).



EX

PE



KEMPF, Miocene megaspores

One of the most important general results is a better knowledge of sporoderm stratification. It becomes apparent that all sporoderms comprise three layers: intine, exine, and perine. In the fossil state normally only two of them are preserved: exine and perine, with *Salvinia* as the single known exception. The fossilization of sporoderm layers depends on their content of sporopollenin. Where this is lacking the layer will also be missing in the fossil record.

The knowledge of sporoderm stratification, mainly obtained from megaspores, also can be applied to pollen grain sporoderms. There the exine has hitherto been named endexine, nexine, or secondary exine, while the perine was described as ektexine, sexine, or primary exine. In pollen grains it is sometimes not easy to recognize where the exine ends and the perine begins, as these two layers are often fused together as in *Alnus* (Pl. 103, fig. 4). There are, however, differences depending on function, which become most distinct in the range of the germinal openings. Apparently sporoderm stratification and fine structure are mainly subject to functional requirements.

Biologically, there are great differences between pteridophyte and spermatophyte megaspores, as well as pteridophyte microspores and spermatophyte pollen grains. However, if one considers the sporoderms alone these differences are less serious. Future work therefore should also consider the megaspore membranes of seed plants, as has been shown for Palaeozoic material by Zimmerman and Taylor (1971).

In general, it is demonstrable that in palynology and in other branches of palaeobotany a vast field is opened up by the use of the transmission electron microscope. Such studies nowadays should be completed by scanning electron microscopy, although due to its poor resolving power this method is incapable of providing sufficient detail.

Acknowledgements. The transmission electron microscope (Zeiss EM 9 A) and the instruments for preparative work (Leitz ultramicrotome, Leitz micromanipulator, etc.) were provided by the Deutsche Forschungsgemeinschaft. Mr. W. Mackowiak carried out the preparative work, as well as the analysis of ultra-thin sections in the electron microscope, with great skill. Megaspores of *Setosporites hirsutus* and *Setosporites brevispinosus* were presented by Dr. H. Grebe (Geological Survey, Krefeld) and Dr. A. Jachowicz (Geological Institute, Sosnowiec). The scanning electron micrographs were taken on a JEOL U 3 SEM (Kontron, LWU, Munich: operator Mrs. Liebel) by courtesy of Mr. G. Cichy (Kontron, Düsseldorf).

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Discussion on Dr. Kempf's paper:

Chaloner: In spores of fossil plants that you cannot immediately attribute to any group of living plants, e.g. to ferns or lycopods, how do you decide what is perine and what is exine?

Kempf: By analogy with spores of modern plants. There the exine plays no part in the ornamentation of the sporoderm surface. The ornamentation of the surface of a megaspore, for instance, is always made up by the perine. If the perine is composed of several zones, each zone follows the ornament observed at the surface. The exine, however, is unaffected. Further, the perine has a functional morphology; it has to protect the spore from the environment, and also it can fill its interstices with gas so that it can float on water.

Chaloner: It is a pity that we do not have 'types' in our terminology as well as in taxonomy. If we had a 'type' for the perine, it would surely be in the fern family Polypodiaceae. For most people, the term perine is more or less confined to this family. Other ferns, *Osmunda*, for example, do not have a perine. So that in *Osmunda* spores the exine must be forming the sculpture.

Kempf: I know of no instance where—according to transmission electron micrographs—the exine forms the sculpture.

Chaloner: How do you define exine then?

Kempf: It is the middle layer of a three-layered sporoderm.

ACRITARCHS OF THE MIDDLE SILURIAN ROCHESTER FORMATION OF SOUTHERN ONTARIO

by BINDRA THUSU

ABSTRACT. The Rochester Formation yields an acritarch microflora containing 24 genera and 46 species and varieties. Genus *Hemideunffia*; Species *Domasia canadensis*, *D. rochesterensis*, *Hemideunffia trifurcata*, *Elektoriskos simplex*, *Filispheeridium bifurcatum*, *Gorgonispheeridium wenlockium*, *Lophospheeridium rugosum* and *L. microgranulosum*; varieties: *Deunffia furcata* var. *niagarensis*, *D. monospinosa* var. *tonowandensis*, and *D. ramusculosa* var. *rochesterensis* are proposed as new.

The Rochester netromorph assemblage, in particular the *Deunffia* and *Domasia* complex, shows a close resemblance to those from the Ilion Shale in Utica, New York, the Rochester Formation in West Virginia, and the Buildwas Beds in Shropshire, Britain. The stratigraphically restricted genus *Deunffia*, in particular *D. ramusculosa* and *D. furcata* which probably made their first appearance during the Lower Wenlockian times, is present in all four areas.

However, the absence of *Deunffia* and the presence of *Domasia* complex in the Wenlockian assemblages from Visby and Belgium suggest some connections with the Rochester assemblage; but the absence of *Deunffia*-*Domasia* complex in the Wenlockian assemblages from Spain and Sahara suggests fewer connections with the Rochester assemblage.

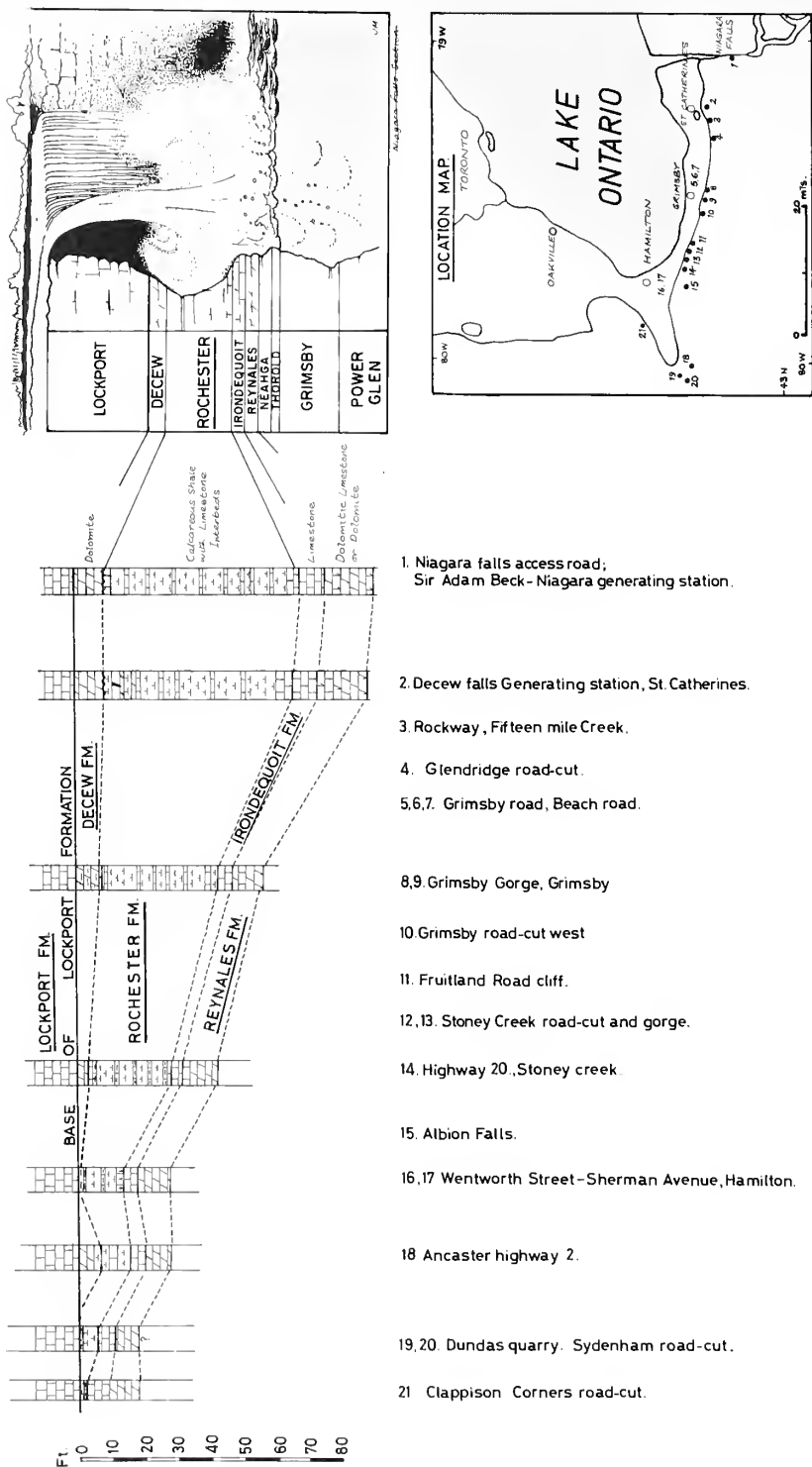
THIS paper contains results of acritarch studies on the Rochester Formation in southern Ontario (text-fig. 1). This region lies south-east of the Canadian shield and forms the marginal areas of the Michigan Basin and the Allegheny Trough.

The Rochester Formation is Tonawandian (Middle Silurian) in age and consists of calcareous shale with interbeds of argillaceous micrite or biomicrite. It is exposed at numerous localities along the Niagara Escarpment in New York and southern Ontario. It has a maximum thickness of 150 feet east of Walcott, New York. To the east the formation grades into the Herkimer Sandstone. To the west it thins successively to 60 feet near Niagara Gorge, 56 to 35 feet in the St. Catharines and Grimsby region, 14 feet at Hamilton, and 2-4 feet in the most northerly exposure at Clappison road cut, near Hamilton, Ontario (text-fig. 1). Well log data (Caley, 1940) indicate a general thinning of the formation from south-east to north-west Ontario without any lithological change.

South-easterly the Rochester Formation extends into Pennsylvania, Maryland, and West Virginia and varies from 20 to 40 feet in thickness, and maintains the same lithic character (Folk 1962).

Investigation by Thusu (1972) shows that the Rochester deposition in southern Ontario took place in a calm, subtidal, inner neritic, low-energy environment with good circulation, interrupted by occasional storms, which extended agitation into the subtidal zone.

However, conditions were not uniform within the Rochester sea and the several resulting environments undoubtedly influenced the distribution of fossils (Thusu 1972). For example, in southern Ontario and western New York bryozoans are present in large numbers, but to the east their number and diversity are greatly reduced. In Pennsylvania and West Virginia a normal marine fauna is absent. Folk (1962) postulates that parts of the Rochester Sea were protected by barrier-bars



TEXT-FIG. 1. Columnar sections of the Rochester and adjacent formations exposed along the Niagara Escarpment in southern Ontario.

which cut off wave action and resulted in lagoonal conditions in eastern West Virginia, while the presence of rich marine fauna in other parts of West Virginia and Pennsylvania suggest the temporary removal of barriers and hence open marine conditions.

PREVIOUS WORK ON PALAEOZOIC ACRITARCHS OF SOUTH-WESTERN ONTARIO AND WESTERN NEW YORK

White (1862, p. 385) reported a variety of acritarchs from Silurian nodules in central and western New York. He identified these as *Zanthidia*, the sporangia of desmids and gemmules of sponges. However, they were neglected and forgotten in North America for 73 years, until Laird (1935, p. 256) again discovered *Xanthidia* in the Lockport Formation (Middle Silurian) of Ontario. Baschnagel (1942, p. 1) reported acritarchs from the Onondaga Chert (Devonian) of central New York. He assigned them to genera and families of freshwater algae. Fisher (1953, p. 13) reported a number of acritarchs from thin-sections of the Neagha and Maplewood Shale in New York. He regarded them to be zygospores of brown algae and compared some of his forms with those reported by Deflandre (1946) from the Silurian of France.

The first major contribution was made by the French palynologist Deunff (1954a, 1955, 1957). He made the first taxonomic studies on some of the Devonian acritarchs of Canada. Recent studies by Staplin *et al.* (1965) and Loeblich (1970) are mainly of taxonomic importance. But Cramer (1968, 1970, 1970b) made the first attempt to use acritarchs in Lower Palaeozoic stratigraphy and correlation.

MATERIAL AND METHODS

Channel samples from the Rochester Formation used in the present investigation consist of dark grey to black fissile calcareous shale, in part dolomitic, and argillaceous grey limestone.

Localities are designated according to the Silurian section numbers (see Map I) given by Bolton (1957). Maximum thickness of the Rochester Formation is given at the end of each locality name.

- | | |
|--------------|---|
| Locality 1. | Niagara Falls, access road, Sir Adam Beck-Niagara generating station, 60 feet. |
| ROC.1 | Basal part of the section, Calcareous Shale, 20 feet. |
| ROC.2692 | Basal part of the section, Calcareous Shale on the American side of the Niagara generating station (sample provided by Geology Department, Sheffield University). |
| ROC.2 | Middle part of the section, Calcareous Shale, 20 feet. |
| ROC.2691 | Middle part of the section, Calcareous Shale, location same as ROC.2692. |
| ROC.7 | Upper part of the section, Calcareous Shale, 20 feet. |
| ROC.2690 | Upper part of the section, Calcareous Shale, location same as ROC.2692. |
| Locality 2. | DeCew Falls Generating station, St. Catherines, 56 feet (locality 1 of Bolton, 1957). |
| ROC.15 | Basal part of the section, Calcareous Shale thin limestone, 20 feet. |
| ROC.16 | Middle part of the section, thin bedded limestone and Calcareous Shale, 20 feet. |
| ROC.17 | Upper part, Calcareous Shale, massive limestone, 16 feet. |
| Locality 14. | Highway 20, Stoney Creek, 24 feet. |
| ROC.8 | Basal part limestone, Calcareous Shale, 12 feet. |
| ROC.9 | Upper part, Calcareous Shale with gypsum, 12 feet. |
| Locality 16. | Jolly Cut, Hamilton, 13 feet. |
| ROC.11 | Basal part, Calcareous Shale, 7 feet. |
| ROC.10 | Upper part, Calcareous Shale, 6 feet. |

- Locality 18. Ancaster, Highway 2, 9 feet.
 ROC.5 Basal part, Calcareous Shale, 4·5 feet.
 ROC.4 Upper part, Calcareous Shale, 4·5 feet.
- Locality 19, 20. Dundas Quarry, Sydenham road-cut, 5 feet.
 ROC.43007 Calcareous Shale 4 to 4·5 feet.
- Locality 21. Clappison Corners road-cut, 2·4 feet.
 ROC.6 Calcareous Shale, 2·4 feet.
 ROC.12 Calcareous Shale, 2 feet (250 feet east of sample ROC.6).

Apart from those from the Rochester Formation, additional samples studied and reported in the present study are as follows:

(i) Ilion Shale (Wenlockian) Utica, New York. Three samples collected from the type area are from south branch of Moyer Creek, Utica, New York. The reader is referred to Zenger (1965, p. 191, section 166) for stratigraphic details of this section. All shale samples yield an abundant microplankton flora characterized by an excellent state of preservation.

(ii) Höglint Shale (Wenlockian) Snäckgardsbaden, Visby, Sweden. One productive sample used is from a Korpklint Bay on the north side of Snäckgardsbaden, five kilometres along the coast north of Visby. The sample comes from behind a small marine swimming pool (material and stratigraphic information provided by Dr. D. Owen of the Manchester University Museum, England).

Standard chemical techniques were employed, similar to those described by Cramer (1970) for the extraction of organic-walled micro-fossils. Most of the specimens were examined at $\times 400$ magnification. All acritarch figures are housed in the micropalaeontological collection of the Geological Survey of Canada in Ottawa. Each specimen is recorded with east-west and north-south mechanical-stage readings of Vickers Photomicroscope M-15.

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SYSTEMATIC PALAEOLOGY

The following list of all acritarch species identified follows the morphographic classification of Downie *et al.* (1963). Most of the species are illustrated in the plates but only those asterisked are described below. All the new taxa are based on a minimum of 25 specimens. Table 1 shows the number of specimens counted in each sample. All slides are deposited with the Palaeontological Division of the Geological Survey of Canada.

Group ACRITARCHA Evitt 1963

Subgroup NETROMORPHITAE Downie, Evitt, and Sarjeant 1963

Deunffia furcata (pl. 104, fig. 20).

**D. furcata* var. *niagarensis* new var. (pl. 104, fig. 14).

D. monospinosa Downie 1960 (pl. 104, fig. 8).

- **D. monospinosa* var. *tonawandensis* new var. (pl. 104, figs. 4, 24).
- D. ramusculosa* Downie, 1960 (pl. 104, figs. 7, 15, 22).
- **D. ramusculosa* var. *rochesterensis* new var. (pl. 104, fig. 18).

Domasia amphora Martin 1969 (pl. 104, figs. 9, 19).

D. bispinosa Downie 1960 (pl. 104, fig. 11).

- **D. canadensis* sp. nov. (pl. 104, figs. 6, 12, 21).
- D. elongata* Downie 1960 (pl. 104, figs. 23, 25).
- **D. rochesterensis* sp. nov. (pl. 104, figs. 2, 5).
- D. trispinosa* Downie, 1960 (pl. 104, fig. 1).

- **Hemideunffia trifurcata* sp. nov. (pl. 104, figs. 10, 16).
- Leiofusa algerensis* Cramer 1970 (pl. 104, fig. 17).
- L. fusiformis* Eisenack 1938 (pl. 104, figs. 3, 13).
- Eupoikilofusa stratifera* Cramer 1964 (pl. 105, fig. 1).

Subgroup ACANTHOMORPHITAE Downie, Evitt, and Sarjeant 1963

Ammonidium cf. *A. microladum* (Downie) Lister 1970 (pl. 105, fig. 5).

Baltisphaeridium longispinosum (Eisenack) Downie 1963 (pl. 105, fig. 19).

