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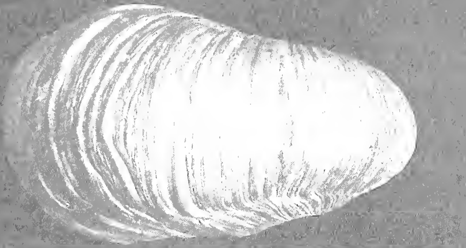

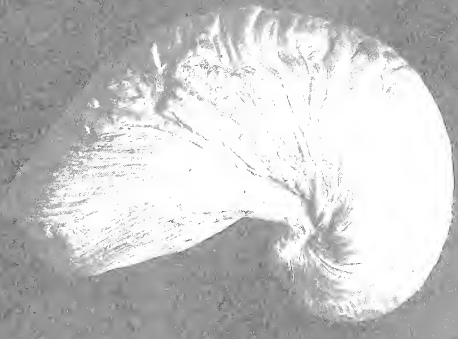

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Cover: The Lower Liassic (Jurassic) oyster *Gryphaea arcuata incurva* J. Sowerby, 1815, from Gloucestershire, England; known popularly as 'The Devil's Toenail'. Specimens in the National Museum of Wales.

MICRO-ORGANISMS FROM THE LATE PRECAMBRIAN NARSSÂRSSUK FORMATION, NORTH-WESTERN GREENLAND

by PAUL K. STROTHER, ANDREW H. KNOLL, *and* ELSO S. BARGHOORN

ABSTRACT. Carbonaceous cherts of the late Proterozoic (*c.* 700 Ma) Narssârssuk Formation, north-western Greenland, contain about twenty microfossil entities distributed in four discrete microbial associations and one allochthonous association. The associations are the preserved remnants of cyanobacterial communities that inhabited different environments within the intertidal and supratidal zones of a hypersaline embayment bordering an arid sabkha-like coast. The palaeoecological distributions of Narssârssuk microbes are comparable to those of other fossil and modern microbial mats from similar environmental settings, suggesting that the Proterozoic evolution of the cyanobacteria has been characterized by physiological as well as morphological conservatism. Environmental explanations for observed differences in Proterozoic fossil assemblages provide the proper null hypothesis against which hypotheses of evolutionary change in stromatolitic cyanobacteria must be tested. Five new taxa are described: *Avictuspirulina minuta* gen. et sp. nov., *Coleogleba auctifica* gen. et sp. nov., *Gyalosphaera fluitans* gen. et sp. nov., *Eosynechococcus thuleënsis* sp. nov., and *Oscillatoriopsis variabilis* sp. nov.

FOSSIL assemblages of planktonic micro-organisms in Upper Proterozoic sedimentary rocks clearly indicate successive morphologic innovations and diversity trends with time (Vidal and Knoll, in press); however, the Precambrian record of benthonic stromatolitic microbiotas shows little evidence of temporal increase in morphologic diversity or complexity. Indeed, although the empirical success of stromatolite-based biostratigraphic correlations would argue for changes in the microbial benthos with time, most of the variation observable in Proterozoic stromatolitic microbiotas is attributable to palaeoecological factors. The reasons for this have to do with both preservational biases in the Precambrian record and the nature of evolution in prokaryotes.

The bulk of our detailed knowledge of Precambrian benthonic assemblages has been derived from the study of carbonaceous cherts in petrographic thin section. Silicification has the advantages that three-dimensional spatial relationships are retained and structures are often preserved at an extremely fine scale (0·5 μm) of resolution. It has the disadvantage that the variety of environments recorded is limited. Proterozoic cherts fall into two general categories: apparently primary cherts associated with iron formation, and silicified beds, lenses, and nodules found in laminated carbonates and stromatolites. Fossiliferous cherts from iron formations primarily contain benthic microfloras dominated by the problematic prokaryotes *Gunflintia* Barghoorn and *Huroniospora* Barghoorn or the trichosphaeric bacterium *Eoastrion* Barghoorn (Barghoorn and Tyler 1965; Cloud 1965; Walter, Goode and Hall 1976; Knoll and Simonson 1981; see also Oehler 1977, for a discussion of silicified microbes from an exhalative oceanic rift environment), although allochthonous elements do occur (e.g. *Leptoteichos*, Knoll, Barghoorn and Awramik 1978). These microbiotas differ considerably from those preserved in stromatolitic carbonates. Two general types of *in situ* stromatolite-building associations are known from the Proterozoic record: those dominated by colonies of the mucilage-producing coccoid cyanobacterium *Eoentophysalis* and those containing densely interwoven populations of filamentous blue-greens. *In situ* benthonic microbes not responsible for mat accretion may also be preserved, as in certain associations here described. Allochthonous elements, including transported fragments of pre-existing mats and plankton, are also found in mat assemblages (Knoll 1982*a*).

[Palaeontology, Vol. 26, Part 1, 1983, pp. 1–32, pls. 1–6.]

In this paper, we describe a microbiota preserved in silicified carbonates of the late Proterozoic Narssârssuk Formation, north-western Greenland. All of the above-mentioned carbonate-facies fossil types, save ripped up mat clasts, are found within this sequence. Actually, four distinct microbial associations and one allochthonous assemblage representing a degree of habitat heterogeneity within the formation are preserved. These are comparable, in part, to both modern microbial communities in analogous depositional settings and to other Precambrian microfossil assemblages, thus, offering some insight into the distribution of cyanobacterial mat communities in time and space.

GEOLOGICAL SETTING AND AGE

The Thule Group is an Upper Proterozoic sedimentary sequence located in north-western Greenland between two structural highs, one south of Wolstenholme Fjord (76° 30′ N.) and the other in southern Prudhoe Land (approximately 78° N.; see text-fig. 1). The geology of the Thule region was outlined in 1959 by Kurtz and Wales, who divided the sequence into three formations: The Wolstenholme Quartzite (lowermost), the Danish Village Formation, and the Narssârssuk Formation. Davies, Krinsley and Nicol (1963) renamed the middle unit the Dundas Formation and, in addition, subdivided the Narssârssuk Formation into three members.

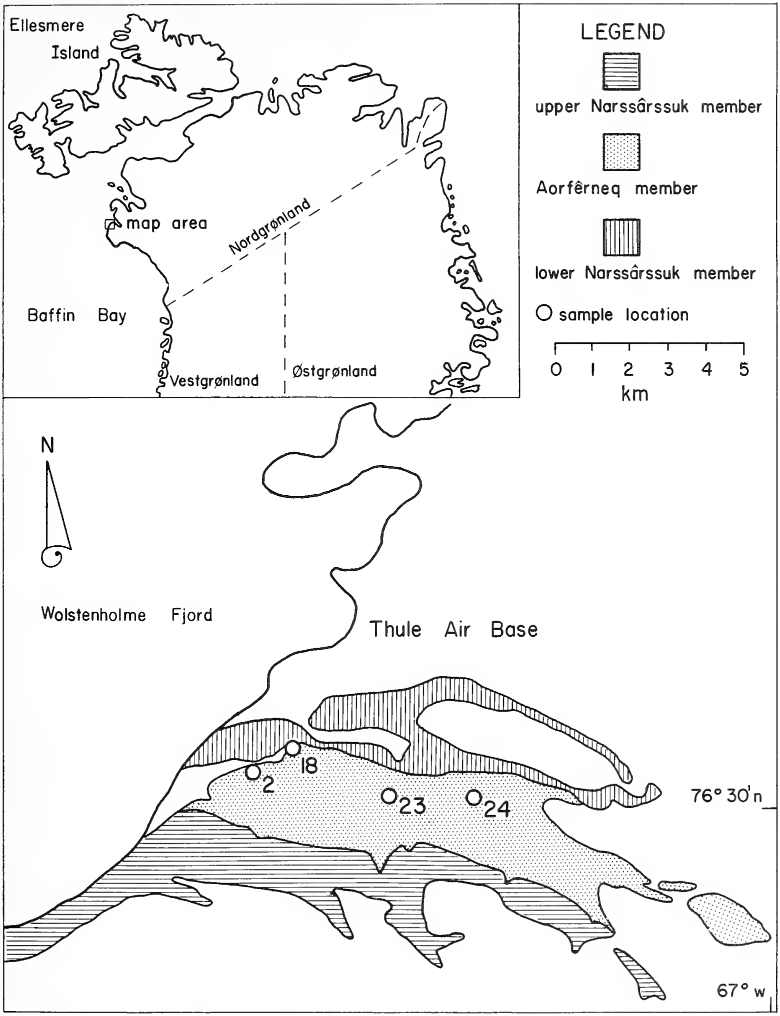
The Wolstenholme Quartzite is a 700 m unit consisting predominantly of white to grey quartz arenites, with subordinate intercalations of reddish sandstones near the base of the formation. Uppermost Wolstenholme beds grade into the dark shales and siltstones of the overlying Dundas Formation. The Dundas consists of approximately 730 m of organic-rich fine-grained detrital rocks with lighter (light-brown) units becoming more common in upper portions of the formation. Ripple marks, desiccation cracks, and load casts below thin sandstone intercalations indicate a near shore sedimentary environment, perhaps a lagoon or periodically flooded mud flat.

The youngest unit in the Thule Group, the Narssârssuk Formation, is characterized by a series of lithological cycles beginning with blocky limestones and grading upward through a succession of stromatolitic limestones and dolomites to thinly laminated dolomites capped by red siltstones. A limonitic erosional surface generally separates red beds from the overlying carbonates of the next cycle. The Lower and Upper Narssârssuk Members contain significant amounts of red siltstone; within the intervening Aorfêrneq Dolomite Member, such detrital beds are few and thin.

Multicycle sections of the Lower Narssârssuk Member record the repeated progradation of a sabkha-like plain across a protected hypersaline embayment which is similar in many respects to Mesozoic sabkha cycles of the Arab-Darb Formation of the Trucial Coast (Wood and Wolfe 1969). Lower Narssârssuk beds contain few sedimentary structures indicative of current movement. Microbially laminated carbonates are common, with low conical, apparently subtidal stromatolites (cf. *Conophyton* sp., see Hoffman 1976, for a paleoenvironmental analysis of this stromatolite type) in lower parts of the cycle giving way to flat, wavy cryptalgal laminites in overlying beds. Vuggy, gypsiferous units are associated with increasing clastic content in upper carbonates that grade into thinly bedded, organic rich shales and, ultimately, silty redbeds.

The Upper Narssârssuk Member is in many respects similar to the Lower, but contains a significantly greater percentage of detrital beds and also shows much more evidence of current activity. Cross-bedded calcareous sandstones often underlie the redbeds in the regressive cycle. Ripple marks are common, as are desiccation cracks in the red siltstones. Stromatolites in the Upper Narssârssuk Member differ from those of the Lower Narssârssuk, presumably in response to a stronger current regime. *Bicaulia*?-type columnar stromatolites were observed at one horizon, and oncolites at several others. Low relief domal stromatolites are also found in the Upper Narssârssuk.

Neither the Upper nor the Lower Narssârssuk Members contain more than rare, scattered patches of chert, and those that do occur contain no fossils. In contrast to this, the Aorfêrneq Dolomite Member contains several horizons of silicified microbial mats, some of which are abundantly fossiliferous. As discussed in more detail below, all cherts appear to be of early diagenetic origin, replacing pre-existing carbonates and permineralizing microbial peats. Although the



TEXT-FIG. 1. Locality map of the Narssârssuk Formation.

Aorfêrneq Member is predominantly dolomitic, thin red siltstone horizons confirm that this member, like the others, comprises a series of progradational cycles. The Aorfêrneq Dolomite differs from the other members in that broad carbonate tidal flats persisted for relatively long periods of time during its deposition. '*Cryptozoon*' type, laterally linked, hemispherical stromatolites are found in subtidal units while oölites attest to shoaling coastal environments. Wavy-laminated, low relief stromatolites are common, and in at least one locality, centimetre-scale mammilate stromatolites occur. Gypsum is common, both as growths disrupting pre-existing microbial laminae and as secondarily developed features in fractures. Although gypsum is a characteristic feature of the Aorfêrneq Dolomite, bedded gypsum horizons characteristic of some evaporitic environments are not found in this member.

The fossiliferous units of the Narssârssuk Formation, then, vary from subtidal to supratidal along the border of a protected embayment in an arid to semi-arid environment. A reasonable modern analogue is the west coast of the Arabian (Persian) Gulf in Abu Dhabi and elsewhere (Purser 1973; Kendall 1979). This provides an appropriate palaeoenvironmental context for the interpretation of Narssârssuk microbial associations.

In Prudhoe Land and the Wolstenholme Fjord region, sedimentary rocks of the Thule Group are cut by doleritic dykes and sills, several of which have been dated by K–Ar whole rock analyses (Dawes, Rex and Jepsen 1976). NW–SE trending dykes cutting the Dundas Formation yield a radiometric age of 676 ± 25 Ma. Similarly trending dykes cut the Narssârssuk Formation south of Wolstenholme Fjord, suggesting that the entire Thule Group is older than the date quoted. Palynomorphs recovered from the Dundas Formation indicate a late Riphean age (Vidal and Dawes 1980), and a single 'peteinosphaerid' (vandalosphaerid *sensu* Vidal 1981) acritarch found in lower Narssârssuk beds suggests an early Vendian age for this formation. Available evidence thus suggests that the Narssârssuk microbes lived during the early Vendian, approximately 700 Ma ago.

MICROFOSSIL ASSOCIATIONS

All samples discussed in this report were collected from the Aorfêrneq Member of the Narssârssuk Formation. Each locality received a locality number which is prefixed by 'KS 78-'. Four of our microfossil associations were restricted to unique localities, the *Gyalosphaera* association, however, was distributed among three separate localities, KS 78-2, KS 78-12, and KS 78-21. In addition, two of the associations, the *Eosynechococcus* and *Eomycetopsis*/*Siphonophycus* associations, occur together at only one locality, KS 78-23. These associations are referred to as '23U' and '23L', since they are derived from the upper and lower portions of the sample respectively. Additional letters suffixed to locality numbers refer to individual thin sections.

The Eosynechococcus *association* KS 78-23 [23U]

Locality KS 78-23, represented by a single chert sample from the middle portion of the Aorfêrneq Member, contains two quite distinct biological assemblages. The lower zone (Pl. 1, fig. 10, 23L) is dominated by vertically oriented filaments in a vuggy carbonate matrix and is capped by a zone of uniform carbonate grains which contains organic laminae but not fossils. The upper zone (Pl. 1, fig. 10, 23U), is a somewhat contorted, laminated siliceous layer containing a distinctive community dominated by a new species of *Eosynechococcus* Hofmann (1976). The basal portion of the upper zone is well preserved; however, subsequent layers are carbonate-rich and preservation is correspondingly variable. There is good evidence in this sample that silica emplacement occurred early during diagenesis, preserving the organisms in their growth positions.

The *Eosynechococcus* zone consists of about seven layers that range in thickness from 0·2 to 2·0 mm, each layer being defined by a kerogenous band at its base (Pl. 6, fig. 5). The layers are composed of equigranular carbonate and microcrystalline quartz (chert) in varying proportions. Carbonate crystals show dissolution surfaces, and void spaces within the carbonate layers are filled with fibrous quartz. The basal layer of the *Eosynechococcus* zone (Pl. 1, fig. 10) is composed entirely of microcrystalline quartz which has faithfully preserved organic structural detail at the cellular level. Fossil micro-organisms are embedded in a homogeneous, amorphous, light-brown organic matrix that does not reflect quartz grain boundaries.

Two discrete microfossil populations dominate this assemblage, a rod-shaped cyanobacterium, *Eosynechococcus thuleënsis* sp. nov. and a problematic globular spheroid informally designated 'spheroid type A'. The filamentous cyanobacteria *Tenuofilum septatum* Schopf and *Oscillatoriopsis variabilis* sp. nov. also occur, but they are not abundant ($< 1\%$ of the total assemblage). Approximately 1% of the assemblage consists of large spherical organisms which probably represent an allochthonous element. The relative and absolute frequencies of microfossils within the basal layer of zone 23U are as follows ($N = 387$):

	Relative frequency	Abundance
Eosynechococcus thuleënsis	0·64	$1{\cdot}6 \times 10^4/\text{cm}^3$
Spheroid type A	0·35	$9{\cdot}0 \times 10^3/\text{cm}^3$
Planktonic spheroids	0·01	$200/\text{cm}^3$
Filaments	0·01	—

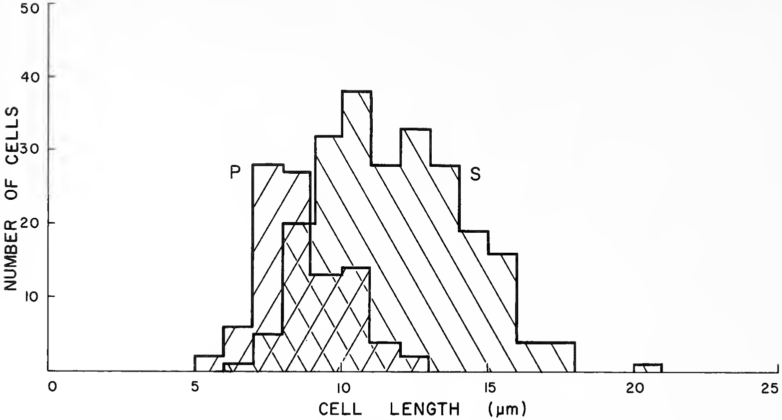
The total concentration of recognizable organisms within this zone is $2{\cdot}6 \times 10^4/\text{cm}^3$.