- **B. pilaris* Cramer, 1964 (pl. 105, figs. 6, 18).
- **Diexallophasis denticulata* (Stockmans and Williere) Loeblich 1970 (pl. 105, fig. 3).
- Elektoiskos pogonius* Loeblich 1970 (pl. 105, fig. 10).
- **E. simplex* sp. nov. (pl. 105, fig. 9).
- **Filisphaeridium bifurcatum* sp. nov. (pl. 105, figs. 8, 12).
- **Gorgonisphaeridium wenlockium* sp. nov. (pl. 105, fig. 11).
- Helosphaeridium latispinosum* Lister 1970 (pl. 105, fig. 16).
- Micrystridium stellatum* Deflandre 1945 (pl. 105, fig. 7).
- Multiplicisphaeridium arbusculiferum* Downie 1963 (pl. 105, figs. 4, 15).
- M. eoplanktonicum* (Eisenack) Lister 1970 (pl. 105, figs. 2, 14).
- M. fisherii* (Cramer) Lister 1970 (pl. 105, fig. 17).
- Quadratum fantasticum* Cramer 1964 (pl. 105, fig. 13).
- Tunisphaeridium tentaculiferum* (Martin) Cramer 1970 (pl. 105, fig. 20).
- Visbysphaera dilatispinosa* (Downie) Lister 1970 (pl. 106, fig. 1).

Subgroup POLYGONOMORPHITAE Downie, Evitt, and Sarjeant 1963

- **Evittia monterrosa* (Cramer) new comb. (pl. 106, figs. 2, 7).
- E. remota* (Deunff) Lister 1970 (pl. 106, fig. 4).
- **Veryhachium lairdi* (Deflandre) ex-Deunff 1954 (pl. 106, figs. 5, 6).
- **V. limaciforme* Stockmans and Williere 1963 (pl. 106, figs. 8, 10).
- V. trispinosum* Eisenack 1931 (pl. 106, fig. 9).
- V. wenlockium* (Downie) Downie and Sarjeant 1964 (pl. 106, fig. 3).

Subgroup HERKOMORPHITAE Downie, Evitt, and Sarjeant 1963

Cymatiosphaera octoplana Downie 1959 (pl. 106, figs. 11, 14).

C. wenlockia Downie 1959 (pl. 106, fig. 19).

Dictyotidium dictyotum (Eisenack) 1955 (pl. 106, fig. 12).

Subgroup PTEROSPERMORPHITAE Downie, Evitt, and Sarjeant 1963

Pterospermopsis cf. *P. martinii* Cramer and Cramer 1968 (pl. 106, fig. 15).*P. onondagaensis* Deunff 1955 (pl. 106, figs. 16, 20).*Duvernaysphaera aranaides* (Cramer) 1970 (pl. 106, fig. 18).

Subgroup SPHAEOMORPHITAE Downie, Evitt, and Sarjeant 1963

Lophosphaeridium rugosum* sp. nov. (pl. 106, fig. 13).L. microgranulosum* sp. nov. (pl. 106, fig. 17).*Leiospheridia* spp.Spores *Punctatisporites* sp. rare.

TABLE 1. Numbers of specimens recorded in sample from localities 1, 14, 18, and 21 out of approximately 250 specimens counted in each sample.

	Loc. 1			Loc. 14		Loc. 18		Loc. 21
	ROC. 2692	ROC. 2691	ROC. 2690	ROC.8	ROC.9	ROC.5	ROC.4	ROC.6
<i>Deunffia furcata</i>	2	6	4	6	6	5
<i>D. furcata</i> var. <i>niagarensis</i>	1	2	3	4	3	..	2	..
<i>D. monospinosa</i>	5	5	5	8	..	6	2	..
<i>D. monospinosa</i> var. <i>tonawandensis</i>	1	2	3	4	1	4	6	..
<i>D. ramusculosa</i>	30	35	30	28	4	18	14	10
<i>D. ramusculosa</i> var. <i>rochesterensis</i>	11	3	9	12	4	4	10	2
<i>Domasia amphora</i>	10	7	3	2	..	2	14	..
<i>D. bispinosa</i>	6	4	2	6	5	6	4	..
<i>D. canadensis</i>	23	15	10	..	3	8	14	18
<i>D. elongata</i>	15	16	22	22	26	10	12	25
<i>D. rochesterensis</i>	12	7	5	6	..	4	4	..
<i>D. trispinosa</i>	21	18	16	16	17	12	8	12
<i>Hemideunffia trifurcata</i>	3	1	1	4	3
<i>Leiofusa algerensis</i>	9	5	3	2	..	4	6	5
<i>L. fusiformis</i>	6	6	4	2	7	4	4	2
<i>E. stratifera</i>	..	1	..	2	1
<i>Ammonidium</i> cf. <i>A. microcladum</i>	4	5	3	6	2	2	6	14
<i>Baltisphaeridium longispinosum</i>	15	7	6	4	8	6	6	16
<i>B. pilaris</i>	7	3	3	2	4	10	2	15
<i>Diexallophasis denticulata</i>	12	12	11	6	14	14	8	20
<i>Elektoriskos pogonius</i>	2	1	2	4	4	3
<i>E. simplex</i>	..	4	4	6	3	4	4	8
<i>Filisphaeridium bifurcatum</i>	1	2	..	2	2	6	4	..
<i>Gorgonisphaeridium wenlockium</i>	2	1	..	2	1	2
<i>Helosphaeridium latispinosum</i>	12	2	18	10	13	10	10	15
<i>Michrystroidium stellatum</i>	11	3	9	6	15	6	4	10
<i>Multiplicisphaeridium arbusculiferum</i>	4	5	4	2	3	8	4	8
<i>M. eoplanktonicum</i>	5	2	2	8	1	4	4	3
<i>M. fisherii</i>	6	3	4	2	??	6	2	6
<i>Quadratum fantasticum</i>	1	1
<i>Tunisphaeridium tentaculiferum</i>	1	2	..	4
<i>Visbysphaera dilatispinosa</i>	1	1

	Loc. 1			Loc. 14		Loc. 18		Loc. 21
	ROC. 2692	ROC. 2691	ROC. 2690	ROC.8	ROC.9	ROC.5	ROC.4	ROC.6
<i>Evittia monterrosa</i>	5	2	2	6	2
<i>Evittia remota</i>	2	2	2	4	2	5
<i>V. lairdi</i>	4	4	7	4	2	4	6	3
<i>V. limaciforme</i>	6	1	7	2	21	4	2	3
<i>V. trispinosum</i>	11	12	14	6	11	2	6	8
<i>V. wenlockium</i>	10	3	2	6	12	2	6	12
<i>Cymatiosphaera octoplana</i>	1	5	3	6	2	..	2	2
<i>C. Wenlockia</i>	3	3	1	4	..	4	2	..
<i>Dictyotidium dictyotum</i>	2	2	11	12	11	8	4	7
<i>Pterospermopsis</i> cf. <i>P. martinii</i>	2	..	1	2
<i>P. onodagaensis</i>	2	..	1	2	1	2
<i>Duvernaysphaera aranaides</i>	1	2	2	2
<i>Lophosphaeridium rugosum</i>	2	2	5	6	4	18	16	..
<i>L. microgranulosum</i>	2	1	..	2	1

Subgroup NETROMORPHITAE Downie, Evitt, and Sarjeant 1963

Diagnosis. Acritarchs having an elongate to fusiform test without an inner body. Surface smooth, granular, striate, spines or with large ornament. One or more spines closed distally may be present at one or both poles. Questionable openings observed in a few species.

Remarks. Well-known genera include: *Deunffia* Downie 1960; *Domasia* Downie 1960; *Leiofusa* Eisenack 1938; *Dactylofusa* Brito and Santos 1965 and *Poikilofusa* Staplin, Jansonius and Pocock 1965. These have a wide geographical distribution and are characteristic of the Silurian strata. Other genera include *Anthatractus* Deunff 1954; *Baiomeniscus* Loeblich 1970; *Disparifusa* Loeblich 1970; *Lunulidia* Eisenack 1958; *Pseudolunulidia* Brito and Santos 1965; *Leiovalia* Eisenack 1965; *Lunulidia*, *Leiovalia* and *Pseudolunulidia* are forms with close morphological relationship with *Leiofusa*. In fact the genotypes of *Lunulidia* and *Leiovalia* were originally described under *Leiofusa* (Eisenack 1938, 1951). These are relatively lesser known genera and range from the Upper Ordovician to the Lower Devonian.

Some of the netromorphs, e.g. *Domasia*, show a close morphological similarity with the polygonomorphs, for example *Veryhachium*. Downie (1963, p. 637) observed *V. elongatum* and found forms with intermediate morphology between *Veryhachium* of the *V. trispinosum*—*V. trisulcum* group, and *Domasia* of the *D. trispinosa*—*D. elongata* group. However, Downie (1963, 633–634) recognized close relationship of *Leiofusa*, *Deunffia*, and *Domasia*.

Deflandre and Deflandre (1964) removed *Deunffia* and *Domasia* from Netromorphitae, considering them simplified Polygonomorphitae.

However, Brito (1967) rejected the views of Deflandre and Deflandre and suggested a close relationship of *Deunffia*, *Domasia*, and *Leiofusa*.

The above-mentioned diagnosis is emended to include:

1. Ornament consisting of one or two hollow processes situated at opposite ends. The long process terminates in a point or branches in various ways, other process is short and terminates in a point and does not exceed more than a few microns.

2. The 100 μ length limit is removed to include larger forms.

Deunffia furcata var. *niagarensis* new var.

Plate 104, fig. 14

Holotype. GSC No. 31615, locality 14, sample ROC.9, Slide No. 9/C.

Remarks. *D. furcata* var. *niagarensis* differs from *D. furcata* by the presence of a small spine at the opposite end of the main shaft.

Dimensions. Size of the vesicle 18 μ (range, 16–18 μ); width of the vesicle 12 μ (range, 10–13 μ); length of the main shaft 16 μ (range, 14–16 μ); length of the small process 1 μ (range, 1–2 μ).

Deunffia monospinosa var. *tonowadensis* new var.

Plate 104, figs. 4, 24

Type specimens. *Holotype* GSC No. 31609, locality 21, sample ROC.12, Slide No. 12/a; *paratype* GSC No. 31609a, locality 18, sample ROC.4, Slide No. 4/A.

Remarks. This variety differs from *D. monospinosa* by the presence of a small spine at the opposite end of the main shaft, and from *L. alegerensis* by a much smaller spine.

Dimensions. Size of the vesicle 18 μ (range, 16–24 μ); width of the vesicle 9 μ (range, 7–11 μ); length of the main shaft 60 μ (range, 50–75 μ); length of the small process 8 μ (range, 6–8 μ).

Deunffia ramusculosa var. *rochesterensis* new var.

Plate 104, fig. 18

Holotype. GSC No. 31618, locality 1, sample ROC.1, Slide No. 1/B.

Remarks. This species differs from *D. ramusculosa* by the presence of a small process (3–4 μ) opposite to the end of the long shaft. Where the process is broken, a small hole or an opening is observed. However, where the vesicle is squashed or folded, *D. ramusculosa* may be confused with *D. ramusculosa* var. *rochesterensis*.

Genus DOMASIA Downie 1960

Type species. *Domasia trispinosa* Downie 1960. Middle Silurian, England.

Diagnosis. Vesicle hollow, elongate, ellipsoidal more or less smooth, about 20 μ in length. Body composed of pale yellow to brown organic membrane. Ornament consisting of two relatively long hollow spines arising near one pole and a single spine of variable length at the opposite end.

Remarks. The two processes arising near one pole may bifurcate at the tips, or a thin hairy process may arise from the middle of the spine. *D. elongata*, *D. trispinosa*, *D. bispinosa*, and *D. amphora* are morphologically very closely related species. However, the nature of the entrance of the processes into the vesicle seems to differentiate these species. *D. elongata* and *D. amphora* have processes merging before entering the vesicle, while *D. trispinosa* and *D. bispinosa* have processes entering the vesicle separately. The Rochester acritarchs show a wide variety of transitional forms between *D. elongata* and *D. amphora*: Downie (1963, p. 637) records a transition between *D. elongata* and *D. trispinosa*.

Domasia canadensis sp. nov.

Plate 104, figs. 6, 12, 21

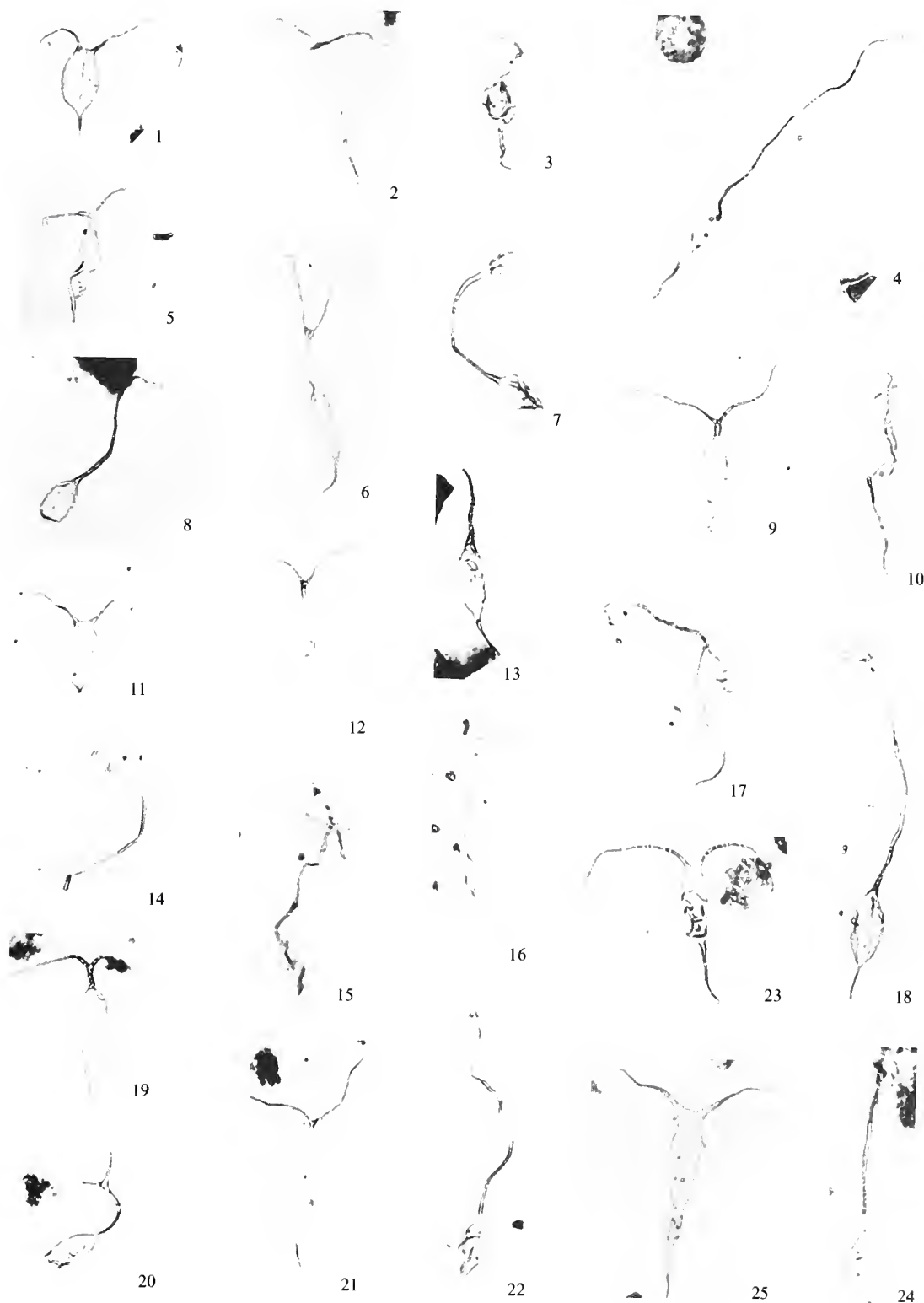
Type specimens. Holotype GSC No. 31610, locality 1, sample ROC.1, Slide No. 1/B; Paratypes GSC No. 31610a-b, locality 1, sample ROC.1, Slide No. 1/A, 1/E.

Description. Vesicle fusiform, pale, smooth or faintly granulose. One pole tapering at first into a stretched, unseptate neck, which is drawn out into two processes. Other pole tapers and terminates into one short process.

EXPLANATION OF PLATE 104

All figures $\times 500$ and from unretouched negatives.

- Fig. 1. *Domasia trispinosa* Downie 1960, GSC No. 31606, locality 14, sample ROC.8, slide number 8/E.
 Figs. 2, 5. *D. rochesterensis* sp. nov. 2, holotype GSC No. 31607, locality 1, sample ROC.1, slide number 1/C. 5, paratype GSC No. 31607a, locality 1, sample ROC.1, slide number 1/B.
 Figs. 3, 13. *Leiofusa fusiformis* Eisenack 1938, GSC Nos. 31608 a-b, 3, locality 1, sample ROC.1, slide number 1/A. 13, locality 21, sample ROC.12, slide number 12/A.
 Figs. 4, 24. *Deunffia monospinosa* var. *tonawandensis* new var. 4, holotype GSC No. 31609, locality 21, sample ROC.12, slide number 12/A. 24, paratype GSC No. 31609a, locality 18, sample ROC.4, slide number 4/A.
 Figs. 6, 12, 21. *D. canadensis* sp. nov. 6, holotype GSC No. 31610, locality 1, sample ROC.1, slide number 1/B. 12, 21, paratypes GSC No. 31610 a-b, locality 1, sample ROC.1, slide numbers 1/A, 1/E.
 Figs. 7, 15, 22. *Deunffia ramusculosa* Downie 1960, GSC Nos. 31611 a-c. 7, locality 21, sample ROC.12, slide number 12/A. 15, locality 14, sample ROC.8, slide number 8/A. 22, locality 1, sample ROC.1, slide number 1/A.
 Fig. 8. *D. monospinosa* Downie 1960, GSC No. 31612, locality 1, sample ROC.1, slide number 1/C.
 Figs. 9, 19. *Domasia amphora* Martin 1969, GSC No. 31613. 9, locality 18, sample ROC.5, slide number 5/A. 19, locality 1, sample number ROC.1, slide number 1/B.
 Figs. 10, 16. *Hemideunffia trifurcata* sp. nov. 10, holotype GSC No. 31614, locality 1, sample ROC.1, slide number 1/C. 16, paratype GSC No. 31614a, locality 1, sample number ROC.2691, slide number 2691/A.
 Fig. 11. *Domasia bispinosa* Downie 1960, holotype 31615, locality 14, sample ROC.8, slide number 8/E.
 Fig. 14. *Deunffia furcata* var. *niagarensis* new var., holotype GSC No. 31615, locality 14, sample ROC.9, slide number 9/C.
 Fig. 17. *Leiofusa algerensis* Cramer 1970, GSC No. 31617, locality 1, sample ROC.1, slide number 1/F.
 Fig. 18. *Deunffia ramusculosa* var. *rochesterensis* new var. Holotype GSC No. 31618, locality 1, sample ROC.1, slide number 1/C.
 Fig. 20. *D. furcata* Downie 1960, GSC No. 31619, locality 1, sample ROC.1, slide number 1/E.
 Figs. 23, 25. *D. elongata* Downie 1960, GSC No. 31620 a-b, locality 1, sample ROC.1, slide number 1/B.



THUSU, Silurian acritarchs

Remarks. *D. candensis* sp. nov. differs from *D. amphora* by the presence of a distinct unseptate and stretched neck. In *D. amphora*, the vesicle terminates into a small neck, but a sharp break is present between the neck and the vesicle.

Dimensions. Length of the vesicle $36\ \mu$ (range, $32\text{--}40\ \mu$); width of the vesicle $7\ \mu$ (range, $6\text{--}10\ \mu$); length of the long processes $41\ \mu$ (range, $39\text{--}45\ \mu$); length of the short process $13\ \mu$ (range, $9\text{--}15\ \mu$); length of the neck $3\text{--}4\ \mu$ (range, $3\text{--}7\ \mu$).

Domasia rochesterensis sp. nov.

Plate 104, figs. 2, 5

Type specimens. Holotype GSC No. 31607, locality 1, sample ROC.1, Slide No. 1/C, Paratype GSC No. 31607a, locality 1, sample ROC.1, Slide No. 1/8.

Description. Vesicle hollow, fusiform, pale yellow, smooth. Two long processes arise near one pole. Each process gives rise to a short secondary process at about the mid-length. A single short process present at the opposite end. Processes septate.

Remarks. The presence of a short secondary process arising from the long processes differentiates this species from *Domasia elongata*.

Dimensions. Size of the vesicle $24\text{--}34\ \mu$ (range, $20\text{--}38\ \mu$); width of the vesicle $8\text{--}10\ \mu$ (range, $7\text{--}12\ \mu$); length of the long processes $33\ \mu$ (range, $30\text{--}45\ \mu$); length of the secondary processes $5\text{--}7\ \mu$ (range, $4\text{--}7\ \mu$); length of the short process $15\text{--}17\ \mu$ (range, $12\text{--}20\ \mu$).

Genus *HEMIDEUNFFIA* gen. nov.

Type species. *Hemideunffia trifurcata* sp. nov.

Diagnosis. Vesicle highly elongate, tapering, pale yellow, thin, smooth walled; one pole simple; opposite pole terminates into three processes, processes may be closed or open at the distal end, septate processes may be present.

Remarks. This genus differs from *Leiofusa* by the presence of a trifurcate process at one pole, and from *Deunffia* by the presence of a long, tapering vesicle. Indeed, this genus is intermediate between *Leiofusa* and *Deunffia*.

Hemideunffia trifurcata sp. nov.

Plate 104, figs. 10, 16

Type specimens. Holotype GSC No. 31614, locality 1, sample ROC.1, Slide No. 1/C; Paratype GSC No. 31614a, locality 1, sample ROC.2691, Slide No. 2691/A.

Description. Vesicle highly elongate, fusiform, tapering, smooth thin walled, pale transparent, fragile often compressed, twisted or folded; one pole simple; opposite pole terminates into a trifurcate process, processes generally closed at the tips, non-septate.

Dimensions. Length of the vesicle $70\ \mu$ (range, $65\text{--}85\ \mu$); width of the vesicle $4\text{--}8\ \mu$ (range, $4\text{--}10\ \mu$); length of the processes $9\ \mu$ (range, $6\text{--}10\ \mu$).

Genus *BALTISPHAERIDIUM* (Eisenack 1958), emend, Downie and Sarjeant 1963,
emend.

Type species. Ovum hispidum longispinosum Eisenack 1931, Baltic, Ordovician.

Remarks. In this work *Baltisphaeridium* is accepted in a broad sense as amended by Downie and Sarjeant (1963) but is restricted to include forms with predominantly homomorphic, unbranched processes, closed or open to the vesicle cavity. Forms with hetromorphic nature of the process termination, and free communication of the process with vesicle, are transferred to *Multiplicisphaeridium*. Processes with equifurcate termination at the tips is transferred to *Ammonidium*. Forms in which processes communicate freely with the vesicle and without any tendency for the processes to close off at its junction with the central body are transferred to *Diexallophasis*. Forms in which the central body is ornamented by numerous prominent pila, rather being smooth or with minor ornamentation are considered to belong to *Pilifero-sphaera*, and forms in which processes are very short and terminate in a point or in short bifurcations with a feather or rosette of small spines, just below their distal end are considered to belong to *Tylotopalla*.

Baltisphaeridium pilaris Cramer 1964

Plate 104, figs. 6, 18

1970 *Baltisphaeridium pilaris* var. *typicum* Cramer, p. 166, pl. 18, figs. 55d-h (gives detailed synonymy).

1970 *Cymbosphaeridium pilar* (Cramer) Lister, p. 63, figs. 256-266.

Remarks. The branching of *B. pilaris* is very complex and considerable variation exists within a species. However, in *B. pilaris* var. *typicum*, the cauliflorate terminations of the processes is seen in most of the specimens studied. *B. pilaris* was transferred by Lister (1970, p. 64) to a new genus *Cymbosphaeridium*. This genus is primarily based on the 'reflected plate formula' proposed by Lister (1970, p. 63-65). This writer does not believe in creating new form-genera on hypothetical characteristics, drawn from the reconstruction of hypothetical thecae of acritarchs. Indeed, such study is important to understand the phylogenetic relationship of acritarchs, but not for creating new genera in a morphographic system of classification.

Diexallophasis denticulata (Stockmans and Williere) Loeblich 1970

Plate 105, fig. 3

1963 *Diexallophasia denticulata* (Stockmans and Williere) Loeblich, p. 715, figs. 8 A-E, 9 A-C.

1963 *Baltisphaeridium denticulatum* Stockmans and Williere, p. 458, pl. 1, fig. 4.

1970 *Baltisphaeridium denticulatum* Cramer, pp. 136-138.

1965 *Baltisphaeridium denticulatum* Martin, p. 5, pl. 1, figs. 5, 6, text-figs. 5, 6.

1966 *Baltisphaeridium denticulatum* Martin, p. 309.

1968 *Baltisphaeridium denticulatum* Jardine and Yapoudjian, pl. 3, fig. 26.

1963 *Baltisphaeridium granulatispinosum* Downie, p. 640, pl. 9, figs. 1, 7.

1966 *Baltisphaeridium granulatispinosum* Martin, p. 310, pl. 1, fig. 24.

1968 *Baltisphaeridium granulatispinosum* Martin, p. 48, pl. 3, fig. 127, pl. 4, fig. 186, pl. 7, fig. 310, pl. 8, figs. 360, 362.

1970 *Evittia granulatispinosa* Lister, p. 67, pl. 4, figs. 2, 3, 5-9, 12, pl. 5, fig. 2: text-figs. 170, 20b.

Remarks. Cramer (1970, pp. 138–140) describes five varieties of *D. denticulata* (*B. denticulatum*). However, Lister (1970, p. 68) and the present writer recognize extreme variability in this group. The character of spines and ornament is continuously variable, thus encouraging the use of this species in a broad sense.

Diexallophasis granulatispinosum (= *Baltisphaeridium granulatispinosum*) is regarded as a junior synonym of *D. denticulata* (= *Baltisphaeridium denticulatum*). However, Lister (1970, p. 68) recognized *Evittia granulatispinosa* (*B. granulatispinosum*) as a valid taxon, and states 'in view of the fact that the process tips of the holotype of *denticulatum* are missing and the character of the process tips is essential to the diagnosis of any species of *Evittia*, the specific name *denticulatum* is considered to be *nomen dubium*'. But the present author rejects the transfer of *denticulatum* to genus *Evittia* for the reasons stated on p. 815, and recognizes the transfer of *denticulatum* in *Diexallophasis*. The diagnosis of *Diexallophasis* broadly defines the character of tips, and hence would not warrant the rejection of the holotype of *denticulatum* because of the missing tips.

Genus ELEKTORISKOS Loeblich 1970

Type species. *Elektoriskos auroa* Loeblich 1970, Middle Silurian Maplewood Shale, New York.

Diagnosis. Circular to subcircular central body, wall apparently single layered,

EXPLANATION OF PLATE 105

All figures $\times 500$ and from unretouched negatives.

Fig. 1. *Eupoikilofusa stratifera* Cramer 1964, GSC No. 31621, locality 14, sample ROC.8, slide number 8/B.

Figs. 2, 14. *Multiplicisphaeridium eoplanktonicum* Downie 1963, GSC Nos. 31622 a–b. 2, locality 1, sample ROC.1, slide number 1/A. 14, locality 18, sample ROC.5, slide number 5/A.

Fig. 3. *Diexallophasis denticulata* (Stockmans and Williere) Loeblich 1970. GSC No. 31623, locality 1, sample ROC.1, slide number 1/A.

Figs. 4, 15. *M. arbusculiferum* Downie 1963, GSC Nos. 31624 a–b. 4, locality 16, sample ROC.11, slide number 11/B. 15, locality 14, sample ROC.8, slide number 8/A.

Fig. 5. *Ammonidium* cf. *A. microcladum* (Downie) Lister 1970, GSC No. 31626.

Figs. 6, 18. *Baltisphaeridium pilaris* Cramer 1964, GSC Nos. 31626. 6, locality 1, sample ROC.2690, slide number 2690/A. 18, locality 21, sample ROC.12, slide number 12/A.

Fig. 7. *Michrhystridium stellatum* Deflandre 1945, GSC No. 31627, locality 14, sample ROC.8, slide number 8/B.

Figs. 8, 12. *Filisphaeridium bifurcatum* sp. nov. 8, holotype GSC No. 31628, locality 1, sample ROC.1, slide number 1/C. 12, paratype GSC No. 31628a, locality 14, sample ROC.8, slide number 8/A.

Fig. 9. *Elektoriskos simplex* sp. nov., holotype GSC No. 31629, locality 18, sample ROC.5, slide number 5/A.

Fig. 10. *E. pogonius* Loeblich 1970, GSC No. 31630, locality 1, sample ROC.1, slide number 1/A.

Fig. 11. *Gorgonisphaeridium wenlockium* sp. nov., holotype GSC No. 31631, locality 14, sample ROC.8, slide number 8/A.

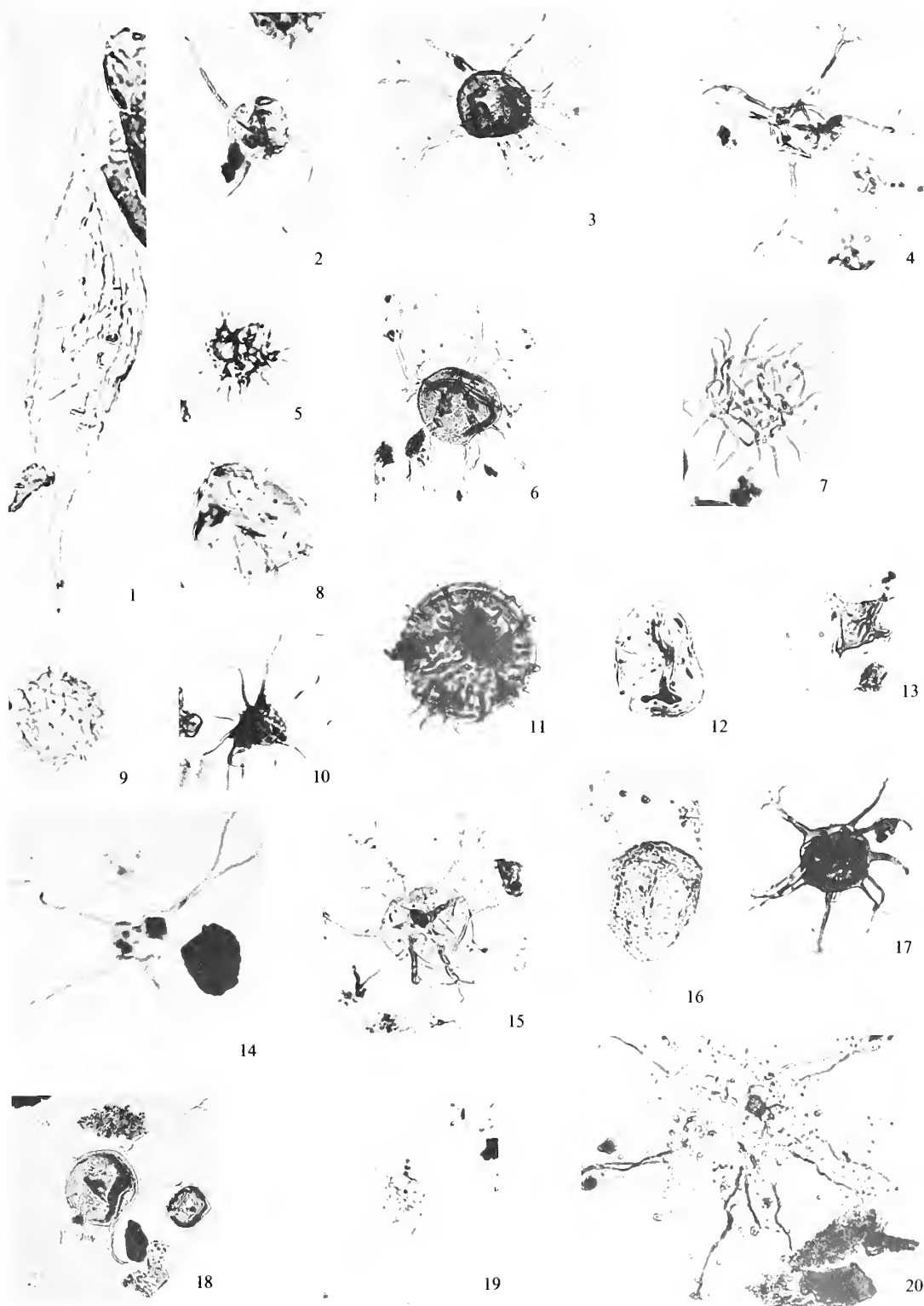
Fig. 13. *Quadradridium fantasticum* Cramer 1964, GSC No. 31632, locality 1, sample ROC.2691, slide number 2691/A.

Fig. 16. *Helosphaeridium latispinosum* Lister 1970, GSC No. 31633, locality 21, sample ROC.12, slide number 12/A.

Fig. 17. *M. fisherii* (Cramer) Lister 1970, GSC No. 31634, locality 14, sample ROC.8, slide number 8/A.

Fig. 19. *B. longispinosum* Downie 1963, GSC No. 31635, locality 1, sample ROC.1, slide number 1/A.

Fig. 20. *Tunisphaeridium tentaculiferum* (Martin) Cramer 1970, GSC No. 31636, locality 6, sample ROC.12, slide number 12/A.



THUSU, Silurian acritarchs

psilate, chagrenate to granulate with numerous slender, flexible but solid processes which do not communicate with the interior of the central body.

Remarks. This genus differs from *Comasphaeridium* in lacking the densely crowded hair-like processes and from *Filisphaeridium* in lacking the distal differentiation of the processes.

Elektoriskos simplex sp. nov.

Plate 105, fig. 9

1970 *Elektoriskos* sp. Loeblich, p. 719, fig. 13C.

Holotype. GSC No. 31629, locality 18, sample ROC.5, Slide No. 5/A.

Description. Vesicle rounded to spherical, thin, smooth, numerous (30–40) short, solid processes, without communicating with vesicle.

Remarks. *E. simplex* sp. nov. differs from *E. sequestratus* Loeblich by the absence of small grana on the vesicle.

Genus FILISPHAERIDIUM Staplin, Jansonius and Pocock 1965

Type species. *Michrhystridium setasessitante* Jansonius 1962, Lower Triassic, Alberta, Canada.

Filisphaeridium bifurcatum sp. nov.

Plate 105, figs. 8, 12

Type specimens. Holotype GSC No. 31628, locality 1, sample ROC.1, Slide No. 1/C; Paratype GSC No. 31628a, locality 14, sample ROC.8, Slide No. 8/A.

Description. Vesicle ellipsoidal to subspherical, smooth, processes 30 or more short tapering about 10% of the vesicle, bifurcating at the tips, process communicate freely with the vesicle.

Remarks. *F. bifurcatum* sp. nov. differs from *F. brevispinosum* Lister by the presence of bifurcating tips.

Dimensions. Size of the vesicle 27–36 μ (range, 25–38 μ); length of the process 3–5 μ (range, 3–5 μ).

Genus GORGONISPHAERIDIUM Staplin, Jansonius and Pocock 1965

Type species. *Gorgonisphaeridium winslowii* Staplin, Jansonius and Pocock 1965, Lower Carboniferous, Southern Alberta, Canada.