Cells of *Eosynechococcus thuleënsis* are usually preserved as straight or slightly curved rods with homogeneous contents that are similar in density to the surrounding organic matrix (Pl. 1, fig. 2). Some specimens exhibit dark, internal granules that are distributed along the long axis of the fossils rather than being condensed into discrete 'spots' as is common with certain Precambrian spheroids. The unilaminar walls of *E. thuleënsis* are uniform and smooth, suggesting that silicification has faithfully preserved the primary morphological features of the organism. Because the cells are never enclosed by concentric or co-parallel laminations that could be interpreted as sheaths, it is inferred that the living organisms did not have well-defined extracellular envelopes. Many *E. thuleënsis* cells are coated with exterior blebs of dense or vesicular organic matter (Pl. 1, figs. 4–6). These structures are probably artefacts of degradation. A degradational sequence runs from cells with a small number of attached blebs (Pl. 1, fig. 5) to clusters of small vesicles and blebs which correspond roughly to the original, elongate cell shape (Pl. 1, fig. 6). Similar structures are found attached to the codominant spheroid type A.

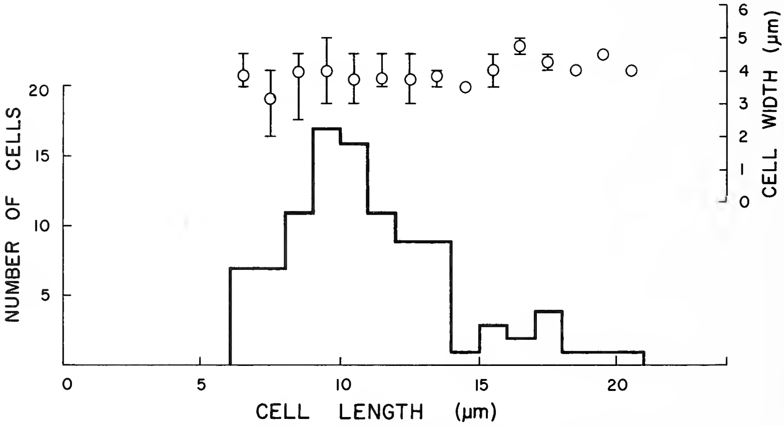
Many of the cells of *E. thuleënsis* are preserved as end-to-end pairs (Pl. 1, fig. 2) and it is this feature that permits elucidation of some growth characteristic of the original organism. Paired cells constitute 30% of the *E. thuleënsis* population ($N = 759$ from three thin sections). The mean length of paired cells is significantly less than that for solitary cells from the same population (text-fig. 2). In addition, the individual cells of a paired set are always approximately the same length. A sample population of forty-three paired sets of cells contained thirty-seven pairs (86%) whose lengths differed by 0·1 μm or less. The maximum difference between any two cells of a paired set was 0·4 μm. The total range in length of all cells of the population was 5 to 25 μm, therefore, paired sets of cells cannot be random associations of solitary cells. Rather, they must represent daughter cells which have remained attached end-to-end during diagenesis.

After dividing transversely, cells of *E. thuleënsis* grew by extension in length with no increase in girth (text-fig. 3). Therefore, cell width in *E. thuleënsis* is approximately constant and, consequently, cell length is proportional to volume.

The uniaxial growth of *E. thuleënsis* permits a more accurate assessment of cell size and increase than is possible with spherical cells. A detailed description of the size-frequency histogram for *E. thuleënsis* is helpful in confirming some of the assumptions about its life-history and ecology. For example, comparisons of paired sets of cells with solitary ones demonstrate that paired cells were derived by single transverse divisions of solitary cells (Strother 1980). The spatial distribution of the *E. thuleënsis* population permits the recognition of growth and development in this fossil form and indicates that the biotic association was of local benthonic derivation.



TEXT-FIG. 2. Length of paired (P) and solitary (S) cells in a population of *Eosynechococcus thuleënsis*.



TEXT-FIG. 3. Cell length vs. width of *Eosynechococcus thuleënsis*. Bar = range, circle = mean width.

Dominating the assemblage with *E. thuleënsis* is an enigmatic, irregularly shaped unicellular organism, spheroid type A (Pl. 1, fig. 3). Its cells are roughly spherical in outline, but cell shape is not uniform; often a spherical dark internal body is present. Cells do not exhibit any particular clustering habits that suggest growth patterns. The irregular envelope shape of spheroid type A suggests that it might be a degradational variant of *E. thuleënsis* which has lost its structural integrity; however, calculated surface areas (for cells of minimum, mean, and maximum size) show no correlation between sample populations of the two organisms and size-frequency histograms for the two populations differ considerably. In addition, distinct cell pairs are absent from spheroid type A populations. The morphology of spheroid type A reveals little of its affinities to any known micro-organisms, extant or fossil.

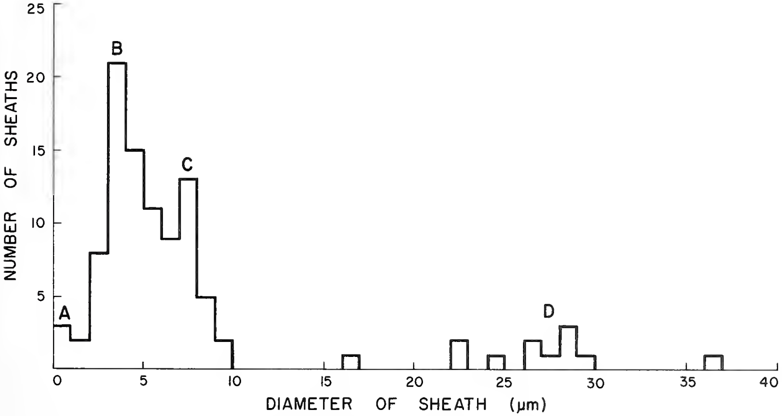
Ecologically, it appears that *E. thuleënsis*, spheroid type A, and the two co-occurring filaments lived as microbenthos in an area of periodic carbonate precipitation. There is little sedimentological or micropalaeontological evidence to suggest that zone 23U was stromatolitic in the sense of active trapping and binding or precipitation by microbes. More likely, this zone represents the passive trapping of surficial micro-organisms in abiogenic carbonates that were subsequently rapidly replaced by silica.

Eomycetopsis/Siphonophycus *association* KS 78-23 [23L]

Underlying the basal layer of the *Eosynechococcus* (23U) assemblage with profound micro-unconformity is a silicified filamentous assemblage named for its principal components. The texture of the filamentous zone is vuggy with densely clustered, vertically aligned, filaments (Pl. 1, fig. 9) interwoven between ovoid to rectangular voids that have been secondarily mineralized. Because they do not disrupt contiguous clusters of filaments, the voids are considered to be primary textural features (Pl. 6, fig. 5). Some filaments have served as nuclei for carbonate crystallization, retaining blocky crystals in their lumens despite general silicification (Pl. 1, fig. 7).

Most microfossils in the filamentous assemblage are empty cylindrical sheaths, although small pockets of spherical cells are sporadically distributed throughout the zone. Most spherical cells belong to *Sphaerophycus parvum* Schopf; however, occasional clusters of *Gloeodiniopsis* cf. *lamellosa* (Schopf) Knoll and Golubic are preserved (Pl. 5, fig. 7).

Filamentous sheaths can be divided into four taxa based on size distributions and sheath morphology. The smallest filaments are assigned to *Tenuofilum septatum* Schopf (text-fig. 4A). These range in diameter from 0·5 to 1·5 μm and consist of dark-brown, condensed strands of poorly preserved granular organic matter. *Eomycetopsis robusta* (Schopf) Knoll and Golubic is



TEXT-FIG. 4. Diameter of filamentous sheaths within KS78-23[L]. Letters mark modes of the four form taxa: A = *Tenuofilum*, B = *Eomycetopsis*, C = *Siphonophycus kestron*, D = *Siphonophycus* sp.

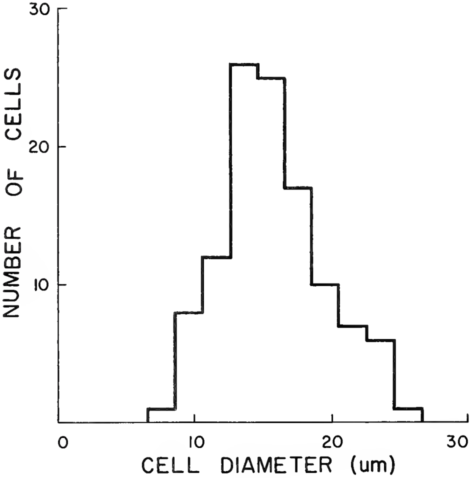
the most common sheath type (text-fig. 4B). Preservation is generally poor and sheath walls are usually composed of dark-brown, granular organic matter. The diameter ranges from over 3 μm to perhaps 6 μm, but at its maximum diameter, *E. robusta* cannot be distinguished with certainty from *Siphonophycus kestron* Schopf, the next larger sheath type in the distribution (text-fig. 4C). Poorly preserved specimens of *S. kestron* have granular walls, but well-preserved ones have discrete, 1 μm thick sheaths composed of light-brown, homogeneous organic matter. The largest sheaths in the assemblage (text-fig. 4D) are comparable to *Siphonophycus* sp. Oehler (1978) in size (20 to 40 μm), but they differ in occasionally containing the remains of internal trichomes (Pl. 1, fig. 8).

The retention of vertical filament orientations, the closely associated carbonate precipitation, and the position of vertical filament tufts as pillars between large voids suggest that this zone is best interpreted as a fossilized tufa deposit (Monty 1976; Hardie and Ginsburg 1977).

The Gyalosphaera *association* KS 78-2/12/21

These three localities from the middle of the Aorfêrneq Member of the Narssârssuk Formation contain microbial assemblages that are indistinguishable from each other and so are discussed as a single recurrent unit. Well-preserved microfossils are found in sinous 2 to 10 cm thick chert bands which are interbedded with fenestrate stromatolitic carbonate and gypsum (Pl. 6, figs. 1, 2). The carbonate portions of these samples are kerogen-rich, but unfossiliferous. Although some recrystallization of carbonate has occurred, certain features of primary mat texture are evident. The abundance of spherical colonies throughout the samples indicates minimal compaction during diagenesis for much of the chert. Euhedral carbonate rhombs with dissolution surfaces and some secondary fluorite crystals are scattered throughout the siliceous zone.

Two spheroidal organic structures dominate the biotic assemblage in these samples. The first is designated 'spheroid type B'. This organism is always faintly preserved because the density of organic matter within the organism is close to the matrix density. High contrast images (Pl. 2, figs. 1–3) reveal a spherical unicellular organism averaging 15·7 μm ($N = 113$) in diameter (text-fig. 5). Cell contents are homogeneous, though generally more dense centripetally. Spheroid type



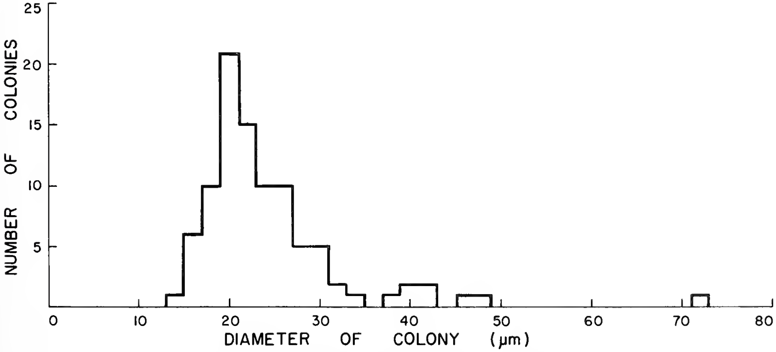
TEXT-FIG. 5. Diameter of a population of Spheroid type B.

B lacks any indication of lamination, either in the form of envelope or intracellular differentiation. Rare specimens of spheroid type B are lobed to elongate (Pl. 2, fig. 2). We have not observed examples with deep median furrows, but shallow furrows on elongate specimens imply a division mechanism. The size-frequency distribution for spheroid type B is leptokurtic and slightly positively skewed. Such a distribution is similar to populations of fossil algal unicells. Spheroid type B constitutes 79% of the organisms in the *Gyalosphaera* association.

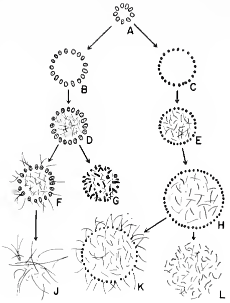
A second spherical structure, *Gyalosphaera*, constitutes 20% of the assemblage, with the remaining taxa comprising less than 1% of the total. *Gyalosphaera* is a spherical colony composed of numerous individual cells which lie at the surface of the sphere. The colony interior shows no evidence of cellular differentiation but is composed of condensed heterogeneous organic debris (Pl. 2, figs. 4–8). Individual cells, or spherules, appear as small (1 to 2 μm) vesicles, or they may be condensed to dark, oblate to polyhedral blebs (Pl. 2, figs. 6–8). Surficial views of large specimens reveal that the spherules are uniformly distributed (Pl. 2, fig. 5). Estimates of number of spherules per colony range from 200 to 4,500 cells. Individual estimates do not correspond to values of 2^n, therefore cell division within colonies was probably not rigidly co-ordinated, and the total number of spherules per colony was indeterminate. Clues to the reproduction of *Gyalosphaera* are lacking. *Gyalosphaera* colonies are never found associated with an encompassing envelope.

Gyalosphaera exhibits gradational variation in size and morphology. Increase in size is expected to reflect colony growth, consequently the histogram for *Gyalosphaera* (text-fig. 6) demonstrates the likelihood that both young and old members of populations have been preserved. Morphologic variation can be biological or diagenetic in origin. As illustrated in text-fig. 7, within *Gyalosphaera* populations, variation is expressed as a change in internal structure from uniform to heterogeneous (e.g. B to D), by the appearance of filamentous structures (F, J, K), in differences in spherule size (B line vs. C line), by spherule loss (J and L), and by coalification and degradation (G).

One specimen of *Gyalosphaera* cf. *fluitans* from slide KS 78-23/f has retained both the surficial spherule pattern and some of the interior structure. The spherules are grouped in sets of four pairs which are orthogonal. In median view (Pl. 2, fig. 11) some spherules can be seen to be attached to bifurcating stalks. This colony organization is similar to that found in the extant cyanobacterial genus, *Gomphosphaeria*, although the size of *Gyalosphaera* cf. *fluitans* is smaller than that of most *Gomphosphaeria* species. In general aspect, *Gyalosphaera* resembles the cyanobacterial genera



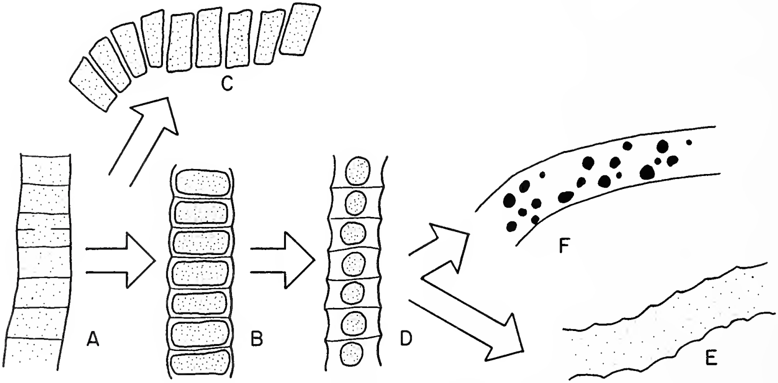
TEXT-FIG. 6. Colony diameter in *Gyalosphaera fluitans*.



TEXT-FIG. 7. Variation in colony form in *Gyalosphaera fluitans*. A–L, see text for explanation.

Gomphosphaeria and *Coelosphaerium* both of which consist of a surficial layer of cells defining a spherical colony. *Coelosphaerium* has an extracellular envelope of mucilage and colonies divide by fragmentation, neither of which has been observed in *Gyalosphaera* populations. In spite of these differences, a general morphological correspondence between *Gyalosphaera* and modern cyanobacteria of the *Gomphosphaeria*/*Coelosphaerium* type seems inescapable. This comparison, coupled with the sporadic distribution of colonies as seen in thin section, suggests that *Gyalosphaera* was a member of the plankton in the restricted waters of the Narssârssuk embayment.

A number of other, less abundant taxa are preserved within this assemblage. The most common filament is *Oscillatoriopsis variabilis* sp. nov. In this cyanobacterium, trichome width ranges from 14 to 16 μm, cell length is about 8 μm, and trichome length reaches 540 μm. Primarily on the basis of cell size, a number of morphological variations, mostly degradational, were recognized as belonging to the same organism (text-fig. 8). Preservation grades from extremely well-preserved trichomes with homogeneous cell contents (Pl. 3, fig. 3; text-fig. 8A) to well-preserved trichomes with condensed contents (Pl. 3, figs. 5, 6, 11; text-fig. 8B, D) to empty trichomes or sheaths with



TEXT-FIG. 8. Degradational forms in *Oscillatoriopsis variabilis*. A–F, see text for explanation.

granular contents (Pl. 3, fig. 7; text-fig. 8E, F). In some specimens, the cell walls have decomposed leaving behind detached cells (Pl. 3, fig. 4; text-fig. 8C). The spool-shaped cells illustrated in Plate 3, fig. 6 and text-fig. 8 correspond to forms from the Bitter Springs and Belcher Islands biotas given the generic name *Halythrix* Schopf (Schopf 1968; Hofmann 1976). Much of this morphological variation is explained by either cell wall collapse (cytorrhysis) or protoplast shrinkage (plasmolysis) due to osmotic change during the early stages of degradation and silicification. *O. variabilis* is sporadically distributed in the sample suites from localities KS 78-2, 12, and 21, and individuals do not show preferential orientation relative to bedding. These facts, as well as the absence of evidence for extracellular sheath or mucilage production, suggest that *O. variabilis* cannot be considered as a major builder of the mats in which it is found.