Gorgonisphaeridium wenlockium sp. nov.

Plate 105, fig. 11

Holotype. GSC No. 31632, locality 14, sample ROC.8, Slide No. 8/A.

Description. Vesical spherical, wall firm and thick, brownish, numerous short spines (30–40) with bulbous base and pointed tip, processes communicate freely with vesicle.

Remarks. This species differs from *G. spicatum* (Staplin) by its larger size, and pointed tips.

Dimensions. Size of the vesicle 80 μ (range, 70–82 μ); length of the spines 6–16 μ (range, 5–18 μ); width of the spines at the base 5–6 μ (range, 5–6 μ); distance between the spines 9–13 μ (range, 9–13 μ).

Genus EVITTIA Brito 1967

Type species. *Evittia sommeri* Brito 1967. Lower Devonian, Brazil.

Restricted diagnosis. Vesicle triangular to polygonal like *Veryhachium* but with the processes typically ramified, vesicle wall and processes sculptured.

Remarks. Cramer (1970, p. 47) considered *Evittia* a partial junior synonym of *Baltisphaeridium* on the grounds that the basal portion of the processes and their number strongly influence the shape of the vesicle. This is possible if *Evittia* possessed many processes. But Brito's generic diagnosis mentions '... having a general structure of *Veryhachium* ...' which in addition to a triangular or polygonal vesicle shape also puts a limit on the number of the processes. In fact the Subgroup Polygonomorphitae to which *Evittia* belongs is characterized by a low-number of processes.

Lister (1970, p. 66) emended *Evittia*, and broadened the genus to include subspherical acanthomorph species of *Baltisphaeridium* thus greatly departing from Brito's original intentions. It should be noted that *Evittia* like *Veryhachium* is defined on subgroup basis by a combination of shell shape and low spine number. Thus introducing within this genus subspherical species regardless of spine number is rejected as contrary to the original intention of Brito.

Evittia monterrosa (Cramer) nov. comb.

Plate 106, figs. 2, 7

1969 *Baltisphaeridium monterrosae* Cramer, p. 490, pl. 1, figs. 5–7.

1970 *Baltisphaeridium monterrosae* Cramer, p. 129, pl. 8, figs. 127–135.

Remarks. The basis for the transfer of this species to *Evittia* is the presence of a polygonal vesicle with a small number of processes (2–5), bifurcating or trifurcating at the distal end.

Genus VERYHACHIUM Deunff 1954, emend. Downie and Sarjeant 1963

Veryhachium lairdi (Deflandre) Deunff 1954

Plate 106, figs. 5, 6

1946 *Hystriosphæridium lairdi* Deflandre, card 1112.

1954 *Veryhachium lairdi* Deunff, p. 306.

1963 *Veryhachium lairdi* Stockmans and Williere, p. 454, pl. 4, fig. 5.

1964 *Veryhachium lairdi* Cramer, p. 309, pl. 11, fig. 16.

1965 *Veryhachium lairdi* Martin, pp. 13–14, figs. 14–15.

1969 *Veryhachium lairdi* Martin, p. 95, pl. 2, figs. 75–83.

1970 *Veryhachium lairdi* Loeblich, p. 741.

Remarks. *V. lairdi* has a maximum of five processes. However a single specimen shown on Plate 106, figs. 5–6 contains six processes and is provisionally placed with the specimens of *V. lairdi*.

Veryhachium limaciforme Stockmans and Williere 1963

Plate 106, figs. 8, 10

- 1963 *Veryhachium limaciforme* Stockmans and Williere, p. 433, pl. 1, figs. 12, 14, 15, 19.
- 1965 *Veryhachium limaciforme* Martin, p. 22, fig. 21.
- 1969 *Veryhachium limaciforme* Martin, p. 96, pls. 7, 8, figs. 354, 402.
- 1963 *Veryhachium elongatum* Downie, p. 637, pl. 92, fig. 10.
- 1963 *Veryhachium delmeri* Stockmans and Williere, p. 453, pl. 1, fig. 17.
- 1965 *Veryhachium delmeri* Martin, p. 22, fig. 22.
- 1966 *Veryhachium delmeri* Martin, p. 316.
- 1969 *Veryhachium delmeri* Martin, p. 90, pls. 4, 6, figs. 176, 346–347.
- 1970 *Domasia limaciforme* (Stockmans and Williere) Cramer, p. 68, pl. 1, figs. 16, 27, 28.

Remarks. This species is retained in the genus *Veryhachium* on three counts: 1. A highly elongate, triangular vesicle. 2. The attachment of the processes to the corners of the vesicle. 3. Absence or very rare septate processes, unlike the species of *Domasia*.

EXPLANATION OF PLATE 106

All figures $\times 500$ and from unretouched negatives.

- Fig. 1. *Visbysphaera dilatispinosa* (Downie) Lister 1970, holotype GSC No. 31637, locality 14, sample ROC.8, slide number 8/A.
- Figs. 2, 7. *Evittia monterrosa* (Cramer) new comb. GSC Nos. 31638 a–b. 2, locality 1, sample ROC.1, slide number 1/A. 7, locality 14, sample ROC.8, slide number 8/A.
- Fig. 3. *Veryhachium wenlockium* (Downie) Downie and Sarjeant 1964, GSC No. 31639, locality 1, sample ROC.1, slide number 1/B.
- Fig. 4. *E. romota* (Deunff) Lister 1970, GSC No. 31640, locality 18, sample ROC.5, slide number 5/A.
- Figs. 5, 6. *V. lairdi* (Deflandare) ex-Deunff 1954, GSC Nos. 31641 a–b. 5, locality 14, sample ROC.9, slide number 9/A. 6, locality 1, sample ROC.1, slide number 1/A.
- Figs. 8, 10. *V. limaciforme* Stockmans and Williers 1963, GSC Nos. 31642 a–b. 8, locality 14, sample ROC.8, slide number 8/E. 10, slide number 8/A.
- Fig. 9. *V. trispinosum* Eisenack 1931, GSC No. 31643, locality 1, sample ROC.1, slide number 1/A.
- Figs. 11, 14. *Cymatiosphaera octoplana* Downie 1959, GSC Nos. 31644 a–b. 11, locality 14, sample ROC.8, slide number 8/B. 14, slide number 8/A.
- Fig. 12. *Dictyotidium dictyotum* (Eisenack) 1955, GSC No. 31645, locality 1, sample ROC.1, slide number 1/G.
- Fig. 13. *Lophosphaeridium rugosum* sp. nov., holotype GSC No. 31646, locality 18, sample ROC.5, slide number 5/A.
- Fig. 15. *Pterospermopsis* cf. *P. martinii* Cramer & Cramer 1968, GSC No. 31647, locality 1, sample ROC.1, slide number 1/C.
- Figs. 16, 20. *P. onondagaensis* Deunff 1955, GSC Nos. 31648 a–b. 16, locality 8, sample ROC.8, slide number 8/A. 20, locality 1, sample ROC.1, slide number 1/A.
- Fig. 17. *L. microgranulosum* sp. nov., holotype GSC No. 31649, locality 14, sample ROC.8, slide number 8/A.
- Fig. 18. *Duvernaysphaera aranaides* (Cramer) 1970, GSC No. 31650, locality 1, sample ROC.1, slide number 1/C.
- Fig. 19. *C. wenlockia* Downie 1969, GSC No. 31651, locality 1, sample ROC.1, slide number 1/E.



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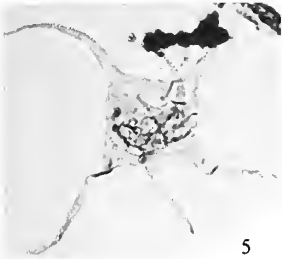
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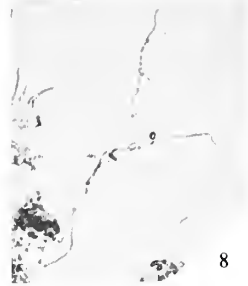
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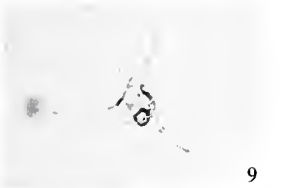
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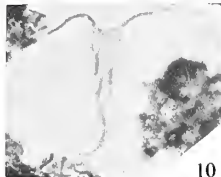
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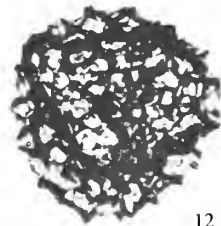
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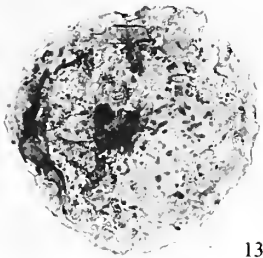
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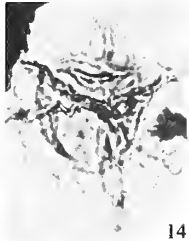
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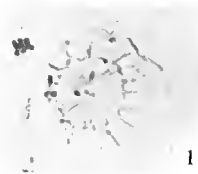
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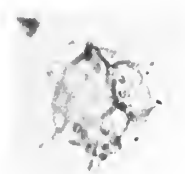
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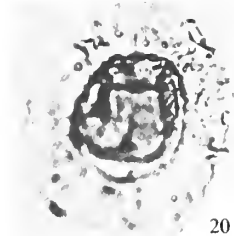
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19



20

Genus *LOPHOSPHAERIDIUM* Timofeyev 1959

Type species. Lophosphaeridium rarum Timofeyev, designated by Downie (1963), Ordovician, Russia.

Lophosphaeridium rugosum sp. nov.

Plate 106, fig. 13

Holotype. GSC No. 31646, locality 18, sample ROC.5, Slide No. 1/G.

Description. Vesicle rounded, orange yellow, thick walled, verrucose ornament, often in crescentric pattern.

Remarks. This species could be an alete spore.

Dimension. 120–130 μ .

Lophosphaeridium microgranulosum sp. nov.

Plate 106, fig. 17

Holotype. GSC No. 31649, locality 14, Sample ROC.8, Slide No. 8/A.

Description. Vesicle rounded, orange yellow, wall thick, finely granulose, granules closely packed, giving the appearance of a finely meshed network.

Dimensions. 160 μ .

DISCUSSION OF THE MICROFLORA

Age of the Rochester Microflora. The presence of highly evolved netromorphs of the *Deunffia* complex (*Deunffia ramusculosa*, *D. furcata*) in the Rochester Formation allows correlation with the Buildwas Beds in Shropshire (Downie 1963). On this basis the Rochester microflora is assigned a Lower Wenlockian age.

Intracontinental comparisons

Power Glen Formation (Lower Llandovery), Niagara Gorge, southern Ontario and New York State. The Rochester acritarchs reported from the Power Glen Formation (Cramer and Cramer 1970) belong to the *Diexallophasis denticulata* and *Veryhachium trispinosum* complex (Table 2). These are forms ranging from the Upper Llandovery to the Emsian.

Neagha and Maplewood Shales (Upper Llandovery) of New York State. The Rochester acritarchs present in these shales (Table 2) are dominantly long-ranging species (Llandovery/Ludlow) also. However, *Baltisphaeridium neagha*, *Dactylofusa neagha*, *Neoverhachium carminae*, and *Carminella maplewoodensis* reported by Cramer and Cramer (1970, p. 713) and *Elektoriskos aurora*, *Holothuriadeigma heterakanium*, and *Multiplicisphaeridium mergaeferum* reported by Loeblich (1970) in the Neagha Shale were not found in the Rochester Formation.

Loeblich (1970) reported a number of species from the Maplewood Shale, in particular *Baimeniscus granulatus*, *Diexallophasis caperoradiola*, *Estiastra stellata*, and species of *Elektoriskos* and *Leiofusa*. Furthermore, both Cramer and Cramer (1970) and Loeblich (1970) record the presence of *Neoverhachium carminae* and *Carminella*

TABLE 2. Selected acritarch species in the Rochester Formation and their reported occurrence in the Middle Silurian strata in North America.

Age Location	Lower Llandovery			Upper Llandovery			Llandovery Wenlock		Wenlock	
	1	2	3	4	5	6	7	8	9	10
<i>Deunffia furcata</i>									X	X
<i>D. monospinosa</i>								*?		
<i>D. ramusculosa</i>									X	X
<i>D. ramusculosa</i> var. <i>rochesterensis</i>										
<i>Domasia amphora</i>				X	?	?				
<i>D. bispinosa</i>				X					X	
<i>D. canadensis</i>										
<i>D. canadensis</i> var. <i>A.</i>										
<i>D. elongata</i>				X			X	X	X	X
<i>D. rochesterensis</i>										X
<i>D. trispinosa</i>							X		X	
<i>Leiofusa algerensis</i>				X						
<i>Eupokilofusa striatifera</i>		X	X	X			X	X	X	X
<i>Ammonidium microcladum</i>					X		X	X		
<i>Baltisphaeridium pilaris</i>				X						X
<i>Diexallophasis denticulata</i>	X	X	X	X			X	X	X	X
<i>Elektroiskos pogonius</i>		X	X	X			X	X	X	X
<i>Helosphaerisphaeridium latispinosum</i>									?X	X
<i>Multiplicisphaeridium arbusculiferum</i>			X							X
<i>M. eoplanktonicum</i>			X							
<i>M. fisherii</i>		X	X	X			X	X		X
<i>Quadraditum fantasticum</i>								X		
<i>Tunisphaeridium tentaculiferum</i>		X	X				X	X	X	
<i>Visbysphaera dilatispinosa</i>										X
<i>Evittia monterrosa</i>			X				X	X		
<i>Cymatiosphaera wenlockia</i>			X	X			X	X	X	
<i>Dictyotidium dictyotum</i>			X							X
<i>Duvernaysphaera aranaides</i>				X			X	X		

*? *D. monocantha*.

Legends for locations:

1. Power Glen Fm., S. Ontario (Cramer & Cramer 1970).
2. Maplewood Shale, New York (Cramer 1968, 1970b).
3. Neagha Shale, New York, S. Ontario (Cramer 1970, Loeblich 1970).
4. Ross Brook Fm., Nova Scotia (Cramer 1970b, Loeblich 1970).
5. Gun River Fm., Anticosti Is. (Cramer 1970).
6. Jupiter Fm., Anticosti Is. (Cramer 1970).
7. Rose Hill Fm., Pennsylvania (Cramer 1969).
8. Tuscarora Fm., Pennsylvania (Cramer 1969).
9. Rochester Fm., Maryland–W. Virginia. Reaugh (pers. comm.).
10. Ilion Shale, New York. This work.

maplewoodensis. These species were not found in the Rochester Formation with the exception of *Elektoriskos pogonius*.

Deunffia furcata, *D. ramusculosa*, *D. ramusculosa* var. *rochesterensis* and *Domasia* spp. are present in the Rochester assemblage and their absence in the Maplewood and Neagha assemblages is the most distinguishing feature.

According to Cramer and Cramer (1970, p. 1080) these differences in the acritarch assemblage are due to the existence of two distinct acritarch biofacies. In other words, Maplewood and Neagha assemblage at one end and the Rochester assemblage at the other, contain two distinct 'biofacies', the *Neoveryhachium carminae* facies and *Deunffia furcata* and *Domasia* facies. Furthermore, Cramer and Cramer do not

believe that this difference between the biofacies was caused by the difference in age. However, although in NW. Spain the *N. carminae* biofacies ranges from Llandovery to Ludlow (Cramer 1970), in eastern North America the *N. carminae* facies is restricted to the *Zygobolba excavata* ostracode Zone, of Late Llandovery age; while the *Deunffia furcata* and *Domasia* facies appear in the *Paraechmina spinosa* ostracode Zone of Basal Wenlock age.

Upper Member of Ross Brook Formation of Nova Scotia. Many Rochester Formation acritarchs occur in the Ross Brook assemblage. The stratigraphically restricted (Upper Llandovery to Wenlock) but geographically well-distributed netromorphs *Domasia amphora*, *D. bispinosa*, *D. elongata*, *Leiofusa algerensis*, *Duvernaysphaera aranaides* are common to both formations (Table 2). However, *Deunffia* spp. present in the Rochester assemblage are absent in the Ross Brook assemblage (Cramer 1970b, p. 747), indicating the younger age of the Rochester assemblage. Cramer (1970b) regards this difference as a function of palaeolatitudes.

Gun River and Jupiter Formations (Upper Llandovery), Anticosti Island, Quebec. There is little in common between the acritarchs of the Rochester Formation and the Gun River and Jupiter Formations (Table 2). However, a number of species abundant in the Gun River and Jupiter assemblages (Cramer 1970b, p. 749) are present in the Wenlock strata of England and Visby, Baltic (see Downie 1963, pp. 646–647).

The Ilion Shale (Wenlock), Utica, New York. The Rochester acritarchs are similar to the Ilion acritarchs (Table 2). The stratigraphically restricted taxa like *Deunffia ramusculosa*, *D. furcata*, *Domasia elongata*, *D. rochesterensis* are common to both the formations, although quantitative differences occur. For example, *Deunffia* and *Domasia* spp. are abundant in the Rochester Formation but rare in the Ilion Shale.

The Rose Hill and Tuscarora Formations (Upper Llandovery), Pennsylvania. In Pennsylvania, the Rose Hill and Tuscarora formations underlie the Rochester Formation. Many long-ranging taxa in the Rochester assemblage in southern Ontario are well represented in Rose Hill and Tuscarora assemblages in Pennsylvania (Cramer 1969, p. 486) (Table 2). However, the presence of *Domasia* and the absence of *Deunffia* spp. in the Rose Hill and Tuscarora assemblages supports the present writer's contention that *Deunffia ramusculosa* appears first in the Rochester assemblage (Lower Wenlock) in the Appalachian region.

The Rochester Formation in West Virginia. The Rochester acritarch assemblage in southern Ontario has many netromorph species in common with the Rochester assemblage in West Virginia (Reaugh, personal communication; Table 2). *Domasia elongata*, *D. bispinosa* and *D. trispinosa* are especially common in the two areas. However, only a few *Deunffia ramusculosa* occur in the Rochester assemblage in West Virginia. This is attributed to its lagoonal conditions (Reaugh, personal communication).

Intercontinental comparison

The Buildwas Beds (Basal Wenlock) in Shropshire, England. The Rochester netromorphs show their greatest similarity with the Downie's assemblage type 1, which is restricted in the Buildwas Beds (Downie 1963, pp. 646–648). *Deunffia* and *Domasia* are locally abundant in both the Rochester and the Buildwas assemblage (Table 3).

TABLE 3. Selected acritarch species in the Rochester Formation and their reported occurrence in the Middle Silurian strata (Wenlock) in Britain, Europe and North Africa.

Locality, age and total number of species		Buildwas Beds (Wenlock) England Downie (1963) (48 sp.)	Hogkint Group (Wenlock) Baltic This work (23 sp.)	Belgium (Wenlock) Martin (1969) (43 sp.)	San Pedro & Furada Fms. Lland./Gedinnian N.W. Spain Cramer 1963, 66, 70 (78 sp.)	Algeria, Sahara (Wenlock) Jardine & Yapaudjian (1968) (13 sp.)
Selected acritarch taxa in the Rochester Formation						
<u>Deunffia furcata</u>		X				
<u>D. ramusculosa</u>		X				
<u>Domasia amphora</u>		?	X	X		
<u>D. bispinosa</u>		X	X	X		
<u>D. elongata</u>		X	X	X		
<u>D. trispinosa</u>		X	X	X		
<u>Eupoikilofusa stratifera</u>			X		X	
<u>Ammonidium microcladum</u>		X				
<u>Baltisphaeridium pilaris</u>			X		X	
<u>Diexallophasis denticulata</u>		X	X	X	X	X
<u>Elektoriskos pogonius</u>			X			
<u>Helosphaeridium latispinosum</u>			?			
<u>Multiplicisphaeridium arbusculiferum</u>		X	X			
<u>M. eoplanktonicum</u>		X	X			
<u>M. fisherii</u>			X			?
<u>Quadraditum fantasticum</u>				X	X	
<u>Tunisphaeridium tentaculiferum</u>			X	X		
<u>Visbysphaera dilatispinosa</u>		X		X	X	
<u>Cymatiosphaera wenlockia</u>		X	?	X		
<u>Dictyotidium dictyotum</u>			X			
<u>Duvernaysphaera aranaides</u>			X		X	X

TABLE 3. Selected acritarch species in the Rochester Formation and their reported occurrence in the Middle Silurian strata (Wenlock) in Britain, Europe and North Africa.

Selected acritarch taxa in the Rochester Formation	Locality, age and total number of species	Buildwas Beds (Wenlock) England Downie (1963) (48 sp.)	Hogkint Group (Wenlock) Baltic This work (23 sp.)	Belgium (Wenlock) Martin (1969) (43 sp.)	San Pedro & Furada Fms. Lland./Gedinnian N.W. Spain Cramer 1963, 66, 70 (78 sp.)	Algeria, Sahara (Wenlock) Jardine & Yapaudjao (1968) (13 sp.)
<u>Deunffia furcata</u>		X				
<u>D. ramusculosa</u>		X				
<u>Domesia asphora</u>		?	X	X		
<u>D. bispinosa</u>		X	X	X		
<u>D. elongata</u>		X	X	X		
<u>D. crispinosa</u>		X	X	X		
<u>Eupoikilofusa stratifera</u>			X		X	
<u>Ammonidium microcladum</u>		X				
<u>Baltisphaeridium pilaris</u>			X		X	
<u>Diexallophasis denticulata</u>		X	X	X	X	X
<u>Elektoriskos pogonius</u>			X			
<u>Melosphaeridium latispinosum</u>			?			
<u>Multiplicisphaeridium arbusculiferum</u>		X	X			
<u>M. eoplanktonicum</u>		X	X			
<u>M. fisherii</u>			X			?
<u>Quadraditum fantasticum</u>				X	X	
<u>Tunisphaeridium tentaculiferum</u>			X	X		
<u>Viebsysphaera dilatispinosa</u>		X		X	X	
<u>Cymatiosphaera wenlockia</u>		X	?	X		
<u>Dictyoptyidium dictyotum</u>			X			
<u>Ouvernaysphaera araneoides</u>			X		X	X

However, the Buildwas acanthomorphs, in particular the *Visbysphaera meson* complex (*V. oliogofurcatum*, *V. meson*, *V. brevifurcata*), were not recorded in the Rochester assemblage. These taxa plus *V. dilatispinosa* (present in both areas) are now known to range from Upper Llandovery to Upper Ludlow (Lister, 1970, pp. 98–100) and their absence or scarcity in the Rochester Assemblage may be attributed to local environmental conditions.

The Höglint Group (Wenlock), Visby, Baltic. The Rochester acanthomorphs show some similarity with those reported by Eisenack (1954, 1955, 1959) in the Middle Silurian of the Baltic region. Of note is the absence in the Rochester assemblage of *Visbysphaera meson* complex with the exception of single specimens of *Baltisphaeridium digitatum* and *B. corallanum*. However, Cramer (1970) reports many Middle Silurian acanthomorph species in the Rochester Formation.

Eisenack obtained acritarchs by hand-picking from aqueous slurry, thus excluding netromorphs from his assemblages. The writer studied an excellently preserved acritarch assemblage from the Höglint Group, Snäckgardsbaden, Visby, and recorded the netromorphs *Domasia amphora*, *D. bispinosa*, *D. elongata*, *D. trispinosa*, and *Eupoikilofusa stratifera*. Cramer (1970, p. 67) recorded *D. elongata* in the uppermost portion of the upper Visby Marl, in Gotland. In addition, numerous species of *Baltisphaeridium*, *Micrhystridium*, *Veryhachium*, *Lophosphaeridium*, and *Leiosphaeridia* were recorded.

The Höglint netromorph assemblage is comparable with that of the Rochester assemblage (Table 3) with the exception of the absence of *Deunffia* spp. in the Höglint assemblage. Further detailed investigation of the netromorph distribution in Höglint group is needed for a more precise correlation.

The Wenlock Assemblage from the Montagne Noire, France. The Rochester acritarchs have little in common with the Wenlock assemblage from France. *Micrystridium*, *Veryhachium*, and *Baltisphaeridium* species common to two areas are long ranging (Llandovery to Emsian). Of the 16 species in France (Deflandre, 1942), 10 were identified in Coalbrookdale Beds (i.e. post-Buildwas Beds) in England (Downie 1963, p. 646). All these taxa are now known to be long-ranging.

The Wenlock Assemblage from Belgium. Of the 21 species in the Rochester Formation 9 occur in the Wenlock of Belgium (Table 3). The Belgian assemblage like the Höglint assemblage shows the presence of *Domasia* and the absence of *Deunffia* (except the rare occurrence of *D. monocantha* in pre-Wenlock strata). The absence of *Deunffia* complex from the Wenlockian of Baltic and Belgium, and its abundance in the Buildwas Beds and the Rochester Formation is worthy of note. However, *Neoveryhachium carminae* present in the Belgian assemblage does not occur in either the Buildwas or the Rochester assemblage.

The San Pedro and Furada Formations in North-West Spain. A small number of Rochester taxa present in the Spanish assemblage range in age from Upper Llandovery to Gedinian (Table 3). There seems to be a provincial differentiation between the two assemblages. The Spanish are dominated by *Neoveryhachium carminae* and numerous local species of *Veryhachium* and *Baltisphaeridium*. In contrast the Rochester is generally dominated by the *Deunffia* and *Domasia* complex, micrhystrids and leiospherids. This striking difference suggests the existence of different micro-

plankton provinces. Cramer (1970) believes such differences to be climatically controlled.

Wenlock Assemblages from the Sahara, Algeria. Little similarity exists between the Rochester taxa and the Wenlockian taxa in the Sahara (Table 3). Long-ranging (Upper Llandovery/Ludlow) species common to both areas are *Diexallophasis denticulata*, *Multiplicisphaeridium fisherri* (*Baltisphaeridium* sp. 5 of Jardine and Yapaudjian 1968), *Evittia remota* (*Veryhachium* sp. 2 of Jardine and Yapaudjian 1968), and *Duvernaysphaera aranaides* (*Pterospermopsis* cf. *Helios* of Jardine and Yapaudjian 1968). Netromorphs (*Deunffia* and *Domasia*) are not reported from the Sahara. The closer link of Saharan and Spanish assemblages is notable, in particular the presence of *Neoverhachium carminae*.

Palaeobiogeographic and palaeoclimatic considerations

Several palaeontologists, especially Bassler (1906, p. 8, 1911) and recently Owen (1969, p. 621), have showed interest in possible links of the Wenlockian Appalachian, Welsh Borderland, and Baltic faunas. It is therefore appropriate to discuss the relationship of the microflora in these regions.

Comparative Microflora. In order to do this, only stratigraphically restricted netromorphs are considered. The species common to more than one locality are as follows:

Species	America (Rochester Fm.)	Britain (Buildwas Beds)	Gotland (Höglint Gp.)
<i>Deunffia furcata</i>	Present	Present	Missing
<i>D. monospinosa</i>	Present	Present	Missing
<i>D. ramusculosa</i>	Present	Present	Missing
<i>Domasia amphora</i>	Present	?	Present
<i>D. bispinosa</i>	Present	Present	Present
<i>D. elongata</i>	Present	Present	Present
<i>D. trispinosa</i>	Present	Present	Present

This comparison suggests that the Rochester microflora had more links with the British than with the Baltic area.

Cramer (1970) suggested that acritarch 'biofaces' are due mainly to climatic factors. He proposed three biofacies: (1) *Neoverhachium carminae*, (ii) *Domasia* and *Deunffia*, and (iii) *Baltisphaeridium corallinum*. The last biofacies partially coincides with the *Domasia* and *Deunffia* biofacies.

In North America and western Europe, Cramer (1970) found the distribution of these biofacies roughly paralleled palaeolatitudes (Cramer 1970, text-fig. 6). The *N. carminae* biofacies occurred in south-east U.S.A. and the Iberian Peninsula and, the *Domasia* and *Deunffia* biofacies in the Central Appalachian region and the Welsh Borderland.

The Rochester acritarch assemblage belongs to the *Domasia* and *Deunffia* biofaces and is similar to the Buildwas assemblage in England. However, the Baltic assemblage (Höglint Beds), although similar, shows the absence of the *Deunffia* complex. The *Deunffia* complex in the Rochester and Buildwas assemblages may represent a local climatic zone, separated by a narrower Atlantic ocean. This independently supports Owen (1969), who on the basis of bryozoa study, suggests similar climatic zones and a narrower Atlantic ocean for the similarity of Wenlockian bryozoa faunas of the

Appalachian and Welsh Borderland. A marked difference between these and the Baltic faunas is attributed to a different climate. However, these suggestions are at variance with those of other workers. Cramer (1970) considers the *Domasia* and *Deunffia* biofacies in the Rochester and Buildwas strata and the *Domasia* biofacies in Höglklint strata to be indicative of a similar climate. Størmer (1967, p. 209) considered the Silurian fossiliferous reefs of Gotland to be facies of the eastern European Platform, having little connection with the Caledonian geosyncline. This would explain the similarity of the Appalachian and Welsh Borderland biota and their differences from those of Gotland. But Paul's (1967) investigations of Silurian cystids suggest that Echinoencrinitidae and Callocystitidae present in Britain originated from the Baltic and North America respectively. This would call for connections between these areas, a suggestion made earlier by Owen (1969).

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TRILOBITE CUTICLE MICROSTRUCTURE AND COMPOSITION

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ABSTRACT. Previous literature on the microstructure and composition of the trilobite cuticle is reviewed. The microstructure of the cuticle of *Asaphus raniceps* Dalman *sensu* Angelin (1854) is described in detail, and a table outlining the major features of the cuticles of fourteen other trilobite species is included. In *Asaphus raniceps* and some other species, two main regions of the cuticle are consistently present: an outer layer characterized by perpendicular prisms, representing about one-fifteenth of the total thickness of the cuticle and an inner area forming the bulk of the cuticle. In the inner area of many cuticles, characteristic primary microstructures are fine perpendicular canals, a variety of wider canals, and horizontal laminae. Three types of tubercle are distinguished from thin-sections. Inorganic analyses of *Asaphus raniceps* show that the cuticle consists largely of calcite. Decalcification of this cuticle with E.D.T.A. left organic residues.

A LARGE number of incidental observations has been made on the trilobite cuticle, usually during the course of systematic descriptions. However, no author has studied the cuticle of a wide range of trilobite species in the thorough way that Lindström (1901) and latterly Clarkson (1967, 1969) have examined visual organs. Attempts at comparing trilobite cuticles with arachnid or crustacean cuticles have therefore often been based on inadequate evidence, and in some cases recent work on extant arthropod cuticles has been totally disregarded.

PREVIOUS LITERATURE

Subdivisions of the trilobite cuticle. The terms 'chitinous' and 'integument' have frequently been used in descriptions of trilobite exoskeletons. Although chitin is the most characteristic organic component of arthropod cuticles, it comprises only a small fraction of the dry weight of calcified cuticles. The use of the term chitinous to describe dark hard fossil material is particularly inappropriate: pure chitin is colourless, soft, and flexible. The term integument includes the cuticle, the underlying epidermal cells which secrete it, and the basement membrane. In trilobite exoskeletons, therefore, only the cuticle is found preserved.

Harley (1861) was probably the first to examine the trilobite cuticle critically, while attempting to establish the systematic position of various 'Astacoderma' from the Ludlow Bone Bed. Thin-sections through the cuticle of *Calymene* (L. Ludlow) showed that it consisted of an outer fibrous layer and an inner prismatic layer, both pierced by canals. However, Harley doubted whether this was the original structural appearance. In his monograph on the visual organs of trilobites, Lindström (1901) figured sections of the cuticles of many species but made very few comments on their structure. Cayeux (1916) compared the structure of trilobite and crustacean cuticles, and Størmer (1930), who gave a detailed account of the 'shell' structure of some Trinucleidae, recognized four main layers in the cuticle of *Tretaspis* and compared these with the four layers in the cuticle of *Homarus*. The microstructure of the cuticle of *Phacops accipitrinus maretiolensis* R. and E. Richter was described by Rome

(1936) who distinguished three main regions of the cuticle besides observing many other features. Hupé (1953) considered that three layers in the cuticle might correspond to the epicuticle, pre- and post-exuvial layers of modern cuticles. Harrington (1959) reviewed the work of Størmer (1930), Hupé (1953), and Kielan (1954) and interpreted the three main layers of Størmer and Kielan as corresponding to those of the modern arthropod endocuticle. However, Rolfe (1962) considered that many of the subdivisions apparent in fossil cuticles were due to diagenetic replacement. More recently, Majewske (1969) and Horowitz and Potter (1971) reviewed some of the previous literature on trilobite cuticles, figured some photomicrographs of thin-sections, but made few observations. Bathurst (1971) has given a more comprehensive account of previous work.

Primary microstructures. The term 'primary microstructures' was introduced by Rolfe (1962) to describe all structures found in fossil cuticles comparable with those in modern arthropod cuticles. A brief review of characteristic structures in extant cuticles has been given by Dalingwater (1973).

Pore-canals: Rolfe (1962) reviewed descriptions of structures from fossil cuticles resembling the pore-canals of extant cuticles, and concluded that the various small canals described by Størmer (1930), Rome (1936), and Evitt and Whittington (1953) were perhaps too large and too sparsely distributed to be true pore-canals. However, Harley (1861) had observed that the cuticle of *Calymene* was traversed by many straight tubes 0.5–1.8 μ in diameter, Lindström (1901) figured many sections of cuticles perforated by numerous minute canals, and Balashova (1948) clearly distinguished very fine 'canalicules' from larger canals perforating the carapace of the Asaphidae.

Larger canals: Rolfe (1962) suggested that many of the larger canals in fossil cuticles should be termed gland or setal ducts. In extant arthropods such ducts are generally larger, are more irregularly placed, and occur less frequently than pore-canals. Larger apertures through trilobite cuticles have been described by Lindström (1901), Richter (1914), Cayeux (1916), Raymond (1920), Størmer (1930, 1931), Whittington (1941, 1956, 1962), Ross (1951), Evitt and Whittington (1953), Hupé (1953), Whittington and Evitt (1954), Richter and Richter (1954), and Harrington (1959).

Laminae: Nearly all extant arthropod cuticles are horizontally laminated and individual laminae are 0.2–10 μ thick. Rolfe (1962) reviewed some of the earlier literature on laminae in trilobite cuticles, commenting on the work of Zittel (1900), Cayeux (1916), Størmer (1930), and Rome (1936). However, Harley (1861) had observed obscure indications of a finely laminated structure in the cuticle of *Calymene*, Sorby's (1879) 'lines of growth' are presumably laminae, and Lindström (1901) also figured many finely laminated cuticles.

Tubercles: Tubercles are defined by Harrington, Moore, and Stubblefield (1959) as small knob-like prominences on any part of the exoskeleton, whereas smaller structures are termed granules. However, the term tubercle has been used imprecisely to describe:

- (i) Structures involving thinning and doming of the cuticle (Raymond, 1920; Størmer, 1930; Kielan, 1954).

- (ii) Domed thickenings differentiated to some extent from the main part of the cuticle (Rome, 1936).
- (iii) Discrete structures embedded in cuticle surfaces (Lindström, 1901; Walcott, 1921).