Similarly, other filaments and unicells found in this assemblage are sporadically distributed; the actual organism or organisms responsible for mat accretion in this environment remain unknown. Post-mortem degradation must have proceeded quite effectively, leaving the preserved biota as scattered remnants of the original community. Thus, the palaeoecological interpretations that can be drawn for other microfossil associations in this formation and others (e.g. Knoll 1982*a*, 1982*b*) based on the spatial distribution of populations are difficult to apply in this case. Mineralogical evidence points toward a supratidal depositional environment; biotic evidence indicates an immediate environment of deposition which was plankton supporting. It is possible that *Gyalosphaera* association was a puddle-dwelling community within a supratidal zone.

Two species of *Eosynechococcus* occur as rare components of the *Gyalosphaera* assemblage. The more common of these is *E. thuleënsis*, found most often in carbonate-rich portions of the chert. Nowhere in this assemblage, however, is *E. thuleënsis* so extensively developed as it is in the *Eosynechococcus* association. The second species of *Eosynechococcus* found in association with *Gyalosphaera* is *E. amadeus* Knoll and Golubic (1979) (Pl. 3, figs. 8, 10), originally described from the Bitter Springs Formation. The similarity in size, shape, and clustering habit between the Bitter Springs and Narssârssuk *E. amadeus* populations (Pl. 3, fig. 8) are among the most striking yet observed in Precambrian palaeontology. Other chroococcalean unicells that occur in the *Gyalosphaera* association include *Sphaerophycus parvum* Schopf; small (2 by 3 μm) paired, ensheathed coccoid cells; and large (15 to 16 μm in diameter) poorly preserved dyads and tetrads (Pl. 4, fig. 1).

Two other filamentous organisms also occur as rare elements in the *Gyalosphaera* association. The first is an *Oscillatoriopsis* sp. which has a trichome width of 8 μm and a cell length of 10 to 12 μm (Pl. 3, fig. 7). Too few specimens have been found to characterize this fossil at the specific level; however, the preservation of internal structure is similar to that in *O. variabilis*. The second is a small spiral trichome found in association with large *Gyalosphaera* colonies or as isolated individuals scattered throughout the fossiliferous horizons. The trichome is 0·8 μm wide, non-septate, and coiled into a loose spiral 5 to 9 μm in diameter. This form is new to Precambrian paleobotany and is placed in the new genus, *Avictuspirulina*, based on morphological congruence with the extant genus, *Spirulina* Turpin em. Gardner (Pl. 3, fig. 9).

The Eoentophysalis *association* KS 78-18

Distinctive, mamillate stromatolites, in part silicified, occur in the lowermost beds of the Aorfêrneq Dolomite Member exposed at an abandoned NIKE site near Thule Air Force Base. The stromatolites (Pl. 6, figs. 3, 4) are centimetre-scale, laterally linked hemispheroids (LLH-type of Logan, Rezak and Ginsburg 1964) similar in morphology to mats accreting in modern intertidal zones bordering protected embayments in Abu Dhabi and the Bahamas (Golubic and Hofmann 1976). The modern stromatolites are built by colonies of the gregarious, mucilage-producing coccoid cyanobacterium *Entophysalis*, and it is clear from *in situ* microfossils preserved in silicified portions of the Narssârssuk structures that these were built by morphologically comparable organisms assignable to the genus *Eoentophysalis* Hofmann (1976).

Eoentophysalis is characterized by small (< 10 μm) cells that divide in three planes to form dense aggregates of monads, dyads, and tetrads embedded in a common mucilage or encompassed by common extracellular envelopes (Pl. 4, fig. 3). Indeed, the extracellular envelopes, which often retain a record of cell-division patterns, are more resistant to post-mortem degradation than are the cells *per se* and may constitute the bulk of the preserved microfossil population (Golubic and Hofmann 1976; Knoll and Golubic 1979). As in modern *Entophysalis* colonies, *Eoentophysalis* aggregates in the Narssârssuk Formation vary in structure from palisade-like arrays (Pl. 4, fig. 7), to globular clusters (Pl. 4, figs. 4–6), to loosely aggregated, irregular groups of cells (Pl. 4, fig. 8). The latter type is the most common cluster arrangement in the fossil populations; individuals (cells or unit envelopes) per cluster range from ten or a few tens to several hundred. Some aggregates contain well-preserved individuals on the cluster periphery with degraded envelopes or amorphous organic matter in the interior. Lack of mineralogical difference between the exterior portions of clusters suggests that this feature is degradational rather than mineralogically produced. Thus, cells grew centrifugally, leaving behind a degraded mucilaginous centre, a pattern common to both modern and fossil entophysalid cyanobacteria (Golubic and Hofmann 1976).

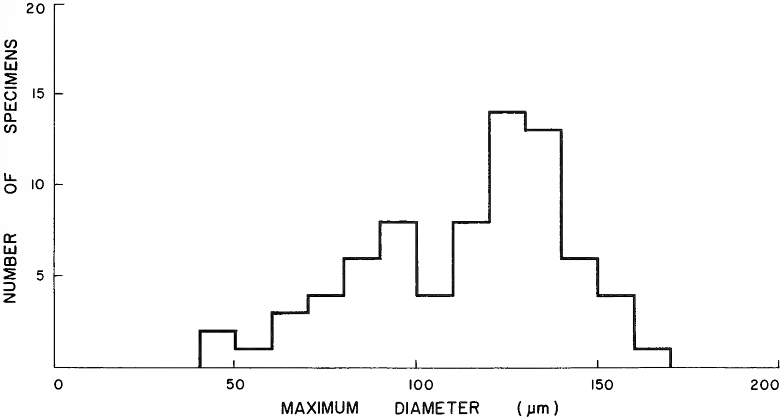
Narssârssuk *Eoentophysalis* individuals are spherical to ellipsoidal and range from 2·5 to 9·0 μm in maximum diameter. Thus, at the lower end of the size range, some populations closely resemble populations of *S. parvum* Schopf (see Knoll and Golubic 1979). Certainly, the types of these two taxa represent different cyanobacteria, but populations of small individuals within *Eoentophysalis* mats that are assigned to *S. parvum* may be biological and/or degradational variants of *Eoentophysalis*. This appears to be the case, in part, in the Narssârssuk Formation; however, we do not wish to extend this interpretation to other formations that contain *Eoentophysalis* and *S. parvum* in intimate association, not having seen the necessary materials in thin section.

Cell contents of Narssârssuk *Eoentophysalis* vary from uniformly dense interiors (Pl. 4, fig. 7) with minimal sheath retention to clear or very lightly stained interiors (Pl. 4, figs. 3, 8). Most of the various degradational forms of individual cells correspond to the '*capsulata*' form of *E. belcherensis* Hofmann (1976). Cell contents are not condensed to dark 'spots', but, rather, degradation has caused either loss of contents with retention of the exterior envelope or uniform condensation of the entire cell. *Eoentophysalis* from the KS 78-18 site does not form the differentially pigmented laminae illustrated in Pl. 4 of Hofmann (1976). The other salient features of *E. belcherensis* are present, however, thus the designation *Eoentophysalis* cf. *belcherensis* is appropriate.

Scattered throughout the preserved entophysalidaceae populations is an organism that is most likely an allochthonous element of the assemblage. *Coleogleba auctifica* gen. nov., sp. nov. is a large, spherical to globose colonial cyanobacterium enclosed within an extensive and well-defined mucilaginous envelope. Colony diameters range from 40 to 180 μm (text-fig. 9). Individual cells (spherules) within colonies are quite small usually 1 to 2 μm, and may be preserved as vesicles (Pl. 5, fig. 1) or, more commonly, as spherical granules of condensed organic matter (Pl. 5, figs. 2, 3). Individuals are distributed uniformly throughout the colony in an amorphous organic matrix. Surrounding sheath material is often laminated in larger specimens (Pl. 5, fig. 3), although smaller colonies may lack extensive extracellular mucilage (Pl. 5, fig. 1). The ensheathing material ranges from amorphous, dark, laminated envelopes (Pl. 5, fig. 3) to light coloured amorphous organic matter containing embedded spherules (Pl. 5, fig. 2).

A population of seventy-four *C. auctifica* colonies distributed along a single bedding plane was measured for maximum diameter and the corresponding histogram plotted in text-fig. 9. The distribution is left-skewed and unimodal with a mean of 114 μm. The shape of the histogram suggests colony replication characterized by peripheral growth of daughter colonies that remain attached to the parent colony. In such a situation, mature colonies do not significantly reduce their diameter during division, and a skewed size distribution results.

In the salient aspects of its colony morphology and divisional pattern, *Coleogleba* closely resembles species of the extant cyanobacterial genus *Microcystis* Kützing, although *Microcystis* colonies do not always retain the tight spheroidal organization exhibited by the fossils. Modern *Microcystis* populations most often occur as plankton in freshwater lakes, but Geitler (1932) does discuss species living as microbenthos in sandy intertidal zones (*M. reinboldi*), as plankton in littoral salt-water puddles (*M. litoralis*), and as plankton in standing water bodies of varying salinities (several species). The distribution of *Coleogleba* within the *Eoentophysalis* stromatolites suggests that it, too, lived as plankton within the Narssârssuk embayment or in local evanescent ponds. *Coleogleba* colonies are, in so far as preservation allows us to comment, restricted to the *Eoentophysalis* association. The ability of entophysalid buildups to pond water in coastal environments has been documented for the Recent (this occurs at Hamelin Pool, Shark Bay, Western Australia) and suggested for other fossiliferous Precambrian formations (Knoll and Golubic 1979); it may be that *Coleogleba* populations thrived in such short-lived, localized habitats within the Narssârssuk intertidal zone.



TEXT-FIG. 9. Colony diameter of *Coleogleba auctifica*.

Poorly preserved filaments are found scattered throughout the silicified *Eoentophysalis* horizons. Almost all are sheaths, of which *Eomycetopsis* is the most common type. Although filaments intertwine, they do not show the preferred orientation that might be expected if they represented *in situ* mat builders. Sheaths of *Siphonophycus*, occasionally containing condensed trichomes, are also found in organic-rich portions of the chert. Only short lengths of these thicker tubes are preserved and, again, no preferred orientation is observed.

Various coccoid cells are common in this association. Several clusters of *Gloeodiniopsis* cf. *lamellosa* with multilaminate, thick-walled sheaths and diameters approaching 20 μm are found (Pl. 5, fig. 6), and one cluster of coccoid cells (Pl. 5, fig. 5) is referable to the genus *Tetraphycus* Oehler (1978). The latter population contains planar tetrads of cells approximately 5 μm in diameter. These fossils differ from other species of *Tetraphycus* by the differentiation of their interior cross walls and exterior envelope. Cell (sheath?) cross walls are smooth, whereas the external envelope is punctate. Such a pattern may be degradational, although too few specimens were located to assess this properly.

KS 78-24 *association*

In one horizon from the lower middle Aorfêrneq Dolomite Member, singularly spheroidal chert nodules have replaced anhydritic laminated dolomites. The microbiota of these nodules consists of sporadically and relatively poorly preserved unicells. Additionally, the nodules preserve 'chicken wire' structures of anhydrite crystals clusters replaced by silica (Pl. 6, fig. 6). Comparable sedimentary features are known to occur in supratidal mats of the Arabian (Persian) Gulf (Wood and Wolfe 1969; Shearman 1978) and provide a unique clue to the palaeoenvironmental position of this sample. *S. parvum* and similarly simple spherical unicells are the most common microfossil types. They often exhibit various stages of degradation, including the condensation of internal granular, carbonized organic matter. A single occurrence of *Gloeodiniopsis* cf. *lamellosa* is similar to that illustrated in Pl. 5, fig. 6, and a second ensheathed chroococcalean cyanobacterium is shown in Pl. 4, fig. 2. Specimens of *Gyalosphaera* also occur, as do scattered carbonate infilled spheres that form clusters of poorly preserved dark, organic polygons (Pl. 5, fig. 4). Hofmann (1976, Pl. 3, figs. 8, 9) found similar fossils in the Kasegalik and McLeary Formations in Canada which he interpreted as acritarchs based on their polygonal shapes. Our specimens appear polygonal due to the inclusion of carbonate in the cell lumens, and it may be suggested that similar non-biological factors determined the morphology of the Belcher Island samples.

Summary of microfossil associations

The distributions and relative abundance estimates of the nineteen microfossil entities found in the Narssârssuk Formation are listed in Table 1. As discussed above, four well-defined microbial associations and one allochthonous assemblage are evident: a filamentous tufa association dominated by sheaths of filamentous cyanobacteria, a non-stromatolitic association dominated by *E. thuleënsis*, an entophysalidacean mat community with associated puddle-dwelling cyanobacteria,

	TAXON	KS78-23L	KS78-23U	KS78-2·12·21	KS78-18	KS78-24
SPHERES · COLONIES	*Gyalosphaera fluitans* n.g., n. sp.		R	A		
	Coleogleba auctifica n.g., n. sp.				C	R
	Tetraphycus sp.				R	
	Sphaerophycus parvum Schopf	R		R	A	R
	Eosynechococcus thuleënsis n. sp.		A	R		
	Eosynechococcus amadeus Knoll and Golubic			R		
	Eoentophysalis cf. *belcherensis* Hofmann				A	
	Myxococcoides sp.					R
	Gloeodiniopsis cf. *lamellosa* Schopf em. Knoll and Golubic	R				R
	Chroococcoid Type A			R		
	Chroococcoid Type B					R
	Spheroid Type A		A			
	Spheroid Type B		R	A		
FILAMENTS	*Siphonophycus* sp.	C				
	Siphonophycus kestron Schopf	C			R	
	Oscillatoriopsis variabilis n. sp.		+	C		
	Eomycetopsis robusta Schopf em. Knoll and Golubic	A			R	R
	Tenuofilum septatum Schopf	R	R			
	Avictuspirulina minuta n.g., n.sp.			R		

TABLE 1. Distribution of Taxa with the Narssârssuk Formation. A = abundant (> 30%). C = common (30—1%), R = rare (< 1%), + = present in a single occurrence. Values are estimates and are, therefore, not quantitative.

an assemblage containing oscillatorian filaments and allochthonous colonial cyanobacteria, and an allochthonous assemblage containing mostly degraded spherical cells. No single association contains more than eight taxa, and in each case, one or two blue-greens completely dominate the preserved biota. The limited taxonomic overlap among associations is also clear from Table 1; no one species is listed as being abundant in more than a single association, although about half are found as rare elements of two or more associations.

The preserved biotas represent the degradation resistant residue of microbial communities distributed across the broad carbonate tidal flats of the Narssârssuk coast. Tufa-encased fossils would appear to have inhabited uppermost intertidal to supratidal habitats, as did the poorly preserved cells found with 'chicken wire' structures in locality KS 78-24. The mamillate entophysalidacean mats grew in the intertidal zone, while transient puddles of water dammed by the accreting stromatolites harboured a distinctive cyanobacterial population. The *Gyalosphaera* association (KS 78-2/12/21) is most difficult to place environmentally, but the combination of its sedimentological setting within the tidal flat zone, the presence of small nobs of disruptive calcium sulfate and fluorite within the microbially laminated dolomite, and the abundance of probable planktonic elements in the preserved assemblage suggests either a frequently flooded position within the intertidal zone or a ponded area higher in the tidal flat range.

DISCUSSION

As discussed above, sedimentological considerations suggest that the Narssârssuk Formation can, in general, be understood in terms of modern and coastal environments such as those bordering protected lagoons of the Arabian (Persian) Gulf. In Abu Dhabi, various microbial mat communities inhabit the broad tidal zone between the Khoral Bazam, a highly saline lagoon, and the prograding sabkha plain to the landward (Kendall and Skipwith 1968). Microbially laminated 'biscuits' built by the filamentous cyanobacterium *Phormidium hendersonii* Howe actually occur subtidally, and those give way sequentially to *Entophysalis*-built mamillate mats, flat mats dominated by *Microcoleus chthonoplastes* Thuret, and 'pinnacle' mats characterized by *Schizothrix splendida* Golubic as one ascends the intertidal zone (Golubic 1976). Park (1977) has discussed this microbial community zonation and suggested that the frequency and duration of wetting, itself a consequence of both tidal oscillations and evaporation rates, exerts a primary control on community distribution. In broad pattern, individual microbial associations occupy discrete zones running parallel to the shore-line, but this distribution can be complicated considerably by the presence of pools, channels, and puddles (Golubic 1976; Knoll and Golubic 1979; see also figure 7-D of Kendall and Skipwith 1968, p. 1050).