Prisms: The surfaces of many arthropod cuticles are covered by a close polygonal network. Each polygon possibly represents the area of activity of an underlying epidermal cell and is formed by inward extensions of epicuticular material at the interfaces between adjacent areas of influence (Dennell 1960). Larger, less regular polygonal areas seen in perpendicular sections of calcified cuticles may represent areas of activity of crystallization centres. Cayeux (1916) figured some relatively large polygonal areas from the cuticles of '*Trinucleus goldfussi*' and Hupé (1953) mentioned 'un fin réseau à mailles polygonales' in his account of the trilobite cuticle.

Inorganic chemistry and mineralogy. It has often been stated, without critical examination of the cuticle itself or of the results of previous research, that the trilobite cuticle contains significant amounts of phosphate. For example, Zittel (1887) described alternate thin layers of calcium carbonate and phosphate, but Cayeux (1916) found no trace of these layers and neither did Bøggild (1930) who clearly thought Zittel was mistaken. Richter (1933) estimated that the trilobite exoskeleton contained up to 30% phosphate, whereas Cayeux's (1933) detailed analyses indicated that phosphates were present only in limited quantities. Only Raw (1952) considered that the cuticle was originally aragonitic, subsequently becoming silicified or coarsely crystallized to calcite. Probably the most significant contribution to a study of the original inorganic composition of the trilobite cuticle was made by Stehli (1955). Although he analysed only one trilobite pygidium, the specimen came from the Middle Permian Buckhorn asphalt deposit in which original shell mineralogies seem to have been preserved. X-ray analysis showed that this pygidium was composed entirely of calcite.

Organic chemistry. Abelson (1954) referred to the presence of three amino-acids in an Ordovician *Calymene*, whereas Fujiwara (1963) found no amino-acids in another species of the same genus.

MATERIAL AND METHODS

Thin-sections provided most of the information for this study but material was also prepared by E.D.T.A. decalcification and acetate-peel preparation. A preliminary study, using the Scanning Electron Microscope (S.E.M.), was made on surfaces as well as on broken and etched material. A wide range of trilobites in varying modes of preservation was examined. The most satisfactory specimens for thin-sectioning were those preserved in fine-grained limestones, with part of the exoskeleton enclosed in matrix. The identity and orientation of these specimens could thus be determined, while the matrix formed a most satisfactory natural embedding medium. Where possible, serial sections were made from a single specimen. Random section series were also made from samples crowded with trilobite remains. Sections were finished by hand using 1200 mesh carborundum and then left relatively thick (20–30 μ). Such thick slices offered much detail, but were unfortunately somewhat

difficult to photograph satisfactorily. All preparations are stored in the Department of Zoology, University of Manchester, England.

The cuticle of *Asaphus raniceps* was in addition analysed in a Phillips X-ray diffractometer, and by X-ray powder photography.

THE CUTICLE OF *ASAPHUS RANICEPS*

Specimens of *Asaphus raniceps* Dalman *sensu* Angelin (1854) were collected from the lower 'Raniceps' Limestone, Haget, Öland, Sweden. About 100 longitudinal, transverse, and tangential perpendicular sections were made across all the calcified areas of the exoskeleton. In addition, a preliminary study of the cuticle of this species was made using the S.E.M. The cuticle of this species is the best documented here and serves as a model for detailed description.

The cuticle is relatively thick compared with that of modern arthropods of comparable size but varies considerably from one area of exoskeleton to another. In a ten-slide series made from block Ö1.0.1 the following ranges of thickness were measured: cephalon 180–450 μ , hypostome 120–560 μ , thorax 100–300 μ , pygidium 160–300 μ .

Surfaces of the cuticle examined with the S.E.M. show a matrix of calcite prisms with morphological indications of c-axes orientated perpendicular to the cuticle surface (Pl. 107, fig. 1). In thin-sections an outer layer comprising one-tenth to one-fifteenth of the total cuticle thickness is seen, composed of fairly regular perpendicular prisms (Pl. 107, fig. 5). However, under crossed-nicols this layer does not extinguish uniformly (Pl. 107, fig. 6) suggesting that although prisms may be orientated with their c-axes normal to the surface, this orientation is not totally uniform. Broken sections of cuticle examined with the S.E.M. confirm light microscope observations that the outer layer is distinct (Pl. 107, fig. 2) from the main part of the cuticle (hereafter termed the inner area). No individual prisms can be seen in the inner area even when it is examined at a magnification of about $\times 1,000$ with the light microscope. Again, total extinction does not occur when particular areas of the cuticle become aligned with the planes of polarization. Under the S.E.M., broken sections of the inner area suggest fibrous crystallites running tangentially to the surface (Pl. 107, fig. 3) but this impression is not confirmed by etched sections (Pl. 107, fig. 4).

The inner area of the cuticle includes fine perpendicular canals approximately 0.1 μ in diameter, and occasionally fine parallel horizontal laminae approximately 1 μ apart can be seen. The cuticle is thicker at the anterior margin of the cephalon, where fine vertical canals are often emphasized by impregnation with pyrite. Wider canals

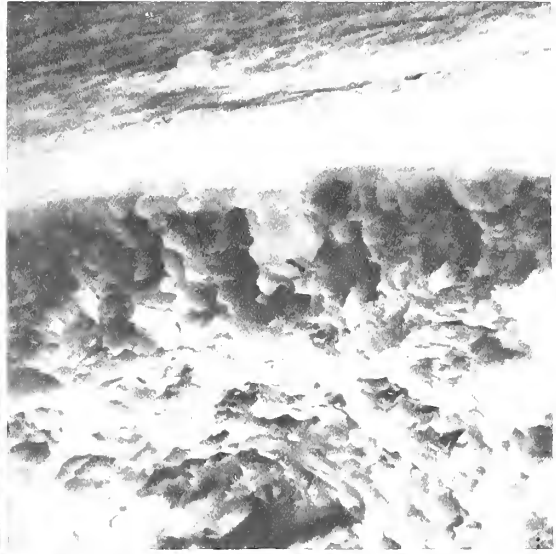
EXPLANATION OF PLATE 107

Figs. 1–4. Scanning electron micrographs of librigenal cuticle of *Asaphus raniceps* Dalman. 1 Upper surface of cuticle, showing fairly regular calcite prisms. $\times 1950$. 2 Broken perpendicular section of cuticle, showing discrete outer layer. $\times 1730$. 3 Broken perpendicular section, showing apparent fibrous crystallites tangential to surface. $\times 420$. 4 Etched perpendicular section of cuticle. $\times 545$.

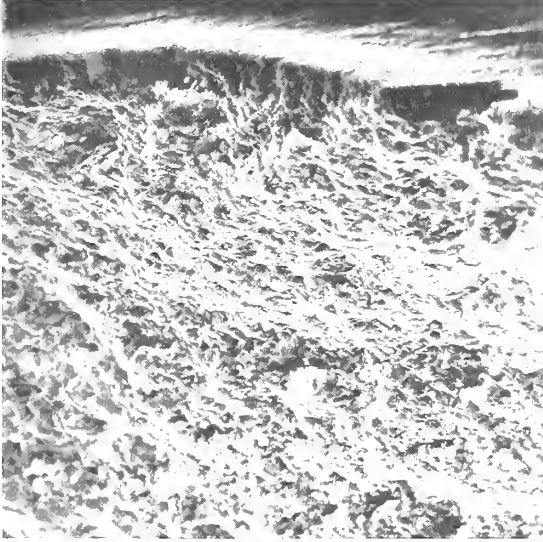
Figs. 5–6. Longitudinal perpendicular section (L.P.S.) of glabella of *Asaphus raniceps* Dalman showing outer layer and inner area of cuticle. Slice Ö1.98.1. 5 Plane-polarized light. 6 Crossed nicols. $\times 125$.



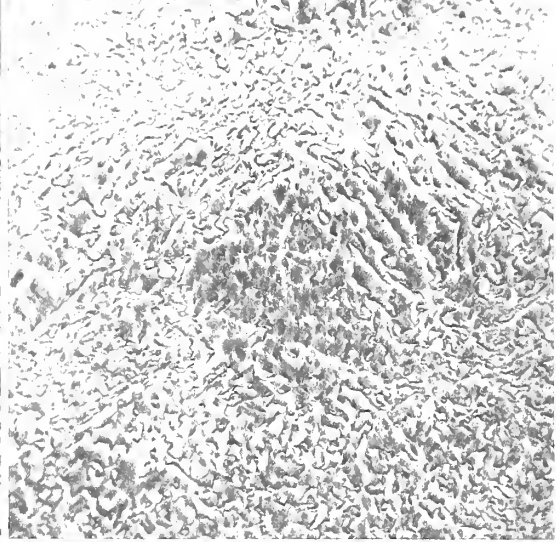
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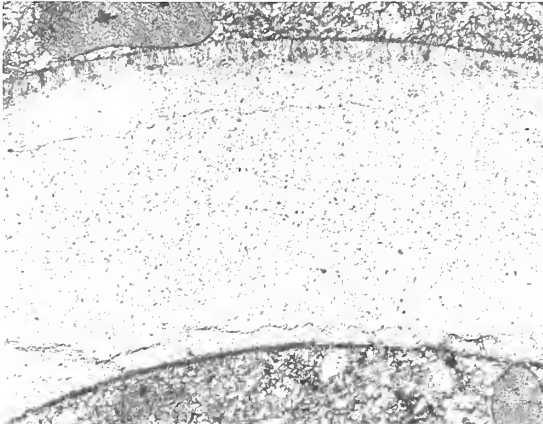
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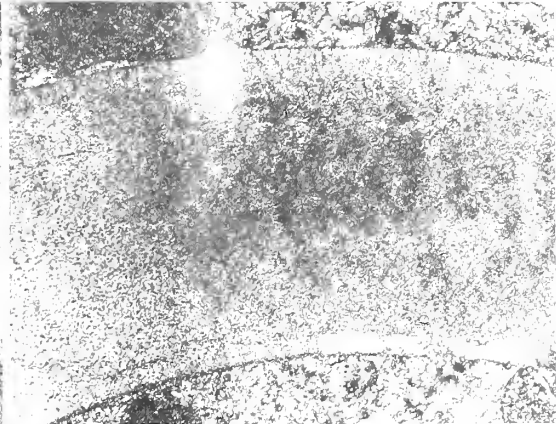
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6

DALINGWATER, trilobite cuticle

approx. $4\ \mu$ in diameter extend to thorn-like projections representing sections through ridges on the anterior part of the cephalon (Pl. 108, fig. 1). This sculpture is even more pronounced on the cephalic doublure, the forward projecting 'thorns' (= sections of terrace lines) becoming flattened and scale-like with canals opening at their bases. The terrace lines on the pygidium are seen in thin-section as thickened ridges of cuticle, but the outer edge of the pygidial doublure is distinctly corrugated. Sculptured ridges on the hypostome are seen in section to be penetrated by canals approximately $4\ \mu$ in diameter.

Several sections were made through the hypostomal maculae where the cuticle is slightly thicker. Here, in contrast to other areas of the hypostomal cuticle, fine perpendicular structures are accentuated by pyrite.

The outer surface of the thoracic cuticle is generally smooth but cuticular sculpturing on the pleural doublure is reflected in thin-sections. Where the cuticle deflects to form the narrow posterior ventral doublure of the thoracic axial rings, the angle is characterized by an area of darker cuticle. This area may represent differentiation of the cuticle to permit flexibility between segments additional to that provided by the soft intersegmental membrane.

Well-preserved material, particularly when freshly broken from the matrix, exhibits a glossy lustre. This possibly represents an extremely thin outermost layer not visible in thin-sections. Isolation of this layer proved difficult but decalcification with a 5% solution of E.D.T.A. (disodium salt) left a residue of brown material with a clear surface layer. In several specimens this surface layer is regularly prismatic in some areas, each prism being $6\text{--}7\ \mu$ across (Pl. 108, fig. 2). The brown residue is usually amorphous but sometimes contains small twisted tubules about $1\ \mu$ in diameter.

X-ray analyses of cuticle from the cephalon, thorax, and pygidium indicated a composition entirely of calcite.

EXPLANATION OF PLATE 108

Figs. 1-2. *Asaphus raniceps* Dalman. 1 L.P.S. anterior of cephalon. Slice ÖI.96.1. $\times 27$. 2 E.D.T.A. preparation, showing prismatic surface layer. E.D.T.A. prep. 19. $\times 360$.

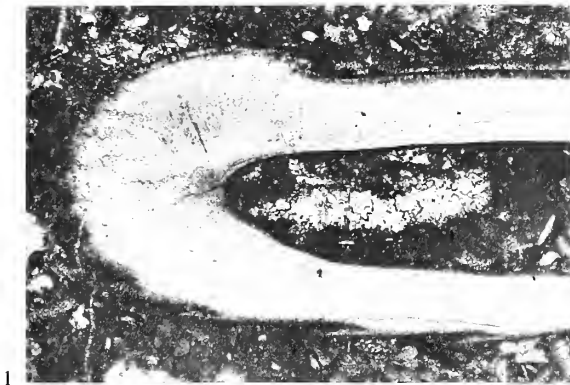
Figs. 3-4. *Iliaenus aduncus* Jaanusson. Slice ÖI.1.1a.2. 3 Tangential perpendicular section (Tan. P.S.) librigena, perforated by large perpendicular canals. These canals are regularly spaced ($50\text{--}150\ \mu$) and were observed in all areas of the exoskeleton examined. $\times 100$. 4 Tan. P.S. edge of thoracic pleura, cuticular sculpturing perforated by 'hair-like' structures. $\times 90$.

Fig. 5. *Bumastus barriensis* (Murchison). L.P.S. pygidial doublure, showing tightly helically coiled fine perpendicular canals accentuated by pyrite. Slice Dy.B.1b.2. $\times 100$.

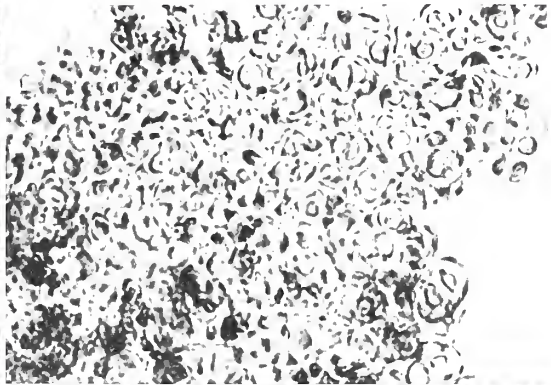
Fig. 6. *Paladin eichwaldi shumnerensis* (King). Transverse perpendicular section (T.P.S.) pygidial margin, showing larger perpendicular canals which are particularly prominent in this region of the cuticle. Slice W.s.1a.1. $\times 90$.

Fig. 7. *Cyrtometopus* sp. L.P.S. glabella lobe, showing irregular undulating laminae which give the cuticle of this genus its characteristic 'cloudy' appearance. Slice C.(FMB)1.2. $\times 90$.

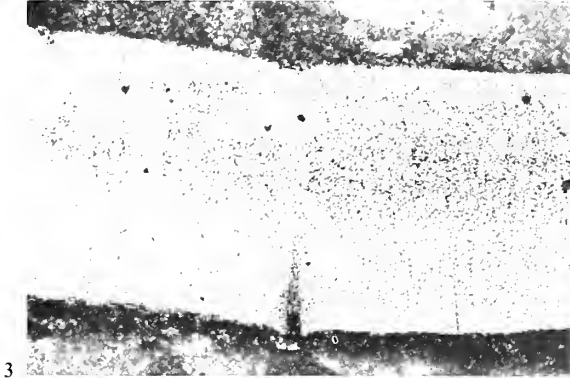
Fig. 8. *Encrinurus punctatus* (Wahlenberg). L.P.S. glabella, showing large tubercles—the cuticle domes and thins. Tubercles of this type are also present in axial regions of the thorax. Small discrete tubercles are present on lateral areas of the cephalon. Slice Dy.E.7.1. $\times 24$.



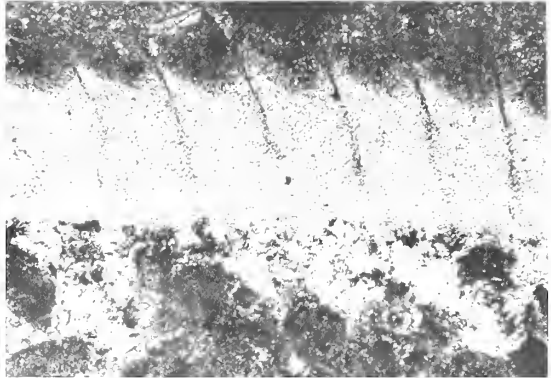
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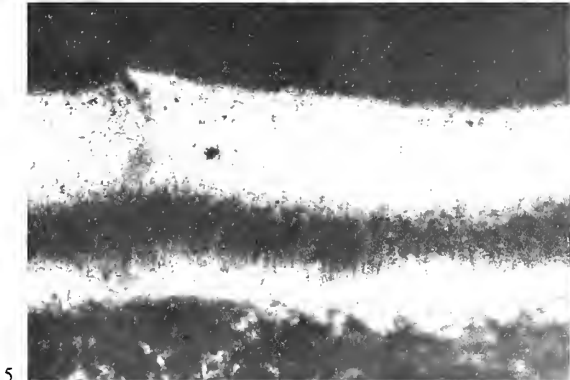
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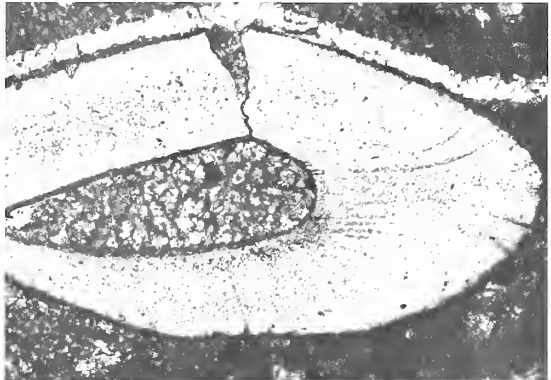
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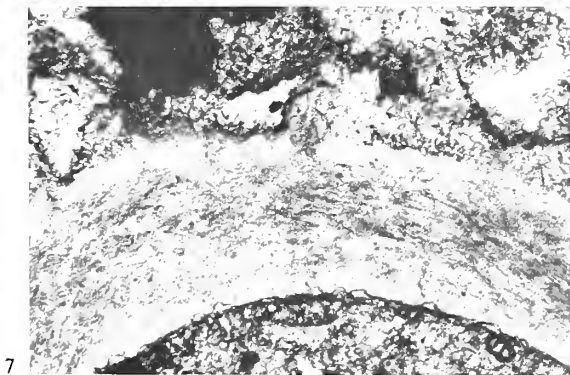
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DALINGWATER, trilobite cuticle

THE CUTICLES OF OTHER TRILOBITE SPECIES

Brief descriptions of the cuticles of fourteen trilobite species are deposited with the British Library, Lending Division, Boston Spa, Yorkshire, reference number SUP 14001. These are illustrated in Plates 108 and 109, and Table 1 summarizes their characteristic features.

TABLE 1. Synopsis of the characteristic features of the cuticles of fourteen trilobite species.

	Material examined	Cuticle thickness (μ)	Duter layer	Larger perpendicular canals	Fine perpendicular canals	Laminae	Special features
<i>Agnostus pisiformis</i> (Linnaeus) Middle Cambrian, Öland.	c., p.	7-30	-	+	-	+	-
<i>Nileus armadillo</i> Dalman 'Raniceps' Limestone, Öland.	c./s.	100-200	-	-	+	-	+
<i>Illaenus aduncus</i> Jaanusson 'Raniceps' Limestone, Öland.	c./s.	180-700	+	+	+	+	+
<i>Bumastus barriensis</i> (Murchison) Wenlock Limestone, Dudley.	c., p.	300-500	-	+	+	+	-
<i>Cyrtosymbole pusilla</i> (Gürich) Famennian Limestone, Poland.	s.	30-100	+	+	-	-	+
<i>Paladin eichwaldi shunnerensis</i> (King) Shunner Fell Limestone, Yorkshire.	p.	150-200	+	+	+	+	-
<i>Ampyx nasutus</i> Dalman Expansus & 'Raniceps' Limestones, Öland.	c.	100-200	+	-	+	+	+
<i>Cyrtometopus clavifrons</i> (Dalman) 'Raniceps' Limestone, Öland.	c.	200-340	-	+	-	+	+
<i>Encrinurus punctatus</i> (Wahlenberg) Wenlock Limestone, Dudley.	c./s.	100-240	+	+	+	+	+
<i>Calymene blumenbachii</i> Brongniart Wenlock Limestone, Dudley.	c./s.	200-400	+	+	+	+	-
<i>Phacops granulatus</i> (Münster) Famennian Limestone, Poland.	s.	100-600	-	+	-	-	+
<i>Trimerocephalus caecus</i> (Gürich) Famennian Limestone, Poland.	s.	120-270	-	+	-	-	+
<i>Acaste downingiae</i> (Murchison) Wenlock Limestone, Dudley.	c.	160-300	+	+	-	-	+
<i>Boedaspis ensifer</i> Whittington & Bohlin Expansus Limestone, Öland.	p.	200-250	+	-	+	-	+

KEY c. = cephalon, p. = pygidium, c./s. = complete specimens, s. = slides,
+ = present, - = not observed, * = figured.

EXPLANATION OF PLATE 109

Fig. 1. *Calymene blumenbachii* Brongniart. L.P.S. glabella lobe, showing a range of perpendicular canals accentuated by pyrite, some of which are similar to the fine canals of other trilobite cuticles. Slice Dy.C.1.2. $\times 160$.

Fig. 2. *Phacops granulatus* (Münster). T.P.S. edge of pygidial axis, showing large tubercle; the cuticle domes and thickens. Slice P.g.(0)1. $\times 92$.

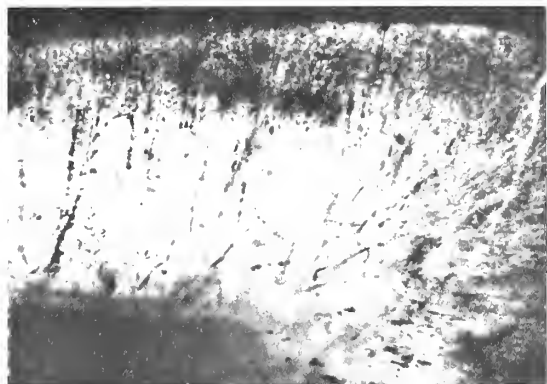
Fig. 3. *Trimerocephalus caecus* (Gürich). T.P.S. large tubercle on edge of librigena. Slice T.c.(O)3. $\times 92$.

Fig. 4. *Acaste downingiae* (Murchison). L.P.S. discrete tubercles on cephalon. Note spine-like structure arising from one tubercle, also canals which may serve the tubercles. Slice Dy.A.d.1.3. $\times 135$.

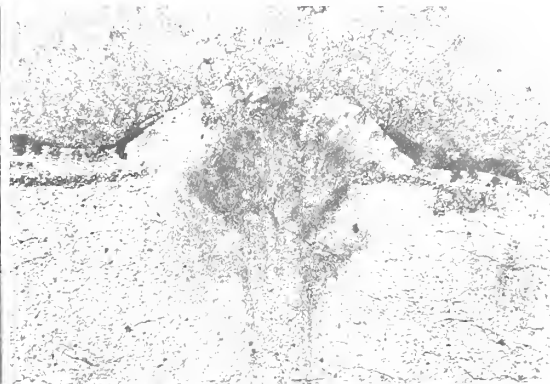
Figs. 5-8. *Boedaspis ensifer* Whittington and Bohlin.

Figs. 5-7. Tan. P.S. edge of pygidium, showing three types (or aspects?) of tubercle involving doming and thinning of the cuticle. Slice Ö1.B.e.1b.2. All $\times 85$.

Fig. 8. Tan. P.S. edge of pygidium, showing discrete tubercle. Slice Ö1.B.e.1a.1. $\times 135$.



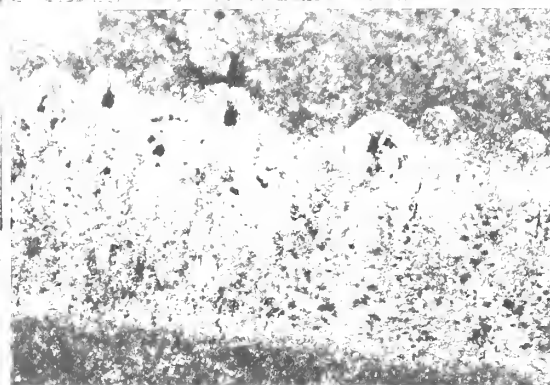
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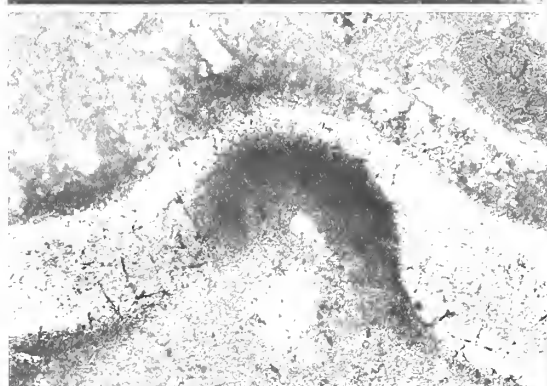
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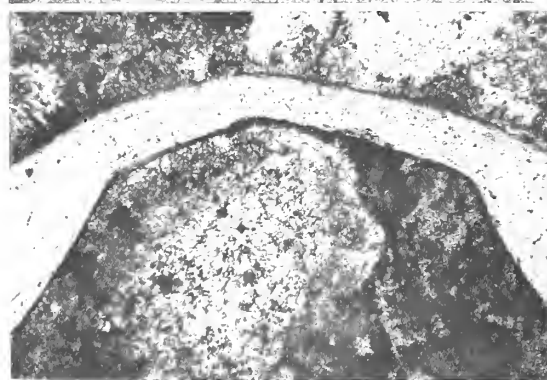
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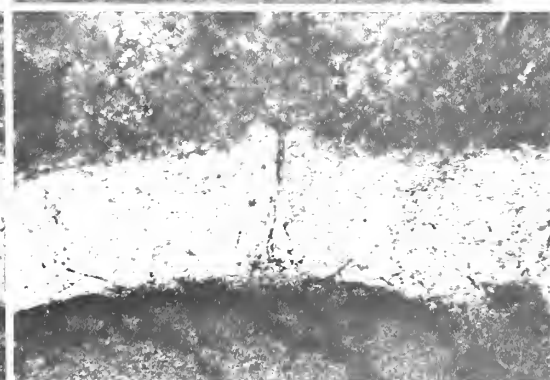
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DALINGWATER, trilobite cuticle

DISCUSSION

Subdivisions. The calcitic composition of *A. raniceps* cuticle agrees with the observations of Bøggild (1930), the detailed analyses of Cayeux (1933), and Stehli's (1956) analysis of a pygidium composed entirely of primary calcite. In most trilobite cuticles, replacement and infiltration of the original inorganic material has probably taken place; this may have been partly inhibited by the organic component. Diagenesis of the calcite in the eye-lenses of *A. raniceps* has been described in detail by Clarkson (1973).

Many previous authors including Sorby (1879), Cayeux (1916), and Majewske (1969) have stated that thin-sections of trilobite cuticle extinguish uniformly when viewed with crossed-nicols, but here it is shown that in *A. raniceps* cuticle (and in most other cuticles examined) extinction is not totally uniform. Moreover, examination of thin-sections of cuticle with the light microscope, and broken sections with the S.E.M. indicates that calcite prisms with any definite orientation occur only in the thin outer layer.

Størmer (1930) suggested that the four cuticular layers of *Tretaspis* were directly comparable with the major structural subdivisions in *Homarus*. However, it is difficult to envisage how an inner uncalcified area of endocuticle (equivalent to the inner layer in *Homarus*) might be preserved when the ventral trilobite cuticle is so rarely encountered. Moreover, an outer epicuticle, if present, is unlikely to be seen in thin-sections of trilobite cuticles prepared by conventional petrological methods. Furthermore, Størmer's 'pigmented layer' is a dense micritic envelope (J. Miller, pers. comm.). Although Richards (1951) established that the subdivision of any arthropod cuticle must be based mainly on histochemical distinctions, Hupé (1953) and Harrington (1959) compared the various layers described by previous authors directly with those of extant arthropod cuticles. Harrington's statement that: 'the exoskeleton of trilobites consists of a thin integument that is directly comparable to the chitinous cuticle of other Arthropoda', seems particularly inappropriate. In contrast, Rolfe's (1962) comment that many subdivisions in fossil cuticles are the result of replacement, may be pessimistic. In the present study the only consistent divisions of the trilobite cuticle seen in thin-section are a thin outer prismatic layer and an inner area. The outer layer, comprising one-tenth to one-thirtieth of the total thickness, was not observed in all cuticles studied, possibly because it is easily eroded and the boundary between it and the inner area seems to be a natural plane of weakness. In broken sections of cuticle examined with the S.E.M., the outer layer appears superficially similar to the tanned calcified exocuticle of *Carcinus maenas*, where the prominent perpendicular elements are pore-canals. Clarkson (1973) has described how the outer layer of the trilobite cuticle corresponds with the cornea; in some modern decapods, the tanned calcified exocuticle also laterally merges with the cornea. The appearance of the prismatic network of thin transparent material obtained on decalcification of *A. raniceps* cuticle resembles that of the epicuticle of some extant arthropods. In the latter, the walls of the regular prisms probably reflect the boundaries of the hypodermal cells responsible for secretion of the cuticle (Dennell 1960).

Thus, although there is some evidence for correlating the subdivisions seen in some trilobite cuticles with those of extant decapod cuticles, no precise comparisons can be made in the absence of histochemical data.

The cuticles of some trilobites (e.g. *Agnostus*) are thin, but most species studied have thick cuticles compared with modern arthropods. Although the general cuticle thickness is rarely greater than 500 μ , the cephalic cuticle of some large trilobites sometimes exceeds 1 mm.

Canals. Fine perpendicular canals, usually less than 1 μ in diameter, occur in the majority of cuticles studied. They are a characteristic feature of the cuticle and occur in large numbers closely packed together. In some cuticles, they appear to be helically coiled. Previous workers, notably Cayeux (1916), have compared these fine canals in the trilobite cuticle with those in modern arthropod cuticles. They are more evident in some species or only locally prominent. Larger canals appear to be more prone to pyrite impregnation and are thus accentuated. The prominence of fine canals in certain areas may also be due to preferential pyrite impregnation.

However, it is more difficult to understand why canal-like structures are accentuated in specialized areas of cuticle such as the hypostomal maculae, dark spots, the cuticle surrounding the eyes, and the anterior margin of the cephalon. Raymond (1920) suggested that the maculae and dark spots represent muscle-attachment sites. In contrast, Lindström (1901) thought that the hypostomal maculae were rudimentary optic organs because in many species the marginal areas of the eyes and the maculae have a similar aspect. Furthermore, he observed that small, closely spaced 'lenses' were present on the maculae of some trilobites. Balashova (1948) also noted the similarity of the eye-margins and maculae in the Asaphidae, but disagreed with Lindström's conclusions and suggested instead that both areas were characterized in life by dense concentrations of sensory setae. Harrington (1959) also thought it unlikely that the hypostomal maculae represented areas of muscle-attachment, partly because he supposed that the 'mineralized integument' was thinner at the maculae. In fact, the cuticle *thickens* at the maculae in the Asaphidae, where perpendicular elements are most prominent in this area. It is suggested here that all these areas were sites of muscle-attachment, and that some of the perpendicular elements may represent tonofibrillae (cuticularized muscle fibres). Their frequent occurrence in multiple units may explain the rudimentary lens-like structure inferred by Lindström (1901). In recent arthropod cuticles it is often difficult to distinguish tonofibrillae from pore-canals (Dr. J. H. Kennaugh, pers. comm.).

A variety of wider canals was observed in the trilobite cuticles studied, some of which are remarkably similar to canals in modern cuticles. However, because conclusive evidence such as the remains of sensory hairs is rare, it is difficult to assess whether these wider canals represent tegumentary or setal ducts. Wide canals are often prominent at the extremities of the exoskeleton. In extant decapods similar regions are plentifully supplied with tegumental glands (Dennell 1960), but in trilobites these canals were probably sensory rather than associated with extensive phenolic tanning. Contrary to Evitt and Whittington (1953), wide canals are present even in 'smooth-shelled trilobites'.

Laminae. The fine parallel laminae described from a few trilobite cuticles are possibly comparable with those in extant decapod cuticles. However, microfibrils were not seen even in the best-preserved material, and it seems more likely that examination

of well-preserved eurypterid cuticles will extend studies of cuticle architecture back into the Palaeozoic.

Tubercles. The various types of tubercles described by previous authors have been recognized in the cuticles studied. Although the term 'tubercle' has been used indiscriminately to describe various structures in modern arthropod cuticles, several authors, notably Kennaugh (1968), have used the term more precisely to describe discrete structures embedded in the cuticle of arachnids. However, as it is difficult to determine which type of tubercle is present without sectioning the cuticle, it seems premature to introduce terminology to distinguish these various structures.

Rome (1936) indicated that *Phacops accipitrinus maretiolensis* was immediately identifiable in thin-section but doubted whether other trilobites could be distinguished so satisfactorily. However, certain species have characteristic, perhaps unique, cuticles which might enable specific identification to be made from a small fragment. When the cuticles of many trilobite species have been described in detail (including variations in structure due to different modes of preservation) this information may prove useful, particularly in borehole work.

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THE PALAEOONTOLOGICAL ASSOCIATION

Annual Report of the Council for 1972

MEMBERSHIP. Over the past two years the ordinary membership has shown a significant rise to c. 760 members from the previous plateau of c. 710 members reached in 1966. This improvement may in part be due to the enlarged circulars with their more informative contents. On 31 December 1972 there were 1321 members (771 Ordinary, 138 Student, and 412 Institutional), a net increase of 85 members during the year.

FINANCE. During 1972 the Association published Volume 15 of *Palaentology* at a cost of £13,221 and *Special Papers* 10 and 11 which are expected to cost £4,758. This printing bill of £17,979 is once again the highest in the Association's history, a reflection of continual price increases in the printing trade.

Total expenditure was £19,038, a decrease over the previous year since we reprinted no back numbers of *Palaentology* or an Index. An excess provision of £895 for 1971 artificially decreased this year's figure. General income was satisfactory, but the high level of subscription income is partly the effect of the postal strike in early 1971, and represents subscriptions held over for a year. Sales of *Palaentology* were encouraging at £7,452, an increase of over £3,000 from 1971, although the latter figure was also adversely affected by the postal strike. The Association is very grateful to those universities and other institutions who gave funds to support individual papers, and in particular to the Royal Society for providing a gift of £400 and a loan of £600 in support of *Special Paper* 11. The more direct grants that papers receive the more the Association can publish.

Although there was a welcome excess of income over expenditure during 1972, our publication reserves were still lower than two years previously. Indeed the reserve of £12,471, although at first sight a high figure, is still well below our aim of being one year's printing costs of *Palaentology* alone. In particular more subscribers, both institutional and private, are needed to *Special Papers* before that series can become self-financing.