The *Eoentophysalis* association of the Narssârssuk Formation provides the best biological point of comparison between the modern and ancient environments. In terms of microbial morphologies, taxonomy, morphology of associated stromatolites, and position within the carbonate intertidal zone, the Greenland example appears to be strikingly similar to the modern. Other Narssârssuk assemblages can be related to the modern model only in more general terms, but it does appear that position along the subtidal to supratidal gradiant, complicated by ponding, controlled microbial distribution.

Entophysalid-dominated mat associations have been reported from a number of Proterozoic formations. The oldest such biota comes from approximately 2,000 m.y. old cherts of the Kasegalik and McLeary formations, Belcher Islands, Canada (Hofmann 1976) and, like the Narssârssuk occurrence, this Early Proterozoic association is strikingly similar to modern entophysalid mats in both biology and inferred environmental setting (Golubic and Hofmann 1976). Younger *Eoentophysalis*-dominated assemblages have been reported from the 1,500 m.y. Amelia Dolomite, Australia (Muir 1976), the slightly younger Balbirini Dolomite, also of Australia (Oehler 1978), the 1,400–1,500 m.y. old Gaoyuzhuang Formation, China (Zhang 1981), the 1,200 m.y. old Dismal Lakes Group, District of Mackenzie, NWT, Canada (Horodyski and Donaldson 1980), and the 750–790 m.y. Bitter Springs Formation, Australia (Knoll and Golubic 1979). Environmental settings appear to be comparable in all cases, documenting the rather remarkable persistence of a unique community-type in a single environment throughout some 2,000 m.y. of earth history.

Filaments found within the Narssârssuk *Eomycetopsis/Siphonophycus* association are widely distributed in Proterozoic stromatolitic microbiotas, but the evolutionary or palaeoecological import of this observation is equivocal because the taxa in question—*Eomycetopsis*, *Syphonophycus*, and *Tenuofilum*—are form genera that in all likelihood were produced by several types of cyanobacteria. Certainly, the filaments of the Narssârssuk association are, to the best of our knowledge, unique among described Proterozoic microfossils in their preservation within a silicified supratidal tufa.

The dominant organisms in the other Narssârssuk associations, *Eosynechococcus thuleënsis*, *Gyalosphaera fluitans*, and *Oscillatoriopsis variabilis*, are sufficiently different from previously described microfossils to preclude meaningful palaeoecological comparisons.

CONCLUSIONS

The importance of environmental setting over age as a major theme in the interpretation of Proterozoic microbial mat assemblages was introduced by Hofmann (1976) and expanded by several other workers (e.g. Peat *et al.* 1978; Knoll and Golubic 1979; Knoll and Simonson 1981). Indeed, given available evidence, one is hard pressed to make a convincing case for either major morphological evolution in the cyanobacteria or increasing ecosystem complexity during the Proterozoic, except, perhaps, for the introduction of colonial planktonic cyanobacteria in the late Riphean. More taxa are known from younger Proterozoic sediments; however, it is clear that in terms of environments the younger Proterozoic is much better sampled than the earlier part of the eon (see Schopf 1977). In cases where the biology of a single environmental setting can be traced throughout most of the Proterozoic, e.g. *Eoentophysalis* mats, little evidence of progressive morphological or ecosystem change is evident.

Care must be exercised in extrapolating records of microbial species diversity based on cumulative tabulations of individual deposits. Evidence from the Aorfêrneq Dolomite Member of the Narssârssuk Formation, the Bitter Springs Formation (Knoll and Golubic 1979; Knoll 1981), and the Draken Conglomerate and Hunnberg Formation, Svalbard (Knoll 1982*a*, 1982*b*), demonstrates that cherty horizons from a single formation often preserve the records of biologically heterogeneous environments. Indeed, multiple assemblages can be found within a series of lamellae within a single hand specimen. Many, if not most, of these silica precipitating environments were hypersaline (e.g. Oehler, D. Z., Oehler, J.H. and Stewart 1979), and today similar habitats support microbial mat communities of low cyanobacterial diversity. The diversity of other bacteria, both photosynthetic and heterotrophic, within modern mats can be impressive (Krumbein *et al.* 1979; Margulis *et al.* 1980); however, the remains of these organisms evidently have a low preservation potential and have not been identified with certainty from ancient mat assemblages.

If one *is* to assess microbial evolution through the Proterozoic, one must base such evaluations on: (1) temporal changes in the diversity and/or community structure exhibited by microfossil associations from specific palaeoenvironments defined sedimentologically, or (2) the appearance of morphological innovations within biologically defined lineages. There is little evidence to support the first criterion; but, as mentioned above, new fossil forms do appear in younger rocks. Organizational complexity does show progressive increase throughout the Proterozoic record of planktonic cyanobacteria. For example, Schopf (1977) has noted a significant increase in the size of both spheroidal and filamentous microfossils approximately 1,400 m.y. BP which he attributes to the evolution of the enkaryotic cell. Evolution may account for some of the observed changes; however, environmental sampling cannot be ruled out as another causative factor. Pre-1400 m.y. microbial assemblages published to date include entophysalid-dominated, arid intertidal zone cyanobacterial biotas and Gunflint-type iron formation or deep water, exhalative ridge environment microfloras. The latter are unrepresented in younger deposits, although for the most part their microfossils have close morphological analogs in the modern prokaryotic biota; the former come from an environment that in post-1,400 m.y. rocks still contains relatively small unicells and filaments.

The colonial chroococcalean cyanobacteria *Coleogleba* and *Gyalosphaera* in the Narssârssuk Formation do add a new element of morphological complexity to the Proterozoic fossil record. Hitherto, the most highly ordered pattern of cell division known in the Precambrian record of the Chroococcales was a report of *Eucapsis*(?) from the 1,600 m.y. old Paradise Creek Formation, Australia (Licari, Cloud and Smith 1969. *Eucapsis*(?) is characterized by regular binary division in three mutually perpendicular planes to form cubical colonies. *Gyalosphaera* represents a subsequent stage of chroococcalean evolution in which division in two planes is ordered on to the surface of a sphere. Still, the limited palaeontological sample of Precambrian ages and environments available to us suggests that it would be hazardous at this point to equate palaeontological first known appearance with evolutionary first appearance.

Certainly, prokaryotes have evolved over the past 2,000 m.y. years; in particular, the existence of specialized parasitic and symbiotic bacteria attest to this fact. Yet, palaeontological evidence indicates that the major features of the prokaryotic biota evolved rapidly and early, and were well-established some 2,000 m.y. ago. More specifically, it is quite possible that the morphological limits of variability of the cyanobacteria were realized during the Proterozoic and that subsequent natural selection has affected physiological processes rather than morphology. The recognition of such physiological evolution is potentially resolvable only through detailed comparative palaeoecological studies.

We do not wish to conclude by leaving the impression that the Proterozoic microfossil record does not and cannot exhibit critical evidence for cyanobacterial evolution. Rather we suggest that environmental explanations for observed differences in fossil assemblages provide the proper null hypotheses against which hypotheses of evolutionary change in mat-dwelling cyanobacteria must be tested.

SYSTEMATIC PALAEONTOLOGY

All specimens described herein are from black cherts from the Aorfêrneq Dolomite Member of the Narssârssuk Formation (Thule Basin) exposed south of Thule Air Base, north-west Greenland. Type material is housed in the Harvard Paleobotanical Collections (HPC) of the Paleobotanical Laboratories, Harvard University, Cambridge, Massachusetts, USA.

Kindom MONERA Haeckel, 1878
Phylum CYANOPHYTA Smith, 1938
Class COCOGONEAE Thuret, 1875
Family CHROOCOCCACEAE Nägeli, 1848
Genus GYALOSPHAERA gen. nov.

Type species. Gyalosphaera fluitans sp. nov.

Diagnosis. Fossilized spherical colony composed of peripheral, organically preserved unicells (spherules) in a common mucilage. Spherules may be spherical, ellipsoidal, vesicular (hollow), or condensed to granular bodies. Colony interior clear, filled with unorganized organic matter, or containing short rod-shaped structures. Spherule distribution uniform over colony surface. Outwardly projecting filaments, if present, attached singly throughout the colony or in tufts at colony surface. Extra-colonial sheath or membranes absent; larger colonies may produce some extra-colonial mucilage.

Etymology. From the Greek for 'hollow sphere'.

Gyalosphaera fluitans sp. nov.

Plate 2, figs. 4–11; Plate 3, figs. 1, 2

Diagnosis. As for genus but with spherules 0·5 to 3·0 μm in diameter; colonies from 12 to 100 μm or greater in overall diameter; attached filaments, if present, 1 μm wide and 5 μm or greater in length.

Holotype. Figured in Pl. 2, figs. 6–8. Slide No. KS78-12h. England finder co-ordinates, H25/3. HPC No. 60465.

Etymology. From the Latin *fluitans* for 'floating', in reference to the planktonic life mode of this organism.

Discussion. *Gyalosphaera fluitans*, as described, may represent at least two biological species. The histogram in text-fig. 6 based on colony diameter reveals a slight break in the size distribution at 35 μm; however, this distinct-size partition is not matched by discontinuous variation in other morphological features—for example, spherule morphology. Thus, many of the larger forms (text-fig. 7H, K, L) are part of the size continuum that includes colonies less than 35 μm in diameter. The nature of associated filaments, which occur in less than 5% of the observed colonies, is obscure; attached filaments may represent biologically distinct degrading organisms. Certain very large spherical masses (Pl. 3, fig. 2; text-fig. 7L) appear to be related to *G. fluitans* based on the similarity of internal organic matter; however, similarities may result from degradational convergence of form and may not necessarily indicate close biological affinity. The geometric construction of *G. fluitans* is most similar to the extant genera *Gomphosphaeria* Kützing and *Coelosphaerium* Nägeli which are found in the plankton of freshwater habitats (although *Gomphosphaeria* has been reported from brackish and marine plankton (Humm and Wicks 1980)).

Gyalosphaera cf. *fluitans*

Plate 2, fig. 11

Discussion. One specimen of colonial form, similar in morphology to *G. fluitans*, was found in the *E. thuleënsis* mat in slide KS 78-23f. It is characterized by an evenly spaced paired arrangement of spherules which are attached to bifurcating stalks. This morphology is exactly analogous to that found in the extant cyanobacteria of the genus *Gomphosphaeria*.

Genus COLEOGLEBA gen. nov.

Type species. *Coleogleba auctifica* sp. nov.

Diagnosis. Fossilized multicellular colonies, organically preserved, spherical to globular, usually with profuse (sometimes laminate) mucilagenous sheath. Daughter colonies often attached. Individual spherules without envelopes, small (0·5 to 2·0 μm), embedded in common mucilage, uniformly distributed throughout colony; spherules spherical, vesicular (hollow), or condensed.

EXPLANATION OF PLATE 1

Figs. 1, 2. *Eosynechococcus thuleënsis*. 1, Holotype, KS78-23a (N15/2), ×2000. 2, end-to-end paired set, KS78-23a, ×2000.

Fig. 3. Spheroid type A., KS78-23e, ×2000.

Figs. 4–6. *Eosynechococcus thuleënsis* in stages of degradation KS78-23a, ×2000. 4, paired cells with attached vesicular blebs. 5, degraded unicell. 6, degraded pair in which one cell is reduced to amorphous organic matter.

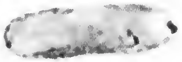
Fig. 7. Carbonate pseudomorph after *Siphonophycus*, filamentous mat, KS78-23d, ×500.

Fig. 8. *Siphonophycus* cf. *kestron* with interior trichome (non-septate) preserved in sheath lumen, filamentous mat, KS78-23a, ×335.

Fig. 9. *Eomycetopsis robusta* in vertically aligned portion of filamentous mat, KS78-23c, ×1000.

Fig. 10. Thin section of portion of slide KS78-23a showing upper *Eosynechococcus thuleënsis* zone (23U) overlying a silicified carbonate transition layer (TZ), which, in turn, overlies the filamentous (23L) mat. Note large sheaths of *Siphonophycus* cf. *kestron* in lower part, ×150.

PLATE 1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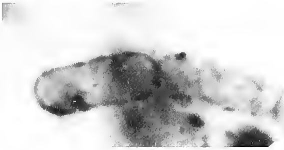
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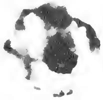
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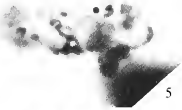
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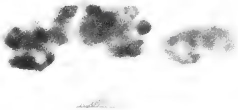
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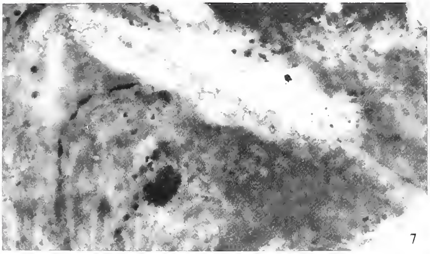
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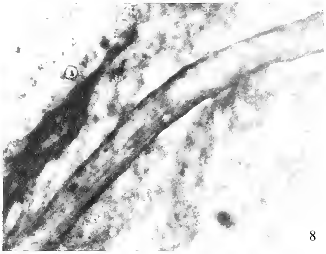
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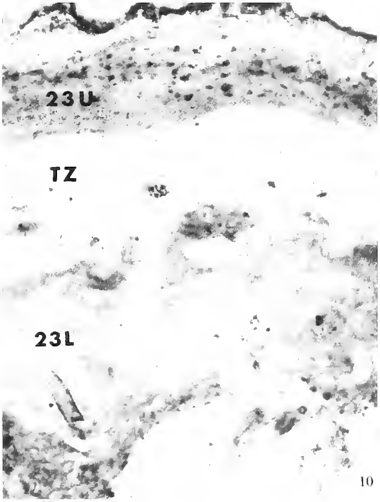

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STROTHER, KNOLL and BARGHOORN, Late Precambrian micro-organisms

Coleogleba auctifica sp. nov.

Plate 5, figs. 1–3

Diagnosis. As for genus but with colony size ranging from 40 to 170 μm in diameter. Sheath may be characterized by containing tangentially oblate spherules or condensed kerogen.

Holotype. Figured in Pl. 5, fig. 3. Slide No. KS78-18a. England finder co-ordinates, J42/1. HPC No. 60468.

Etymology. From the Latin for 'growing' as indicated by the tendency for daughter colonies to remain attached to parent colonies.

Discussion. Morphologically *C. auctifica* is certainly related to *Microcystis* Kützing, a multicellular chroococcalian cyanophyte found in freshwater plankton blooms. Most species of *Microcystis* are irregularly shaped, but spherical colonies do occur—for example, *M. incerta* and *M. pulvera* (Smith 1933, p. 61). Daughter colony formation in *C. auctifica* is similar to that in *Microcystis*. The sporadic distribution of *C. auctifica* throughout the Aorfêrneq cherts suggests that the organism was planktonic in ephemeral ponds.

Genus EOSYNECHOCOCCUS Hofmann, 1976

Type species. *Eosynechococcus moorei* Hofmann, 1976, p. 1057, Pl. 2, fig. 4.

Eosynechococcus thuleënsis sp. nov.

Plate 1, figs. 1, 2, 4–6

Diagnosis. Rods 3·0 to 4·6 μm wide, 5 to 25 μm long (mean 3·9 × 10·8 μm); cell contents usually absent, when present, they are homogeneous and never condensed to discrete granules or 'spots', cell surface microgranulate; smaller cells often attached in end-to-end pairs, rarely in chains of four or more cells; rods straight or slightly bent, rarely clustered laterally: sheath absent; cell division transverse; cells often associated with surficial blebs of vesicular to condensed organic matter.

Holotype. Figured in Pl. 1, fig. 1. Slide No. KS78-23a. England finder co-ordinates, N15/2. HPC No. 60470.

Etymology. With reference to the Thule district of north-west Greenland.

Discussion. Morphologically and with respect to cell division, *E. thuleënsis* is remarkably congruent with the extant *Synechococcus* Nägeli. This similarity extends to the tendency for paired cells to remain attached end-to-end after division (*synechos* is Greek for 'holding together'). Unfortunately for the purposes of palaeoenvironmental reconstruction, the physiological tolerances of the extant *Synechococcus* are very wide, so that living species range from marine planktonic (Waterbury *et al*. 1979) to freshwater thermophilic (Brock 1978). *Synechococcus* is not known as a mat-former from marine environments, but Desikachary (1959) reports species from soils and submerged

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EXPLANATION OF PLATE 2

Figs. 1–3. Spheroid type B. 1, typical form, KS78-12h, × 1500. 2, elongate, possibly dividing form, KS78-12i, × 1500. 3, cluster within banded chert, KS78-12h, × 1000.

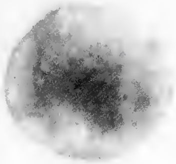
Figs. 4, 5. *Gyalosphaera fluitans* KS78-12k, × 1000. 4, view in median focus with degraded, unorganized interior contents. 5, surficial view showing spherule arrangement.

Figs. 6–8. *Gyalosphaera fluitans*. Holotype. Three optical planes of the specimen, KS78-12h (H25/3), × 1500.

Figs. 9, 10. *Gyalosphaera fluitans*. 9, degraded specimen with attached filaments, KS78-12h, × 1000. 10, median focus view of degraded specimen with interior rod-shaped structures, KS78-12h, × 1500.