PUBLICATIONS. Four parts of *Palaentology* were published during 1972; they contained 47 papers and consisted of 693 pages and 132 plates. The cover of *Palaentology* was redesigned during the year at Oxford University Press, and was issued from Volume 16 part 1. *Special Papers in Palaentology* 11 (for 1972) was published, and *Special Paper* 12 (for 1973), the Cambridge symposium volume 'Organisms and continents through time', early in 1973. Advance publicity matter for this *Special Paper*, widely distributed in N. America through the good offices of Dr. Ellis Yochelson, the S.E.P.M., and the Paleontological Society, resulted in many orders. A sales campaign to promote the *Special Papers* generally was mounted during the year, most of the work being undertaken by Dr. W. J. Kennedy. It is hoped that members will encourage subscription to this series.

The *List of British Palaentologists* referred to in the last annual report was issued to Ordinary and Student Members during the year. All the work entailed in the compilation of the volume, and the costs of production, were borne by Robertson Research International Limited, and the Association is greatly indebted to Dr. R. H. Cummings and his staff for their efforts so generously given.

MEETINGS. Six meetings were held during 1972-3. The Association is greatly indebted to Professor P. C. Sylvester-Bradley (Leicester University), Dr. R. H. Cummings (Robertson Research International Limited), and Professor E. A. Vincent (Oxford University) for granting facilities for meetings, to Dr. C. T. Scrutton for leading the field meeting and to the local secretaries for their efficient services.

- a. The *Fifteenth Annual General Meeting* was held in the rooms of The Geological Society of London on Wednesday, 1 March 1972. The Annual Report of the Council for 1971-2 was accepted and the Council for 1972-3 elected. Dr. C. Downie of Sheffield University delivered the *Fifteenth Annual Address* on 'The Palaeozoic acritarchs'.
- b. A *Field Demonstration Meeting* on 'Devonian corals and stromatoporoids of the Torbay area' was led by Dr. C. T. Scrutton on 6 May 1972.
- c. A most successful innovation during the year was a *Teach-in* 'Analysis of processes in carbonate environments', organized by Dr. Julia A. E. B. Hubbard and led by Dr. R. G. C. Bathurst. Numbers

were restricted to 40 (including the 11 speakers), but were drawn from a wide sector of interests, and from a wide geographic area. This cross-cutting meeting gained many new friends for the Association from neighbouring disciplines.

- d. A *Symposium* on 'The application of electron microscopy to palaeontology' was held at EMCON 72—the 5th European Congress on Electron Microscopy, at Manchester University on 11 September 1972. About 60 people attended, 12 papers were presented, some of which will appear in 'Palaeontology'. The meeting was organized by Dr. Marjorie D. Muir.
- e. A *Joint Demonstration Meeting* on 'The electron microscope in micropalaeontology' was held with the British Micropalaeontological Group at Leicester University on 25 October 1972. This was a sequel to the above meeting, and 22 demonstrations were provided. The local secretary was Mr. R. Clements.
- f. An *Open Discussion Meeting* was held at Oxford University on 17–20 December 1972. Over 120 people attended to hear 24 papers, to see the remarkable film of echinoid behaviour brought along by Dr. Porter Kier (arrangements are in hand to obtain a hire copy for the British Film Institute), and to view the 20 demonstrations. This was the first of a new style of open meeting organized by the Association; its undoubted success will encourage the adoption of this pattern for future annual meetings. A welcome feature of this year's meeting was a choice of two field excursions, run jointly with the British Sedimentological Research Group. The local secretary was Dr. W. J. Kennedy.

COUNCIL. The following were elected members of Council of the Association for 1972–3 at the Annual General Meeting on 1 March 1972: *President*: Professor M. R. House. *Vice-Presidents*: Dr. Gwyn Thomas, Mr. N. F. Hughes. *Treasurer*: Dr. J. M. Hancock (Deputy Treasurer during Treasurer's absence abroad: Dr. L. R. M. Cocks). *Membership Treasurer*: Dr. A. J. Lloyd. *Secretary*: Dr. W. D. I. Rolfe. *Editors*: Dr. I. Strachan, Dr. R. Goldring, Dr. J. D. Hudson, Dr. D. J. Gobbett, Dr. L. R. M. Cocks. *Other members*: Dr. M. G. Bassett, Dr. E. N. K. Clarkson, Dr. R. H. Cummings, Professor D. L. Dineley, Dr. Julia A. E. B. Hubbard (Circular Reporter), Dr. J. K. Ingham, Mr. M. Mitchell, Dr. Marjorie D. Muir, Dr. B. Owens, Dr. W. H. C. Ramsbottom, Dr. P. Rawson, Dr. P. L. Robinson, Dr. A. D. Wright.

CIRCULARS. These continued in the enlarged form instituted last year, and there was evidence that the fuller information provided was welcomed; as a result of the Circular Reporter's initiative, copies were now sent to 99 Institutional Members and interested bodies. Four Circulars (nos. 69–72) were distributed during the year.

COUNCIL ACTIVITIES. Besides continuing the planning of the meetings throughout the year, Council has given thought to the following new ventures. On the suggestion of the Stimulus Committee it was agreed that an International Symposium on 'The Ordovician System' should be held at Birmingham in 1974. Plans for the meeting and publications have been made by the sub-committee appointed for this task (convener Dr. A. D. Wright) and advance publicity circulated. It was decided to institute a series of handbooks of fossils of various formations, under the general editorship of Dr. J. D. Hudson. The first volume will be 'Fossils of Wren's Nest, Dudley' by Dr. I. Strachan.

Besides being represented on the British National Committee for Geology, the Association is now represented on the Botany and Zoology subcommittees of the National Committee for Biology by Professor W. G. Chaloner and Professor M. R. House respectively. During the year, the Association applied for and was recognized by The Geological Society of London as a society, ten years' membership of which entitles new Fellows to exemption from the usual Admission Fee.

BALANCE SHEET AND ACCOUNTS FOR THE YEAR ENDING 31 DECEMBER 1972

BALANCE SHEET AS AT 31 DECEMBER 1972

1971	LIABILITIES	1971	ASSETS	
	Publications Reserve:		5 Office Equipment for Membership	
13,504	Balance at 31 December 1971	8,530-94	Treasurer	.
-4,973	Excess of Income 1972	3,939-92	Investments at cost:	.
			Chester City Loan	1,000-00
183	Subscriptions for 1973	12,470-86	£2000 Treasury 9% 1994	.
	in advance	273-01	£860 L.C.C. 6 $\frac{3}{4}$ % 1974	.
	Provision for printing		Kirkby U.D.C. Loan	1,000-00
	<i>Palaeontology</i> Vol. 15 as per		Industrial & Commercial Finance	
	Income and Expenditure A/c	13,320-95	Corp. £200 Loan Stock B 1974	195-25
2,744	Less Expenditure already incurred	6,720-95	£2000 Agricultural Mort. Corp.	
			9 $\frac{1}{4}$ % 1980-85	1,937-60
4,650	Provision for printing <i>Special Papers</i>		Wagon Finance Corp. Loan	2,000-00
	as per Income and Expenditure A/c	3,863-10	Equities Fund for Charities	3,047-07
	Less Expenditure already incurred	563-10	750 shares Foreign & Colonial	
			Inv. Trust	1,073-93
1,440	Royal Society Loan	3,300-00	4000 Income shares New Throg-	
—	Adelaide University Loan	1,300-00	morton Inv. Trust	1,116-86
1,555	Sundry Creditors:	505-05	450 shares New Court European	
	Advance payments for		Trust	450-00
	Special Papers	974-69		14,518-66
	Audit Fee	30-00	Sundry Debtors:	
			Authors for Offprints	536-21
			Income Tax refund due	176-00
				712-22
			Cash at Bank:	
			Deposit Account	4,372-54
			Current Account	5,815-19
				10,187-73
				25,453-61

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31 DECEMBER 1972

1971	EXPENDITURE	1971		INCOME	
	To provision for cost of publication of <i>Palaeontology</i> :			By Subscriptions for 1972	7,953.42
	Vol. 15 part 1	3,272.06		" " 1971	1,791.02
	part 2	3,356.85			
	part 3	3,300.00		Sales of <i>Palaeontology</i>	9,744.44
	part 4	3,300.00		Sales of Offprints	7,122.53
				Profit on Sales of Shares	329.69
				Interest received (gross):	367.88
				L.C.C. 6 $\frac{3}{4}$ % 1974	58.04
12,368	Add extra cost of Vol. 14 part 4	13,228.91		Wagon Finance Loan	155.23
		92.04		Westland Aircraft	15.00
			13,320.95	Charifund	258.35
2,508	To reprinting Vol. 1 and Index			Agricultural Mortgage	185.00
	To provision for cost of publication of <i>Special Papers</i> :			New Throgmorton Inv. Trust	97.50
	No. 10	1,458.40		Foreign & Col. Inv. Trust	21.93
	No. 11	3,300.00		Kirkby U.D.C.	67.50
				Chester City Loan	53.70
4,650	Less excess prov. for 8 and 9	4,758.40		I.C.F.C. 1972	50.00
		895.30		" 1974	20.00
			3,863.10	9% Treasury 1994	90.00
				Gratton Warehouses	13.13
				Deposit Account	88.22
	To Postage	181.96			1,173.60
	Stationery	173.24		Less holding charges	10.95
	Audit Fee	30.00			
	Circulars	716.84		By Donations	1,162.65
	Meetings	89.14		Special Papers Sales	896.00
	Honorarium to Membership			Sale of copy of Raup Film to BFI	3,276.99
	Treasurer's assistant	75.00		Miscellaneous Receipts	21.78
	Advertisements	188.51			60.69
	Storage of backstock	208.80			
	Insurance of backstock	85.31			
	Distribution of membership list	55.66			
	Membership other societies	19.31			
1,377	Depreciation of equipment	34.91			
			1,853.68		
-4,973	Excess of Income over Expenditure		3,939.92		
					22,982.65

L. R. M. Cocks, Deputy Treasurer

Report of the Auditors to the Members of the Palaeontological Association. We have examined the above balance sheet and annexed Income and Expenditure Account which in our opinion give respectively a true and fair view of the state of the Association's affairs as at 31 December 1972 and of its income and expenditure for the year ended on that date.

Sheffield

THORNTON, BAKER & Co.
Chartered Accountants, Auditors

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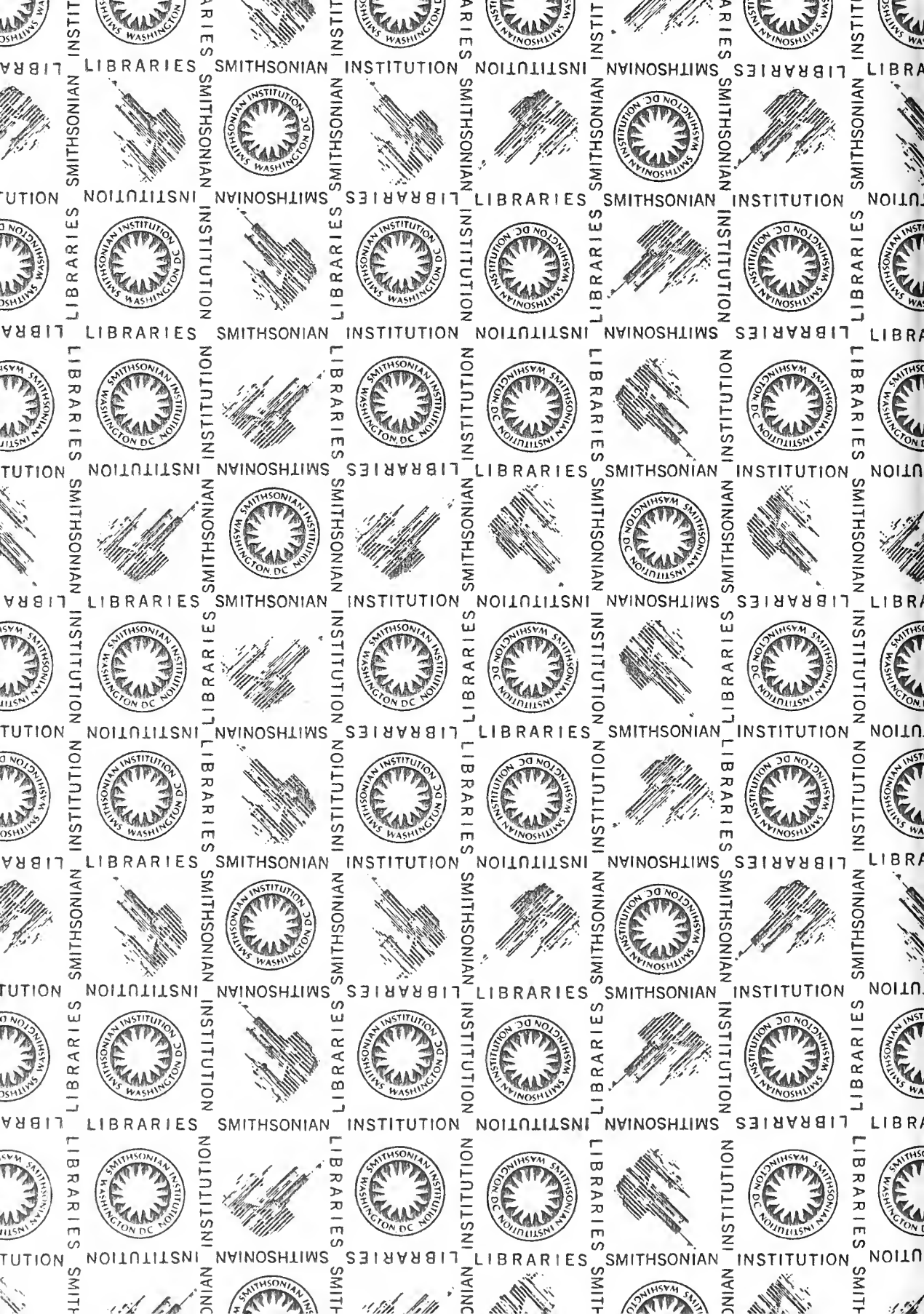
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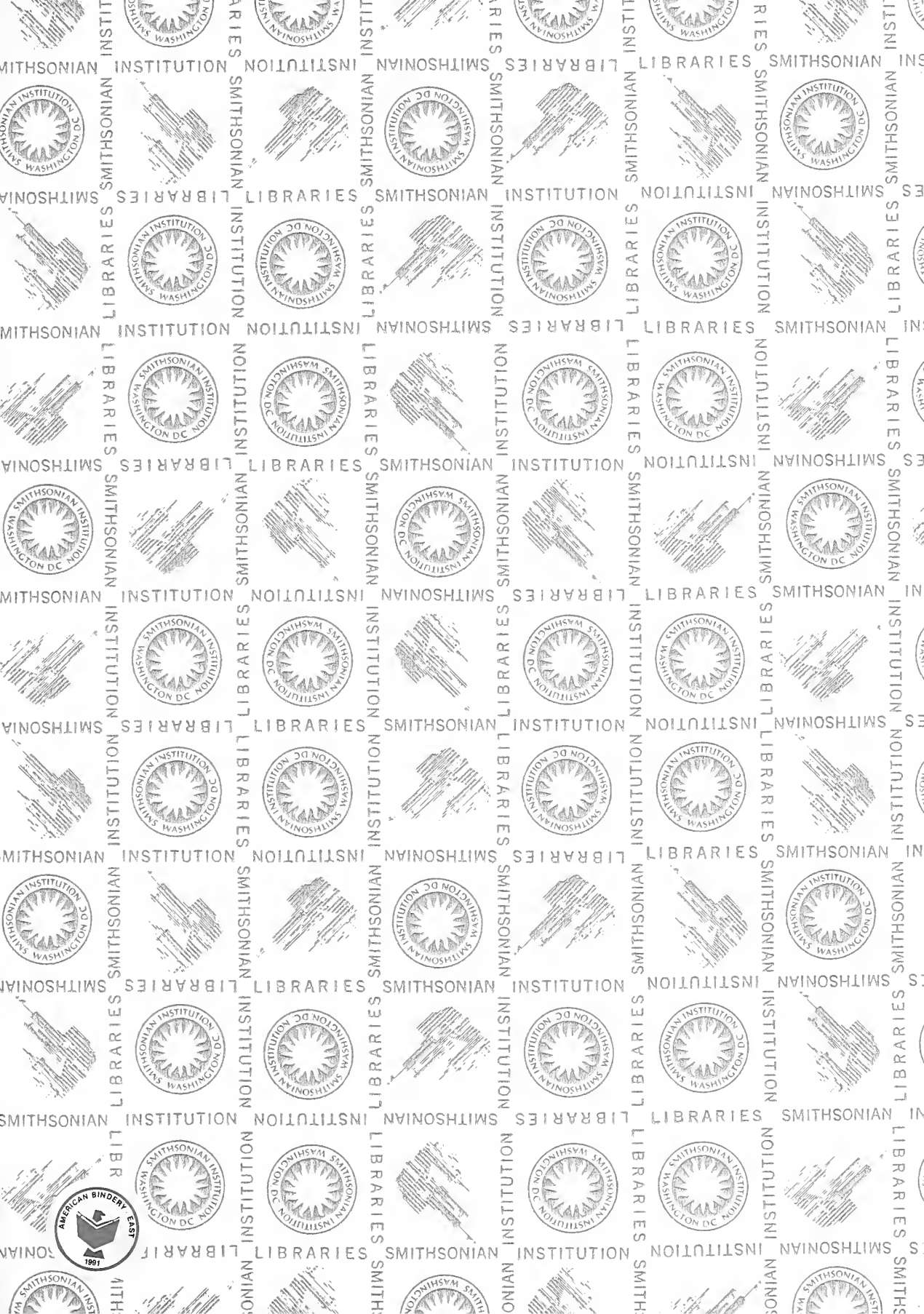
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