Fig. 11. *Gyalosphaera* cf. *fluitans*. Spherules attached to radially bifurcating stalks are apparent in this median section, KS78-23f, × 1500.

PLATE 2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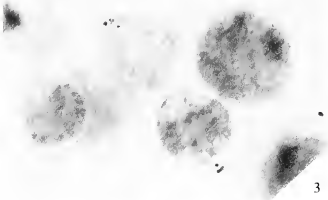
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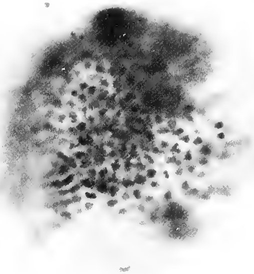
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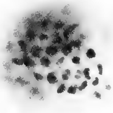
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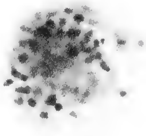
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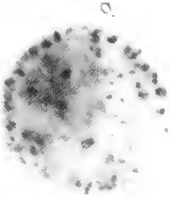
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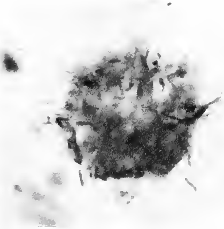
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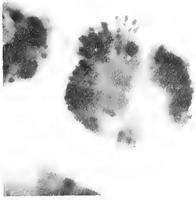
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STROTHER, KNOLL and BARGHOORN, Late Precambrian micro-organisms

aquatic habitats and *Synechococcus lividus* is found in hot springs mats in associations with *Chloroflexis* (Doemel and Brock 1974).

E. thuleënsis is distinguished from other species primarily on the basis of size and tendency for its width to remain constant. It is most similar to *E. medius* Hofmann, which is known from only three specimens.

Eosynechococcus amadeus Knoll and Golubic, 1979

Plate 3, fig. 8

1979 *Eosynechococcus amadeus*; Knoll and Golubic, p. 148, fig. 4*c*.

Discussion. The single figured cluster of cells is remarkably similar to the type material from the Bitter Springs Formation. This includes in addition to the size and shape of individual cells, the construction of packets of cells which occur in 'densely packed clusters and curved palisade-like arrangements' (Knoll and Golubic 1979, p. 148).

Eosynechococcus cf. *amadeus* Knoll and Golubic, 1979

Plate 3, fig. 10

Discussion. On the basis of size and shape, cells from clusters that do not mimic exactly the packets formed by *E. amadeus* are considered as *Eosynechococcus* cf. *amadeus*. This type of *Eosynechococcus* is found rarely throughout the *Gyalosphaera* association and parts of the *E. thuleënsis* (23U) association.

Genus MYXOCOCCOIDES Schopf, 1968

Type species. *Myxococcoides minor* Schopf, 1968, p. 676, pl. 81, fig. 1.

Myxococcoides sp.

Plate 5, fig. 4

1976 Acritarchs (Evitt); Hofmann, p. 1072, pl. 3, figs. 8, 9.

Discussion. Many of the unicells from sample KS78-24 resemble what Hofmann (1976, pl. 3, figs. 8, 9) labelled 'Acritarcha'. In the Aorfêrneq chert, the polygonal outlines of these specimens (Pl. 3, fig. 4) are in all likelihood produced diagenetically as they often contain carbonate crystals in their lumens. *Myxococcoides* Schopf is a form genus encompassing smooth-walled spheroids in the size

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EXPLANATION OF PLATE 3

Figs. 1, 2. *Gyalosphaera fluitans*. 1, degraded specimen with attached filaments, KS78-12c, × 1900. 2, large form with dense interior, KS78-12c, × 1000.

Figs. 3–6. *Oscillatoriopsis variabilis*. 3, type specimen exhibiting well-preserved homogeneous contents and straight walls, KS78-12c (K17/2), × 500. 4, specimen with spool-shaped cells including terminal cell, KS78-12D/2, × 500. 5, filament with well-preserved spherical (plasmolysed) protoplasts, KS78-12j, × 1000.

Fig. 7. *Oscillatoriopsis* sp. with dark, granular internal bodies, KS78-12L, × 1000.

Fig. 8. *Eosynechococcus amadeus* showing typical clustering arrangement also in the Bitter Springs samples, KS78-12k, × 1500.

Fig. 9. *Avictuspirulina minuta* type specimen, shown attached to the perimeter of a large *Gyalosphaera*, KS78-12c (G13/4), × 2000.

Fig. 10. *Eosynechococcus* cf. *amadeus* showing a different clustering habit from that in fig. 8, KS78-12i, × 1500.

Fig. 11. *Oscillatoriopsis variabilis* with condensed cell contents and remnant cytoplasm, KS78-12L, × 1000.

PLATE 3


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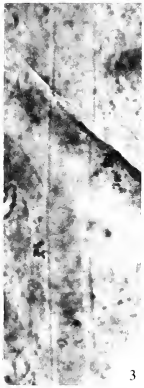
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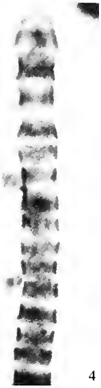
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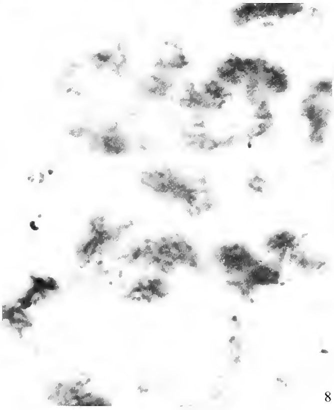
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STROTHER, KNOLL and BARGHOORN, Late Precambrian micro-organisms

range of 3 to 30 μm. Certainly, the Aorfêrneq spheroids belong to this genus, but preservation is too poor to permit specific designation.

Genus GLOEODINIOPSIS Schopf, 1968

Type species. Gloeodiniopsis lamellosa Schopf, 1968, p. 684, pl. 84, fig. 2.

Gloeodiniopsis cf. *lamellosa* (Schopf) Knoll and Golubic, 1979

Plate 5, figs. 6, 7

Discussion. The Aorfêrneq specimens occur in loosely aggregated clusters of solitary cells that vary from those containing well-laminated sheaths (Pl. 5, fig. 6) to those without thick sheath (Pl. 5, fig. 7). They vary from *G. lamellosa* Knoll and Golubic in their larger size, approaching 20 μm in diameter.

Genus TETRAPHYCUS Oehler, 1978

Type species. Tetraphycus gregalis Oehler, 1978, p. 294, fig. 9J.

Tetraphycus sp.

Plate 5, fig. 5

Discussion. One cluster of cells occurring consistently in planar tetrads and with differentiated cross walls can be placed into the genus *Tetraphycus*, although the distinct wall morphology is unknown from other *Tetraphycus* specimens. Too few cells were found to characterize a new species, the distinguishing characteristics of these cells may have been degradationally induced.

'Chroococcoid unicells'

Chroococcoid unicell type A

Plate 4, fig. 1

Discussion. One population of thirty-two cells contained poorly preserved dyads and tetrads of ensheathed cells. Cells are large, about 30 μm including the thick, conspicuous sheath. The presence of a distinct sheath and the clustering of cells in dyads and tetrads indicates an affinity with *Chroococcus* Nägeli or perhaps *Gloeocapsa* Kützing.

Chroococcoid unicell type B

Plate 4, fig. 2

Discussion. A single, large cell with distinct sheath occurred in sample KS78-24. The morphology is decidedly chroococcalean. Elliptical shape and median constriction of the protoplast suggest that this specimen entered into early stages of binary fission shortly before death.

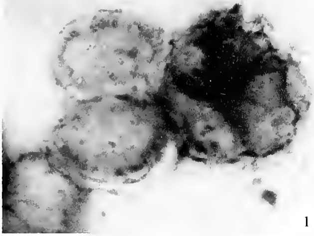
EXPLANATION OF PLATE 4

Fig. 1. 'Chroococcalean unicell' type A, dyad and tetrad with sheath, KS78-12j, × 875.

Fig. 2. 'Chroococcalean unicell' type B, single cell with distinct sheath and constricted median zone, KS78-24g, × 1150.

Figs. 3–8. *Eosynechococcus* cf. *belcherensis*. 3, small clusters of tetrads, KS78-18/f2, × 2000. 4, typical large loosely aggregated cluster, KS78-18/f2, × 500. 5, radially aligned colony, KS78-18A, × 1000. 6, small cluster, KS78-18/f2, × 2000. 7, palisade-forming colony, KS78-18/f2, × 600. 8, loosely associated cells showing variation in size and contents, KS78-18/f2, × 2000.

PLATE 4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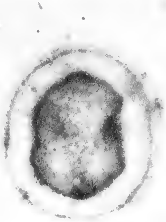
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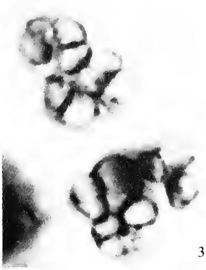
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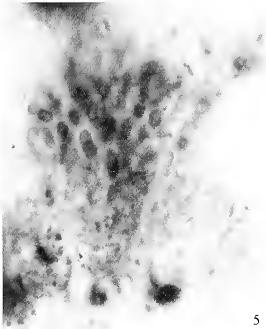
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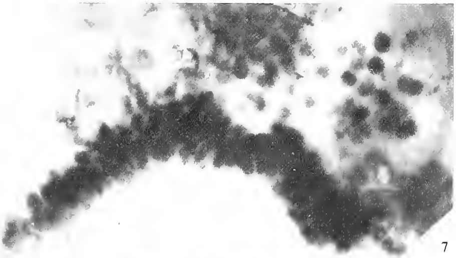
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STROTHER, KNOLL and BARGHOORN, Late Precambrian micro-organisms

Family ENTOPHYSALIDACEAE Geitler, 1925
Genus EOENTOPHYSALIS (Hofmann) Mendelson and Schopf, 1982

Type species. Eoentophysalis belcherensis Hofmann, 1976, p. 1070, pl. 6, fig. 13.

Eoentophysalis cf. *belcherensis* Hofmann, 1976

Plate 4, figs. 4–8

Discussion. Numerous colonies of cells dividing in three planes produce a variety of cluster morphologies. These arrangements differ from *E. belcherensis* Hofmann in that forms with internal contents and peripheral colony pigmentation are not apparent in the Greenland material. Their absence may well reflect degradational differences and be of little taxonomic importance. Specimens may be preserved as individual cells embedded in common mucilage or as envelopes of multiple cells in common mucilage. Growth of the clusters is centrifugal, with the result that degraded cores are common in larger aggregates.

Class HORMOGONEAE Thuret, 1875
Order NOSTOCALES Geitler, 1925
Family OSCILLATORIACEAE (S. F. Gray) Dumortier ex Kirchner, 1898
Genus OSCILLATORIOPSIS (Schopf) Mendelson and Schopf, 1982

Type species. Oscillatoriopsis obtusa Schopf, 1968, p. 667, pl. 77, fig. 8.

Discussion. Oscillatoriopsis differs from *Paleolyngbya* Schopf in lacking definite remains of sheath (see Mendelson and Schopf 1982, p. 63).

Oscillatoriopsis variabilis sp. nov.

Plate 3, figs. 3–6, 11

Diagnosis. Organically preserved, fossilized, three-dimensional filaments with cells 14 to 17 μm broad by 7 to 9 μm long; terminal cell hemispherical; cross walls evenly spaced near apices. Cell contents homogeneous, condensed ellipsoidal, condensed spheroidal, or condensed multiple smaller spheroidal bodies; filament margins smooth or crenulate.

Holotype. Figured in Pl. 3, fig. 3. Slide No. KS78-12c. England finder co-ordinates, K17/2. HPC No. 60469.

Etymology. In reference to the variable morphology of cellular contents (which are diagenetically induced) found in this species.

Discussion. O. variabilis is most similar in size to *O. robusta* Horodyski and Donaldson, which is 18 μm wide. *O. robusta* is known from only one specimen in which the cross walls are not organically preserved. *O. variabilis* demonstrates a remarkable sequence of degradational variation (text-fig. 8). The best-preseved specimens are similar to modern *Oscillatoria* in lacking a sheath or having only minimal sheath.

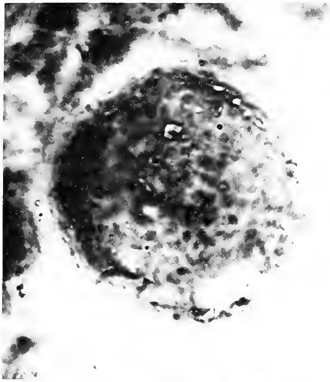
EXPLANATION OF PLATE 5

Figs. 1–3. *Coleogleba auctifica.* 1, small colony with vesicular spherules and minimal sheath, KS78-18/1, ×1000. 2, specimen with condensed spherules and moderate extracolonial mucilage containing flattened spherules, KS78-18/fs, ×1000. 3, type specimen with abundant kerogenous extracolonial mucilage, KS78-18a (J42/1), ×800.

Fig. 4. *Myxococcoides* sp. from thin section KS78-24g, ×1000.

Fig. 5. *Tetraphycus* sp. from KS78-18A showing differentiated wall structure, ×2000.

Figs. 6, 7. *Gloeodiniopsis* cf. *lamellosa.* 6, more typical form with thick laminate sheath, KS78-23c, ×2000. 7, forms with thin sheath and internal protoplasts present, KS78-23a, ×1000.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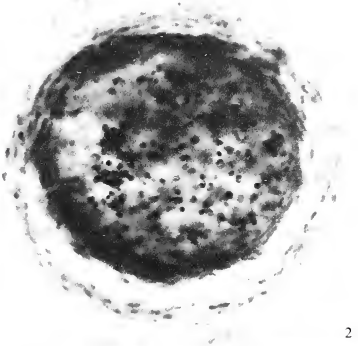
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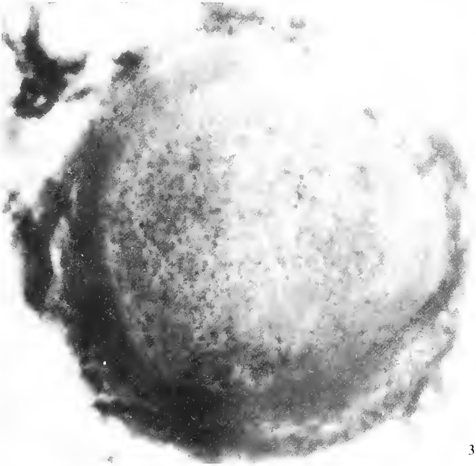
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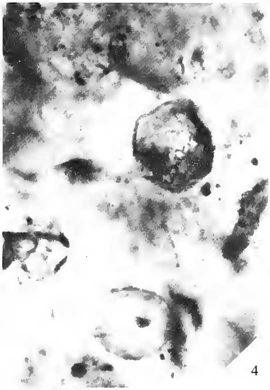
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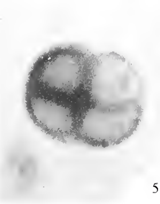
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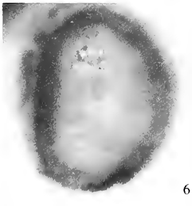
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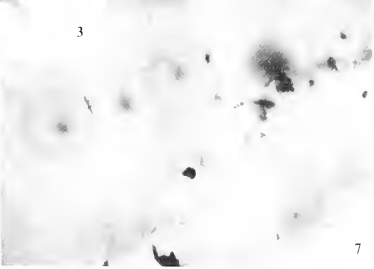
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STROTHER, KNOLL and BARGHOORN, Late Precambrian micro-organisms

Genus AVICTUSPIRULINA gen. nov.

Type species. Avictuspirulina minuta sp. nov.

Diagnosis. Fossilized spiral, cylindrical filament three-dimensionally preserved; more or less regularly coiled; cross walls absent; sheath absent; apices rounded; cell contents uniform and dense; filaments 2 μm or less in diameter.

Etymology. From the Latin *avictus* meaning 'ancestral' and the extant genus *Spirulina* (Turpin) Gardner.

Discussion. Avictuspirulina differs from species of *Heliconema* Schopf in not having a flattened thallus, coils at a 45° angle, and in size and surface texture. It differs from *Obruchevella* Reitl., a Vendian to Ordovician coiled tube, in being less regularly coiled and in size (see Cloud *et al.* 1979).

Avictuspirulina minuta sp. nov.

Plate 3, fig. 9

Diagnosis. As for genus but with filament diameter 0·8 μm wide; filament coiled into three to four spirals 5 to 9 μm in diameter and spaced 2 to 4 μm apart; end spirals often of lesser diameter than middle spirals.

Holotype. Figured in Pl. 3, fig. 9. Slide No. KS78-12c. England finder co-ordinates, G13/4. HPC No. 60466.

Etymology. From the Latin for 'small'.

Discussion. About fifteen specimens of this taxon have been found in association with extracellular organic matter surrounding large *Gyalosphaera*-type organisms. The fossil is morphologically allied to the extant genus *Spirulina* because of its spiral nature and lack of cross walls. *A. minuta* is similar to *Spirulina laxissima* West (Desikachary 1959).

Genus SIPHONOPHYCUS Schopf, 1968

Type species. Siphonophycus kestron Schopf, 1968, p. 671, pl. 80, figs. 1–2.

Siphonophycus sp.

Plate 1, figs. 7, 8, 10

1978 *Siphonophycus* sp. Oehler, p. 300, figs. 12N–12R.

Discussion. Short segments of large (20 to 40 μm) tubes are common in the filamentous (23L) association. Specimens are occasionally infilled with carbonate (Pl. 1, fig. 7) or may contain one or two non-septate trichomes (Pl. 1, fig. 8). Sheath wall is often thick and may consist of a double organic layer. They are comparable to the *Siphonophycus* sp. of Oehler (1978), but preservation is too variable to ascertain useful taxonomic designation.

EXPLANATION OF PLATE 6

Fig. 1. Hand sample, KS78-12, showing carbonate-filled vugs in lower portion and black, fossiliferous chert in upper portion, ×1·4.

Fig. 2. Thin section, KS78-12j, showing dark, sinuous fossiliferous chert bands, ×3.

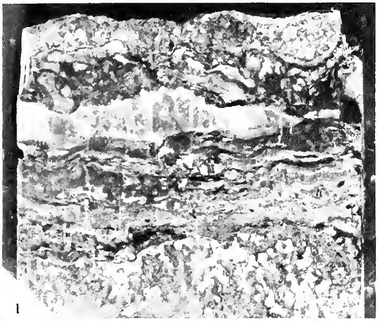
Fig. 3. Small pustular stromatolites from locality KS78-18. Sample is partially silicified carbonate, ×1·5.

Fig. 4. Thin section, KS78-18a/5. Gray-laminated portion is unfossiliferous carbonate, dark areas contain abundant *Eoentophysalis* preserved in chert, ×3.

Fig. 5. Thin section, KS78/23f, showing lower vuggy *Eomycetopsis*/*Siphonophycus* association topped by laminate *Eosynechococcus thuleënsis* zone, ×4.

Fig. 6. Thin section KS78-24 with chert-replaced radiating anhydrite structures, ×4.

PLATE 6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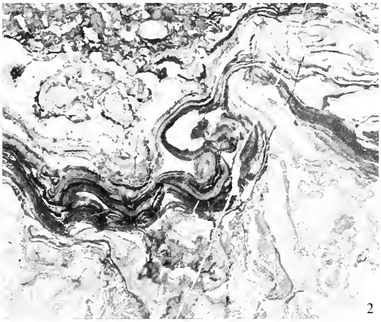
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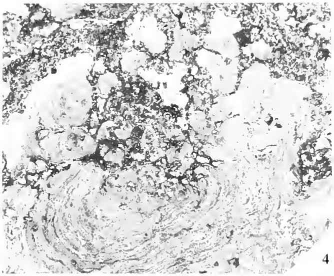
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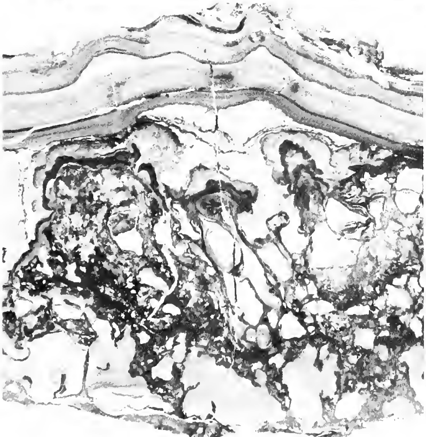
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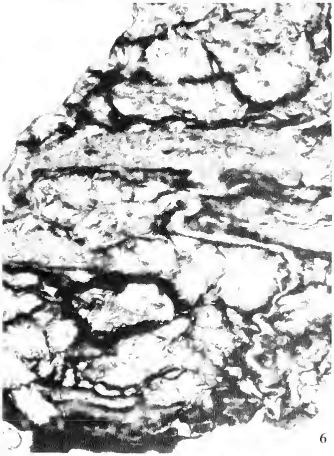
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STROTHER, KNOLL and BARGHOORN, Late Precambrian micro-organisms

Genus EOMYCETOPSIS (Schopf) Knoll and Golubic 1979

Type species. Eomycetopsis robusta Schopf, 1968, p. 685, pl. 83, fig. 1.

Eomycetopsis robusta Schopf

Plate 1, fig. 9

(for synonomy, see Mendelson and Schopf 1982)

Discussion. Numerous filaments, aseptate and unbranched fit the size characteristics established for this form taxon (2 to 4 μm). The filaments occur in dense, poorly preserved, intertwined mats often with gross vertical alignment. They dominate the filamentous mat (23L) section of sample KS78-23.

Incertae sedis
Spheroid type A

Plate 1, fig. 3

Description. Organically preserved, irregularly shaped, subspherical fossilized envelope often with dense central body; envelope 3 to 12 μm in diameter, inner body up to 5 μm in diameter; granular to microgranular surface texture.

Discussion. Spheroid type A has been found only in the *Eosynechococcus* zone from sample KS78-23. A population of $N = 50$ has the following parameters based on diameter: $\bar{x} = 6{\cdot}8$ μm, range from 3 to 12 μm, $s = 1{\cdot}8$ μm. Spheroid type A codominates the community along with *E. thuleënsis*. The irregularity of its envelope is not characteristic of any known cyanobacteria, nor is it similar to degraded cyanobacterial envelopes. It is possible that spheroid type A represents a non-photosynthetic component of the *Eosynechococcus* community.

Spheroid type B

Plate 2, figs. 1–3

Description. Spherical organism, outline faintly preserved but usually quite spherical; interior contents homogeneous or characterized by lighter spherical blebs embedded in a homogeneous organic matrix; extracellular sheath or mucilage absent; mean diameter 16 μm.

Discussion. Spheroid type B dominates the *Gyalosphaera* assemblage. Its simple morphology and faintly preserved interior structure do not allow its classification even to the kingdom level. The size-frequency characteristics for a population of $N = 113$ (text-fig. 5), show a range of 8 to 28 μm ($\bar{x} = 15{\cdot}7$ μm) in diameter with a leptokurtic distribution reminiscent of algal unicell populations. Spheroid type B probably represents a planktonic organism, but its biological affinities are obscure.

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REFERENCES

BARGHOORN, E. S. and TYLER, S. A. 1965. Microorganisms from the Gunflint Chert. *Science*, **147**, 563–577.
BROCK, T. P. 1978. *Thermophilic microorganisms and life at high temperatures.* New York, 465 pp.

CLOUD, P. E., Jr. 1965. Significance of the Gunflint (Precambrian) microflora. *Science*, **148,** 27–35.

——AWRAMIK, S. M., MORRISON, K. and HADLEY, D. G. 1979. Earliest Phanerozoic or latest Precambrian fossils from the Arabian Shield. *Precambrian Res.* **10,** 73–94.

DAVIES, W. E., KRINSLEY, D. B. and NICOL, A. H. 1963. Geology of the North Star Bugt Area, northwest Greenland. *Meddelelser om Grønland*, **162,** 47 pp.

DAWES, P. R., REX, D. C. and JEPSEN, H. F. 1976. K/Ar whole rock ages of dolerites from the Thule District, western North Greenland. *In* ESCHER, A. and WATT, W. S. (eds.). *Geology of Greenland.* Copenhagen, pp. 61–66.

DESIKACHARY, T. V. 1959. *Cyanophyta.* New Delhi, 686 pp.

DOEMEL, W. N. and BROCK, T. P. 1974. Bacterial stromatolites: origin of laminations. *Science*, **184,** 1083–1085.

GEITLER, L. 1932. Cyanophyceae. *In* RABENHORST, L. (ed.). *Kryptogamen-Flora von Deutschland, Osterreich und der Schweiz*, **14,** Jena, 1196 pp.

GOLUBIC, S. 1976. Organisms that build stromatolites. *In* WALTER, M. R. (ed.), *Stromatolites.* Amsterdam, pp. 114–140.

——and HOFMANN, H. J. 1976. Comparison of Holocene and mid-Precambrian entophysalidaceae (Cyanophyta) in stromatolitic algal mats: cell division and degradation. *J. Paleont.* **50,** 1074–1082.

HARDIE, L. A. and GINSBURG, R. N. 1977. Layering: the origin and environmental significance of lamination and thin bedding. *In* HARDIE, L. A. (ed.). *Sedimentation on the Modern carbonate tidal flats of northwest Andros Island. Bahamas.* Baltimore, pp. 50–123.

HOFFMAN, P. 1976. Environmental diversity of middle Precambrian stromatolites. *In* WALTER, M. R. (ed.). *Stromatolites.* Amsterdam, pp. 599–611.

HOFMANN, H. J. 1976. Precambrian microflora, Belcher Islands, Canada: significance and systematics. *J. Paleont.* **50,** 1040–1073.

HORODYSKI, R. J. and DONALDSON, J. A. 1980. Microfossils from the Middle Proterozoic Dismal Lake Group, arctic Canada. *Precambrian Res.* **11,** 125–159.

HUMM, H. J. and WICKS, S. R. 1980. *Introduction and guide to the marine blue-green algae.* New York, 194 pp.

KENDALL, A. C. 1979. Continental and supratidal (sabkha) evaporites. *In* WALTER, R. G. (ed.). *Facies models.* Toronto, pp. 145–158.

——and SKIPWITH, P. A. 1968. Recent algal mats of a Persian Gulf lagoon. *J. Sedim. Petrol.* **38,** 1040–1058.

KNOLL, A. H. 1981. Paleoecology of late Precambrian microbial assemblages. *In* NIKLAS, K. J. (ed.). *Paleobotany, Paleoecology, and Evolution.* New York, pp. 17–54.

——1982*a*. Microorganisms from the late Precambrian Draken Conglomerate, Ny Friesland, Spitsbergen, *J. Paleont.* **56,** 755–790.

——1982*b*. Microbiotas of the late Precambrian Hunnberg Formation, Nordaustlandet, Svalbard. Ibid., in press.

——BARGHOORN, E. S. and AWRAMIK, S. M. 1978. New microorganisms from the Aphebian Gunflint Iron Formation, Ontario. Ibid. **52,** 976–992.

——and GOLUBIC, S. 1979. Anatomy and taphonomy of a Precambrian algal stromatolite. *Precambrian Res.* **10,** 115–151.

——and SIMONSON, B. 1981. Early Proterozoic microfossils and penecontemporaneous quartz cementation in the Sokoman Iron Formation, Canada. *Science*, **211,** 478–480.

——and VIDAL, G. 1980. Late Proterozoic vase-shaped microfossils from the Visingso Beds, Sweden. *Geol. Foren. Stockholm Forh.* **102,** 207–211.

KRUMBEIN, W. E., BUCHHOLZ, H., FRANKE, P., GIANI, D., GIELE, C. and WONNEBERGER, K. 1979. Oxygen and hydrogen sulfide coexistence in stromatolites: a model for the origin of mineralogical lamination in stromatolites and banded iron formations. *Naturwissenschaften*, **66,** 381–389.

KURTZ, V. E. and WALES, D. M. 1959. Geology of the Thule Area, Greenland. *Proc. Okla. Acad. Sci.* 1950, 83–89.

LICARI, G. R., CLOUD, P. E. and SMITH, W. D. 1969. A new chroococcaceaen alga from the Proterozoic of Queensland. *Proc. natn. Acad.* **62,** 56–62.

LOGAN, B. W., REZAK, R. and GINSBURG, R. N. 1964. Classification and environmental significance of algal stromatolites. *J. Geol.* **72,** 68–83.

MARGULIS, L., ASHENDORF, D., BANERJEE, S., FRANCIS, S., GIOVANNOI, S., STOLZ, J., BARGHOORN, E. S. and CHASE, D. 1980. The microbial community in the layered sediments at Laguna Figueroa, Baja California. *Precambrian Res.* **11,** 93–124.

MENDELSON, C. V. and SCHOPF, J. W. 1982. Proterozoic microfossils from the Sukhaya Tunguska, Shorikha, and Yudoma Formations of the Siberian Platform, USSR. *J. Paleont.* **56,** 42–83.

MONTY, C. 1976. The origin and development of cryptalgal fabrics. *In* WALTER, M. R. (ed.). *Stromatolites.* Amsterdam, pp. 193–249.

MUIR, M. D. 1976. Proterozoic microfossils from the Amelia Dolomite, McArthur Basin, Northern Territory. *Alcheringa*, **1,** 143–158.

OEHLER, D. Z. 1978. Microflora of the middle Proterozoic Balbarini Dolomite (McArthur Group) of Australia. Ibid. **2,** 269–309.

—— OEHLER, J. H. and STEWART, A. 1979. Algal fossils from a late Precambrian hypersaline lagoon. *Science*, **205,** 388–390.

OEHLER, J. H. 1977. Microflora of the H.Y.C. Pyritic Shale Member of the Barney Creek Formation (McArthur Group), middle Proterozoic of northern Australia. *Alcheringa*, **1,** 315–349.

PARK, R. K. 1977. The preservation potential of recent stromatolites. *Sedimentology*, **24,** 485–506.

PEAT, C. J., MUIR, M. D., PLUMB, K. A., MCKIRDY, D. M. and NORVICK, M. S. 1978. Proterozoic microfossils from the Roger Group, Northern Territory, Australia. *BMR J. Australian Geol. Geophys.* **3,** 1–17.

PURSER, B. H. 1973. *The Persian Gulf: Holocene carbonate sedimentation and diagenesis in a shallow epicontinental sea.* Berlin, 471 pp.

SCHOPF, J. W. 1968. Microflora of the Bitter Springs Formation, late Precambrian, central Australia. *J. Paleont.* **42,** 651–688.

—— 1977. Earliest evidence of fossil eukaryotes. *In* PONNAMPERUMA, C. (ed.). *Chemical evolution of the Early Precambrian.* New York, pp. 107–109.

SHEARMAN, D. J. 1978. Evaporites of coastal sabkhas. *In* DEAN, W. E. and SCHREIBER, B. C. (eds.). *Marine evaporites.* SEPM Short Course No. 4, pp. 6–42.

SMITH, G. M. 1933. *The fresh-water algae of the United States.* New York, 716 pp.

STROTHER, P. K. 1980. *Microbial communities from Precambrian strata.* Thesis, Harvard University.

VIDAL, G. 1981. Micropalaeontology and biostratigraphy of the Upper Proterozoic and Lower Cambrian sequence in East Finnmark, northern Norway. *Norges geol. Unders.* **362,** 1–53.

—— and DAWES, P. R. 1980. Acritarchs from the Proterozoic Thule Group, north-west Greenland. *Gronlands geol. Unders. Rap.* **100,** 24–29.

—— and KNOLL, A. H. (in press). Proterozoic plankton. *Geol. Soc. Amer. Mem.*

WALTER, M. R., GOODE, A. D. T. and HALL, W. D. M. 1976. Microfossils from a newly discovered Precambrian stromatolitic iron formation in western Australia. *Nature*, **261,** 221–223.

WATERBURY, J. B., WATSON, S. W., GUILLARD, R. R. L. and BRAND, L. E. 1979. Widespread occurrence of a unicelular, marine, planktonic cyanobacterium. Ibid., **277,** 293–294.

WOOD, G. V. and WOLFE, M. J. 1969. Sabkha cycles in the Arab/Darb Formation of the Trucial Coast of Arabia. *Sedimentology*, **12,** 165–191.

ZHANG, Z. 1981. Precambrian microfossils from the Simian of South China. *Nature*, **289,** 792–793.

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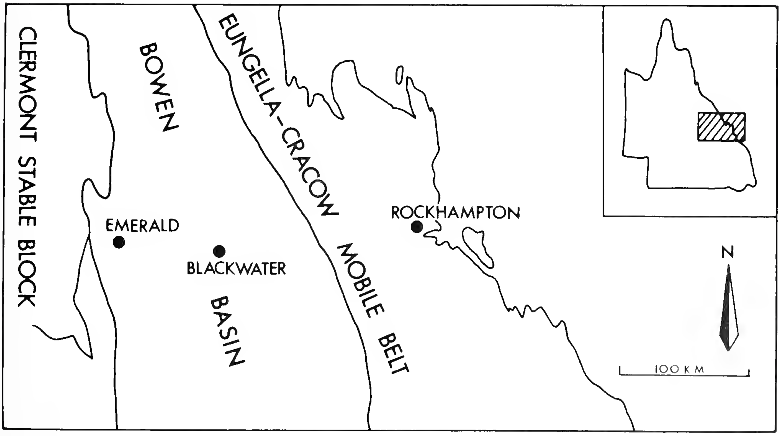
A LATE PERMIAN ACTINOPTERYGIAN FISH FROM AUSTRALIA

by K. S. W. CAMPBELL *and* LE DUY PHUOC

ABSTRACT. *Ebenaqua*, a new genus of deep-bodied palaeoniscoid fishes, type species *E. ritchiei* sp. nov., is described from the Late Permian Rangal Coal Measures at Blackwater, central Queensland. It is interpreted as an early member of the Bobasatraniformes. Examination of a large number of characters on specimens from the Kupferschiefer suggests that the genus *Platysomus* is also a bobasatraniform. The homologies of the bones in the suborbital and maxillary regions of members of this order are reinterpreted. A functional study of the jaw mechanics suggests that the forward position of the jaw articulation, the loosely articulated bones of the face, and the markedly upright suspensorium of *E. ritchiei* are adaptations to a distinctive mode of feeding and gill ventilation. These features should not be used to infer halecostome or neopterygian relationships. The pectoral and pelvic fins are vestigial, and their functions in the control of manœuvre and stability are inferred to have been taken over by the dorsal and anal fins, which nevertheless retain a paleoniscoid structure. The versatility of palaeoniscoid fins movements was greater than has been accepted previously.

A COLLECTION of actinopterygian fishes belonging to nine genera has been made from two localities at Blackwater in the Upper Permian Blackwater Group, a coal measure sequence lying between the marine Permian Back Creek Group and the Lower Triassic Rewan Formation (text-fig. 1). The material was first found in outcrop in a complex area where the shales have been baked by a fire in one of the seams. Subsequently, more prolific and better preserved specimens were found in



TEXT-FIG. 1. Locality map of Blackwater Mine, Queensland.

[Palaeontology, Vol. 26, Part 1, 1983, pp. 33-70, pls. 7-10.]

position in the Utah Development Company's open-cut mine. The fauna at the two sites is apparently identical.

The assemblage includes members of the Palaeonisciformes, Redfieldiiformes, and Bobasatraniformes. The palaeonisciforms are the most diverse, including seven distinct types, four of which are sufficiently well preserved and distinct to warrant description as new genera. One of the remainder may be a species of *Cycloptychius* Young, a European Carboniferous genus, but no head has been found and this assignment must be tentative.

The most abundant species is the bobasatraniform *E. ritchiei* gen. et sp. nov., described below. It makes up about one-third of the total collection available to us, and the specimens are commonly found completely articulated. The species is important for several reasons. It has some of the most highly specialized features, such as reduced pectoral and pelvic fins and protruding snout, known from the Bobasatraniformes. Its skull bones are well enough preserved to permit a functional analysis to be made, and this analysis suggests that the similarities between bobasatraniforms and holostean, or more advanced, fishes are superficial. The extreme reduction of pectoral and pelvic fins implies that the fish manœuvred by the action of the anal and dorsal fins, which nevertheless retain a primitive structure. The capacity of paleoniscoid fins to produce flexible movements comparable to those of more advanced fishes will therefore need further investigation. And finally, the presence of the genus in freshwater deposits whereas all other occurrences of the Order are marine, poses interesting questions for biogeography.

STRATIGRAPHY

The stratigraphic sequence in the Blackwater area is shown below (after Staines 1975).

Lower Triassic	Mimosa Group	Rewan Formation
Local minor disconformity		
Upper Permian	Blackwater Group	Rangal Coal Measures Burngrove Formation Fair Hill Formation
Lower to Upper Permian	Back Creek Group	MacMillan Formation German Creek Formation Ingelara Formation Freitag Formation

The fishes are from the Rangal Coal Measures, a unit which is 90–135 m thick in the vicinity of Blackwater. It contains several coal seams that split and rejoin, producing difficulty in correlation and a resultant complex nomenclature which has been stabilized by Staines (1972, 1975). His work is followed here. The chief fossiliferous locality is 6 m above the Argo (or Main Lower) Seam which, as the name implies, lies towards the bottom of the Rangal Coal Measures.

The fishes occur in a light-grey, soft shale in which there is abundant comminuted plant material. On exposure to the weather the shale rapidly breaks down. A similar lithology at the top of the Argo Seam contains more carbonaceous layers from which specimens of *Phyllotheca*, *Glossopteris*, *Vertebraria*, *Taeniopteris*, and equisetalean stems have been recovered. Occasional specimens of *Glossopteris* and *Vertebraria* are found in the fish bed.

A specimen of mudstone from the fish bed was examined for palynomorphs by Dr. Elizabeth Truswell who has supplied the following list. Spores: *Dulhuntyispora dulhuntyi* s.l., and *D. parvithola* (very rare); *Granulatisporites micronodosus*; *Horridotriletes ramosus*; *Granulatisporites* sp.; *Dictyotriletes* sp. nov. (common); *Didecitriletes* cf. *ericianus*; and *Laevigatosporites colliensis*. Pollens: *Marsupipollenites triradiatus*; *Praecolpatites sinuosus*; *Platysaccus* spp.; *Protohaploxypinus limpidus*, *P. amplus*, and *P.* cf. *varius* (common); *Scheuringipollenites* spp.; *Vitreisporites pallidus*; *Striatopodocarpidites* cf. *pantii*; and *Parasaccites* sp. She has indicated that this assemblage implies a position high in the Upper Stage 5 of Kemp *et al.* (1977), which is at the top of the Permian. There are no distinctive elements of the basal Triassic Trla assemblage.

SYSTEMATIC PALAEONTOLOGY

Order BOBASATRANIFORMES
Genus *EBENAQUA* gen. nov.

Derivation of name: *Latin ebenus* black; *aqua* (f) water.

Diagnosis. Body deeply rhombic in profile, with dorsal and ventral angles approximately equal; laterally compressed. Facial contour steep and with a strongly protruding snout based on an enlarged maxilla. A large suborbital attached to the maxilla and bearing a branch of the lateral line canal. Postspiraculars present. Maxilla and suborbital overlapped by infraorbitals forming a loose junction. Two preoperculars without a lateral line canal. Opercular and subopercular separated by an oblique suture, the subopercular extending almost to the ventral edge of the animal. Branchiostegal rays greatly reduced in number. Mandible small, about two-thirds the length of the maxilla, and slung well forward. Jaws edentulous. Cleithrum strong; supracleithrum present, but no anocleithrum or clavicle. Twenty-seven rows of scales between the posterior end of the cleithrum and the caudal peduncle, and another ten rows extending forward under the pectoral fin. Posterodorsal and posteroventral scale rows much reduced in width, very regular compared with *Bobasatrania*, and running at a low angle to the body margins. Flank scales elongate, rhomboid, with steeply inclined unornamented leading and trailing edges, and only slight overlap; long, spiked scale articulation. Lateral line canal well-defined throughout, and with a regular posteroventral branch and a highly irregular anterodorsal branch on the body; short dorsal and, less commonly, ventral tubules branch from the main canal. Pectoral and pelvic fins small, the pelvic being situated a short distance in front of the ventral angle. Dorsal and anal fins extending from dorsal and ventral angles to the caudal peduncle, and consisting of a group of long rays at their distal extremities, but much shorter, more uniform rays over most of their length; dorsal and anal fin rays more numerous than their baseosts. All fin rays jointed. Tail strongly heterocercal with the scales on the dorsal lobe extending to its extremity; ventral lobe slightly expanded; fin rays on ventral lobe more crowded, stronger and with longer segments than those on the dorsal lobe; outline of the caudal fin symmetrical.

Ebenaqua *and the Bobasatraniformes*. If Westoll's (1941) assessment of *Lekanichthys* is correct, the only genera confidently placed in this group are *Bobasatrania* and *Ecrinesomus*. Several features of *Ecrinesomus* remain unknown—e.g. the details of the caudal fin and of the lower dermal bones of the branchial chamber. However, they have in common the following features: deep body; extended dorsal and anal fins; jaw slung well forward; maxilla large and placed well forward; edentulous; 'suspensorium' vertical; a large suborbital (the supramaxilloquadratojugal of Neilson 1952) between the preoperculars and the maxilla; peculiar development of paired preoperculars, and suboperculars; branchiostegal rays reduced or absent; postspiraculars present; clavicles reduced or absent; flank scales elongated and vertically striated; scale rows swing forward to meet the posterodorsal and anteroventral margins obliquely; pelvic fin small or absent; dorsal and anal fins extended from dorsal and ventral extremities to the caudal peduncle; caudal fin heterocercal, but the approximately symmetrical development of dorsal and ventral lobes.

Of course, not all these features are unique to the Bobasatraniformes, but their combination defines a distinctive group. *Ebenaqua* shares all the above characters. The case for its inclusion in the group is made even stronger by comparison with *Bobasatrania* itself. Both genera have a lateral line canal on the suborbital, the jaw articulation strongly overlapped by the posterior part of the maxilla, long rays at the anterior ends of the dorsal and anal fins, clearly differentiated rays on the dorsal and ventral lobes of the dorsal and anal fins, and a row of spines on the anterodorsal and anteroventral body margins.

The main differences between *Ebenaqua* and *Bobasatrania* are the existence in the latter genus of (*a*) a short rostral region; (*b*) an entirely free suborbital; (*c*) a lacuna in the cheek below the orbit; (*d*) a lateral line canal on the preoperculars; (*e*) an elongate pectoral fin; (*f*) an entire ventral edge with no gap for a pelvic fin; (*g*) a greatly reduced squamation on the caudal lobe; (*h*) baseosts approximately equal in number to the rays of the dorsal and anal fins.

These differences are considered to be of generic significance only. It is noted that *Ecrinesomus* is more similar to *Ebenaqua* than *Bobasatrania* in characters *b*, *c*, *d*, and *h* above.

This relatively straightforward situation is complicated by difficulties with the interpretation of the genus *Platysomus*. As indicated in the Appendix, this genus has to be interpreted on the Permian species which are in urgent need of revision, and not on such Early Carboniferous species as *Platysomus superbus* Traquair, which are almost certainly not congeneric with the Permian forms. Specimens from the Late Permian Kupferschiefer described in the Appendix do not have the head structure figured by Traquair (1879) for *P. gibbosus*; nor do they resemble the reconstructions of *P. parvulus* (Traquair 1879) or *P. superbus* (Moy-Thomas and Bradley Dyne 1938). On the other hand, the skull roof and circumorbital bones, the opercular and preoperculars, the edentulous jaws, the peculiar forward position of the mandible with its distinctive cross-section and its overlapped relation with the maxilla, the shape and arrangement of the scales, the lateral line with its crossbar-like tubules, the overall fine linear ornament that breaks up into pustules on the dorsal parts of the animal, and the shape and position of the ceratohyal, all show similarities with *Ebenaqua* and with Bobasatraniformes. More importantly, there is a lateral-line-bearing bone behind the maxilla, and it has the same shape and relationships as the bone designated as a suborbital in *Ebenaqua*, and by inference in the Bobasatraniforms, the only other groups in which it is known to occur. If further study confirms our interpretation of the Kupferschiefer specimens, and *Platysomus* and the Bobasatraniformes are shown to be more closely related than has been previously accepted, there will be difficulty with the nomenclature of some of the higher taxa covering these groups (see Moy-Thomas and Miles 1971). Meanwhile we propose to assign *Ebenaqua* to the Bobasatraniformes pending further investigation of the Permian platysomids.

Relationships of the Bobasatraniformes. We are in agreement with Gardiner's view (1967*a*, p. 195) that the group is most clearly allied with the palaeoniscoids and did not give rise to any subsequent group. In our view bobasatraniids are essentially primitive fishes with some specialized characters that it would be incorrect to term 'advanced', if by that term is meant having characters in common with holosteans or even teleosts (see Patterson 1973, p. 296).

Evidence of the essentially palaeoniscoid structure of the group is found in the complex development of the dorsal caudal lobes; the small number of baseosts in comparison with the number of dorsal and anal fin rays in *Ebenaqua* and *Ecrinesomus*; the degree of segmentation of the fin rays; the absence of undivided rays in the dorsal and anal fins; the posterior position of the pelvic fin (when present); the well-developed postrostral bone; and the presence of postspiracular bones.

The so-called advanced features that cause most concern are the mobile maxilla and the vertical suspensorium (see Schaeffer and Rosen 1961, for a discussion of the significance of these features). Patterson (1973, p. 296) has indicated that the mobile maxilla of *Bobasatrania* is a halecostome character and that the reduced clavicles, vertical suspensorium, and equal numbers of fin rays and baseosts in both dorsal and anal fins, are neopterygian characters. On the other hand, he goes on to point out (p. 297) that as the maxilla in *Ecrinesomus* is fixed, that bone must have become free more than once in actinopterygians. This is supported by the new evidence from *Ebenaqua*. Moreover, as is shown in the functional section of this work, the peculiar maxilla-suborbital arrangement and the forward jaw articulation are related to distinctive feeding and gill ventilation systems of a kind quite different from the jaw-gape changes associated with evolution of the holosteans. Mobile maxillae *ipso facto* do not indicate relationships, though different styles of mobility *may* do so. As for the upright suspensorium, in the bobasatraniids, as judged from Neilsen's figures, the hyomandibula has completely lost its connection with the jaw suspension and the jaw is articulated, and presumably supported, in a manner different from that shown by neopterygians. Consequently, this feature cannot be regarded as indicating relationships either. Finally, *Ecrinesomus* and *Ebenaqua* show the normal palaeoniscoid baseost numbers relative to fin ray numbers, and the fin rays in *Bobasatrania* are proportionately more numerous and more closely spaced than in neopterygians. Judging from the close spacing of its baseosts, it seems probable that the approximately equal numbers of baseosts and rays in *Bobasatrania* resulted from an increase in the number of baseosts rather than a decrease in the number of rays as in neopterygians. Consequently, only the reduced clavicles remain from the list of 'advanced' features mentioned by Patterson, and even they may be explained in terms of the narrow ventral body form in bobasatraniids.

Schaeffer and Mangus (1976, p. 559) concluded that in *Bobasatrania* 'the open cheek, free maxilla and vertical suspensorium indicate a holostean-halecostome arrangement of the jaw musculature', though they did not imply that this judgement had taxonomic implications. Our reconstruction of the adductor musculature of Bobasatraniformes is not holostean-halecostome in character (see below).

It goes without saying that suggestions of a relationship between *Bobasatrania*, the pycnodonts and *Dorypterus* (see Westoll 1941, for discussion), were based on convergent characters.

The bobasatraniids, in our view, form an aberrant group retaining many primitive characters, but developing several unique ones that show convergent similarities to holosteans and halecostomes. The question that remains to be discussed is—which palaeoniscoid group is likely to be its closest relative? Gardiner (1967*a*, p. 195) allied the group with the amphicentrids, and Westoll (1941, p. 47) considered that *Bobasatrania* is probably derived from *Platysomus* or one of its near allies, thus supporting the conclusions of Stensiö (1932) and Woodward (1939). These suggestions will be discussed in turn.

Gardiner's (1967*a*, p. 195) proposal that bobasatraniids 'are an offshoot from the same palaeoniscoid stock which gave rise to the amphicentrids', rests on 'the make-up of the shoulder girdle and the unpaired fins, and in the much deepened, laterally compressed body'. However, body form is scarcely a differentiating character in this instance, and the other features are too poorly defined to be applicable. It is difficult to escape the conclusion that he preferred an amphicentrid to a platysomid origin because he considered the bobasatraniids to have crushing teeth (see his p. 185 for discussion).

Westoll's assessment of Bobasatraniform relationships was based on comparisons with English Late Permian specimens assigned to *P. gibbosus*, and the similarities he emphasized were the skull roof and circumorbitals, two preoperculars, sigmoid axonosts, elongate rhomboid scales with longitudinal striae, and paired tubules on the body lateral line. As indicated above, we have additional characters indicating a close relationship between at least some Permian forms of '*P. gibbosus*' type and the Bobasatraniformes. This relationship is of importance in the search for possible ancestors because '*P. gibbosus*' is the oldest known member of this group, and it has such features as a few free branchiostegal rays and several suborbitals in front of the preopercular that are not known in *Ebenaqua*, *Ecrinesomus*, or *Bobasatrania*. Assuming that the features these three genera and '*P. gibbosus*' have in common are jointly inherited, it should be possible to infer the minimal characters of an ancestral group. To these should be added those features which, though they are not equally represented in all members of this group, are interpreted as having been modified from an ancestral form of specified type. For example, all four taxa have different branchiostegal plate arrangements, '*P. gibbosus*' being the most complex and *Ecrinesomus* apparently being without plates on the ventral surface apart from the gular. In view of the common occurrence of multiple branchiostegals in Late Palaeozoic actinopterygians, and the fact that the greatest number of plates occurs in the oldest form, we infer that the ancestral group had a number of free branchiostegal rays. A similar argument might be used with respect to the preoperculars of which there are two without a lateral line in the above taxa except *Bobasatrania*. In that genus there is a larger plate that is readily interpreted as a fusion of the second preopercular and the subopercular, and a lateral line occurs on this plate and the isolated preopercular. Since late Palaeozoic actinopterygians normally have a preopercular canal, and since the forward movement of the mandible in the group under discussion has produced a profound modification in the canal system on the lower part of the head, we infer that the ancestral group had two canal-bearing preoperculars.

Using the above approach we conclude that the ancestor of this group had the following features: dermosphenotic, dermopterotic, at least three postspiraculars, paired extrascapulars, two preoperculars with lateral line canal, three or more suborbitals in a postorbital position, clavicles, deep body, elongate body scales with long spike-and-groove articulation and fine linear ornament, long dorsal and anal fins, caudal fin with ridge scales and rays of ventral lobe strengthened to produce an isobatic structure. In addition, the ancestral group should have structures that can be transformed to give the unique Bobasatraniform structures.

At present, no genus with this group of characters is known, but that causes little concern given the extremely patchy sampling of late Palaeozoic fish faunas and the incomplete descriptions available for many known species. What is clear is that deep-bodied species such as '*Platysomus*' *superbus* Traquair, '*Platysomus*' *parvulus* Williamson, *Chirodopsis geikiei* Traquair, and *Amphicentrum granulosum* Young, which are among the best-known species in the groups cited as possible ancestral groups for the Bobasatraniformes, have little in common with such an hypothetical ancestor.

Ebenaqua ritchiei sp. nov.

Derivation of name: In honour of Dr. A. Ritchie.

Holotype. F58674 AM and counterpart F58695 AM. Two specimens on the slab, the larger and more complete individual being the holotype.

Paratypes. (*a*) F10135 QM, an almost complete fish and the largest specimen available. (*b*) F53871 AM, part and counterpart, preserved in pink, baked shale. (*c*) F58676 AM, an almost complete small individual. (*d*) F58680 AM, part and counterpart, almost complete. (*e*) F56881 AM, a single whole individual. (*f*) F58683 AM and counterpart F58693 AM, three incomplete individuals on a slab. (*g*) F58684 AM, a single large but partly effaced individual. (*h*) F58699 AM, a fragment of a large individual.

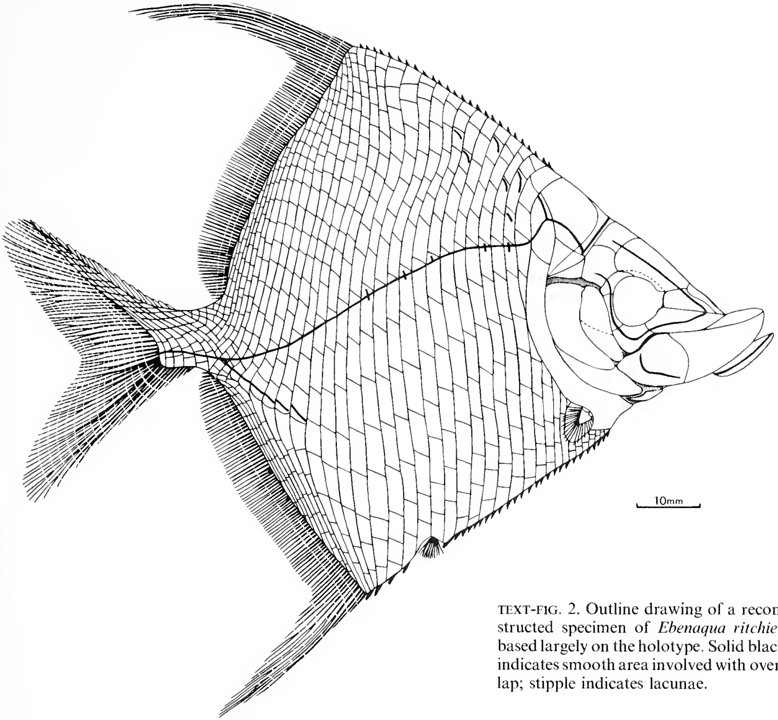
Description. The specimens are preserved compressed almost into a plane, and when split the shale parts along a surface that approximately corresponds with the median plane of the animal. This means that many specimens are viewed from the inside out. However, in places the split surface passes around one side of the animal or the other, leaving a confusing superimposed set of bones or scales from the two sides. This can usually be detected, but in areas of strong ossification it leads to difficulty of interpretation.

The skeletal material has been completely replaced by kaolinite. The manner of such replacement is difficult to understand, not only because of the mechanism involved, but also because of the fidelity of the structural preservation. The finest surface details of the scales, for example, are recorded. Unfortunately, no details of the bone histology remain, and consequently some important criteria of relationship are unavailable.

The body form of the animal is deep but variable, as is shown in text-figs. 2–3. (The position of the orbit is chosen as the anterior measuring point because several specimens have lost their snouts.) This variation in form is not the result of compression as there has been no shearing of the rock, and opposite sides of the one animal seem to be almost exactly superimposed. The body must have been very slender over almost its entire length. Four reasons may be advanced to support this conclusion. (*a*) The scales have remained almost exactly in contact edge-to-edge on *all* parts of the trunk, and not only along the posterodorsal and posteroventral edges where the scale pattern indicates that the body was blade-like. (*b*) The anterodorsal and anteroventral edges of the body are preserved as only gently convex curves, whereas they would be markedly convex if there were any body swelling. (*c*) The cleithrum has sprung apart at the symphysis with almost no displacement of the scales lying immediately behind it, and with a minimum amount of fracturing. (*d*) The dimensions of the bones flooring the branchial chamber indicate that the animal was narrow in this region.

There is some variation in the straightness of the anteroventral and anterodorsal margins, in general the larger specimens being the more convex. All specimens have gently convex posteroventral and posterodorsal margins.

Skull roof and cheeks. The post-temporals are the largest bones in the roof. Their posterior edges swing forward to the mid-line where they are separated by three or four spine-bearing scales. The junctions with all the surrounding bones are strong. No specimens show the sutures opened up, though they are commonly slightly depressed, probably reflecting a life condition.

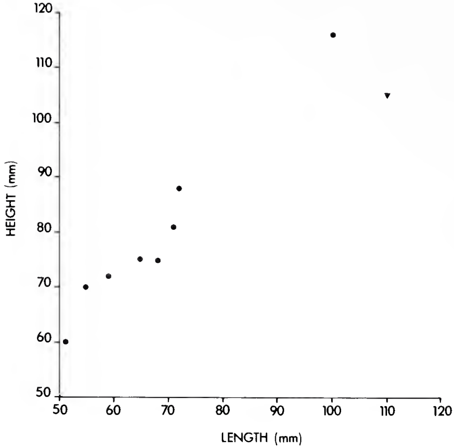


TEXT-FIG. 2. Outline drawing of a reconstructed specimen of *Ebenaqua ritchiei*, based largely on the holotype. Solid black indicates smooth area involved with overlap; stipple indicates lacunae.

The extrascapulars are narrow but expand towards the mid-line, particularly between the posttemporals. On most specimens the suture between the lateral and median components is not clear, but where it is visible the median is the smaller.

The parietal is clearly defined on all specimens, but there is difficulty with the interpretation of the frontal. Lying between the frontal and the orbit on all specimens there is a thickened ridge of bone that is firmly attached to the frontal. It is not common for the frontal to be in contact with the orbit in the deep-bodied palaeoniscoids. However, signs of a suture are seen on three specimens, and a peculiar angular junction against the dermosphenotic has been observed on others. Consequently we have tentatively shown a supraorbital in the reconstruction.

The boundary between the nasal and the frontal is clear on several specimens, lying at the upper edge of the posterior nostril. The anterior nostril cannot be seen clearly on any specimen. The possibility that both nostrils lay within the deep embayment of the orbit has been considered and rejected because of the position of the lateral line canal in front of this embayment. We conclude that the anterior nostril is a very small opening near the anterodorsal corner of the nasal.



TEXT-FIG. 3. Plot of length/width for nine specimens. The length has been measured from the posterior edge of the orbit to the posterior edge of the caudal peduncle. The large specimen indicated by the triangle is F10135 QM.

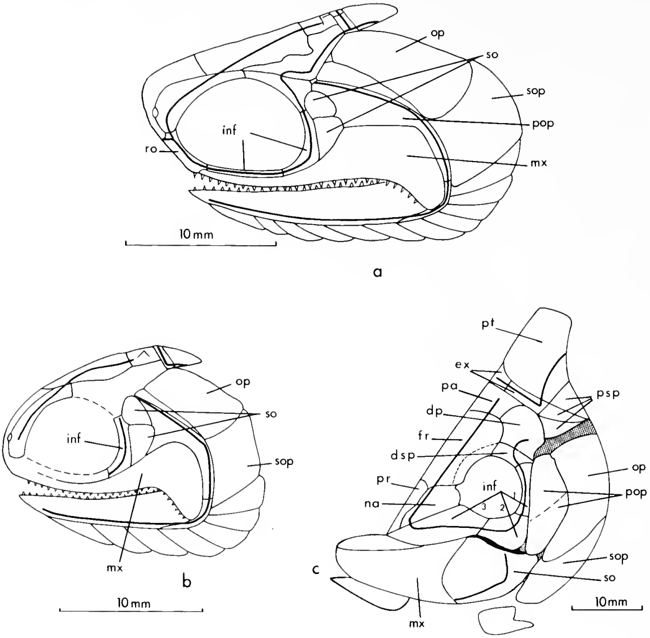
The area between the nasal and the rostral projection is not well preserved on any specimen, but there is a long thin bone lying in this area anterior to the frontal. It is not known if this is a single bone crushed on itself or a paired bone. It has no lateral line canal. This, together with its position, indicates that it can only be a postrostral. There is no space for the rostral or for the rostropremaxilla, which are found in this region in *Bobasatrania*. The lateral line passes directly from the nasal to the infraorbital 3 (see below). It may be suspected that the nasal and infraorbital 3 have undetected sutures across them, the front of the so-called nasal being the rostral, and the front of the infraorbital 3 being the rostropremaxilla. Apart from the fact that we cannot detect sutures on these bones, this solution is not reasonable because it places the rostral behind the postrostral. Nor does it take account of the fact that a rostral commissure of the lateral line and canal has not been found. We conclude that this commissure has been lost along with the rostral and rostropremaxilla during remodelling of the rostrum.

The maxilla is a remarkable, elongate bone, most of the lateral surface of which is flat and highly ornamented, but its upper edge is smooth and is overlapped by the infraorbital 3. It is clear that the two bones could move relative to each other. Posteriorly it meets the suborbital, which is also overlapped by the infraorbitals on a similar smooth surface. The posterior boundary of the maxilla is always clear, and is usually represented by a depressed suture whose outline is convex forwards. An occasional specimen is split along the suture. We have little doubt that the two bones were flexibly joined. The ventral edge of the maxilla is markedly convex and edentulous. The best-preserved specimens show a smooth lenticular strip of bone forming the upper edge of the rostrum and running back into the overlapped part of the maxilla. This lenticle must have been thin, but at its anterior end it has a slight swelling. On some specimens it shows a slight emargination where it joins the ornamented part of the maxilla, but on others this junction is even. We can find no suture between it and the maxilla, though it always lies in a plane at an angle to the plane of the main part of the maxilla.

Its upper edge is invariably sharp, so that it must have been sutured against its antimere. Such a suture would have been very weak. There is a natural tendency to regard this structure as a 'rostral' that has become fused to the maxilla, but its continuity with the smooth dorsal overlapped strip of the maxilla, and the absence of a lateral line canal on it, suggest that this explanation is not acceptable. We conclude that it is a differentiated strip of maxilla.

The bone that is clearly homologous with the one labelled 'supramaxillaquadratojugal' by Nielsen (1952), Lehman (1956), and Schaeffer and Mangus (1976), in *Bobasatrania* and *Ecrinesomus*, is a distinctive structure. Schaeffer and Mangus expressed doubt about the homology of this bone, but did not reach any positive conclusions. It has a flat, highly ornamented body, but its upper edge has a smooth overlapped surface separated off by a slight kink, and its posterior edge has a powerful subtriangular smooth projection that is overlapped by the preopercular 2 and fits into a slight notch in the anterior edge of the subopercular. It carries a clearly defined segment of the lateral line canal which runs from a dorsal direction into the bone just below the dorsal overlap, contains an angular bend, and then runs forward without dividing. Anteriorly it runs off the bone near its anteroventral corner, and it is directed towards the mandible. We believe that it is almost certainly the upper part of the mandibular canal. The precise homology of this bone is unlikely to be finally determined without further material intermediate between *Ebenaqua* and its ancestors, but some points can be made.

There seem to be three possible homologies—supramaxilla, quadratojugal, or suborbital—apart from the complex suggestion of Nielson which requires fusions for which we can see no firm evidence. Gardiner (1967*b*, p. 200) has regarded the bone as a supramaxilla, but he gave no supporting argument. The supramaxilla *sensu stricto* first appeared in Mesozoic holosteans as a consequence of disarticulation of the cheek when the mouth was widely opened, and it lay on the dorsal edge of the maxilla for this reason. In the Bobasatraniformes the bone in question occupied a different position from the supramaxilla and, as explained elsewhere in this article, it originated with a different function and at an earlier time. Consequently, we cannot accept this hypothesis. The second view is that it is a highly modified quadratojugal, a bone known in various palaeoniscoids in which it is usually 'a small, plate-like bone which is in contact with the quadrate and is overlapped externally by the maxilla and preopercular' (Patterson 1973, p. 249). In this position the mandibular lateral line canal from the preopercular to the mandible passed in the soft tissue over its surface. It could be that as the lower jaw moved forwards in Bobasatraniformes the quadratojugal became exposed and greatly enlarged, and incorporated the lateral line connection from the preopercular to the mandible. Then as the distance between preopercular and mandible increased even more, the canal connections were modified. A virtue of this hypothesis is that although the quadratojugal is primitively not a canal bone, it apparently becomes canal-bearing in some palaeoniscoid groups—for example, the Haplolepidae (Westoll 1944). On the other hand, we consider it significant that there are no known Palaeozoic forms with an anteriorly displaced jaw articulation in which there is an exposed quadratojugal with a canal from the preopercular. The hypothesis that the bone is a modified suborbital is supported by the following arguments. Several palaeoniscoids have one or more suborbitals between the infraorbitals, the preopercular, and the maxilla—for example, *Mesopoma* and *Rhadinichthys* (see text-fig. 4). The Late Permian holostean *Acentrophorus* has a short maxilla with a suborbital immediately behind it and out of contact with the quadrate articulation, as is the bone in question in the Bobasatraniformes. And the Late Permian platysomid described in the Appendix has a row of suborbitals forming a series that includes the bone under discussion. Consequently, it would not be surprising if, in a late Palaeozoic form, a suborbital moved forwards to occupy a space created by the progressively more anterior suspension of the mandible. One difficulty with this interpretation is that suborbitals are not lateral line bones, but this is not a fatal objection as canals are able to invade non-canal bones (Graham-Smith 1978). The Bobasatraniform canal, moreover, is unique, in that no other group of fishes has a canal directed towards the infraorbital. We note also that in *Bobasatrania* the preopercular canal is still present though connection with the mandible has been lost. In Nielsen's figure of *B. groenlandica* it is directed ventrally off the bone, suggesting that if such a connection existed it passed in the skin ventral to the bone under discussion. Schaeffer and Mangus (1976, fig. 9) also show the canal rising off the bone in a ventral direction in



TEXT-FIG. 4. Lateral views of skulls of (*a*) *Radinichthys*, (*b*) *Mesopoma*, and (*c*) *Ebenaqua* to show the position of the suborbital bones. Figures (*a*) and (*b*) modified from Moy-Thomas and Dyne 1938. dp, dermopterotic; dsp, dermosphenotic; ex, extrascapulars; fr, frontal; inf 1, 2, 3 infraorbitals; mx, maxilla; na, nasal; op, operculum; pa, parietal; pop, preoperculum; pr, postrostral; psp, postspiracular; pt, post-temporal; ro, rostral; so, suborbital; sop, suboperculum. Solid black indicates smooth area involved with overlap; stipple indicates lacunae.

B. canadensis. Presumably this connection in the skin was broken when a new line developed from the infraorbital. As indicated above, we find none of these arguments conclusive, but on balance we prefer the suborbital to the quadratojugal hypothesis.

Below the post-temporal and the extrascapulars is a group of three triangular bones. These are bordered below by the opercular from which they are separated by a gap. Although the three bones are usually preserved in a confused state, F58699 AM shows them all with great clarity. Nielsen (1952, p. 203) refers to the two bones in this position of *B. groenlandica* as postspiraculars, noting that there is a single bone in this position in *Pteronisculus*. There is also a bone in a similar position in *Moythomasia* (Jessen 1968). Although Lehman (1956, pp. 20–21) considered these bones in *B. mahavavica* to be postspiraculars, White (1932) thought that they may be postorbitals, or the bone Y of Traquair. The examples of *Pteronisculus*, *Moythomasia*, and the Bobasatraniformes suggest either that in primitive palaeoniscoids bones were developed in the angle between the shoulder girdle, the cranial roof, and the opercular, but that they were later lost in many genera; or alternatively that bones developed in this position to fill space as required. (The causal mechanisms for the independent development of these bones may be different in each case.) We cannot choose between these alternatives on the basis of evidence known to us, but for simplicity we refer to these bones as postspiraculars.

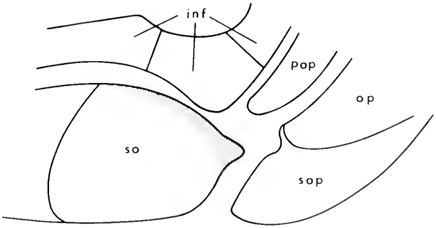
Anterior to these is a large bone which is sharply defined around its upper edges, but it is always broken ventrally. We are satisfied that it is a single bone and that it carries the lateral line canal to the dermosphenotic. The reason for the poor preservation seems to be that only the lower part of the plate is well ossified, and on crushing cracks develop across the plate. It can only be the dermopterotic.

The dermosphenotic is a clearly defined thick bone that in structure and form is really one of the circumorbitals. It carried a thick bony crest and is traversed by the lateral line canal in the usual way.

Infraorbital 1 is a long narrow bone also with a thick crest, but infraorbital 2, though thick close to the edge of the orbit, has a wide outer flange that becomes quite thin towards its ventral edge. The boundaries between infraorbital 2 and infraorbitals 1 and 3 are not clear. Infraorbital 3 is a large, flat, triangular bone, the thickened ridge around the orbit having faded away on infraorbital 2. The bone extends forwards to the rostral protuberance, and its junction with the nasal and the postrostral is straight and frequently open. This may be the result of compaction, but we suspect that it was probably a very weak suture. There is no sign of bone overlap along this line.

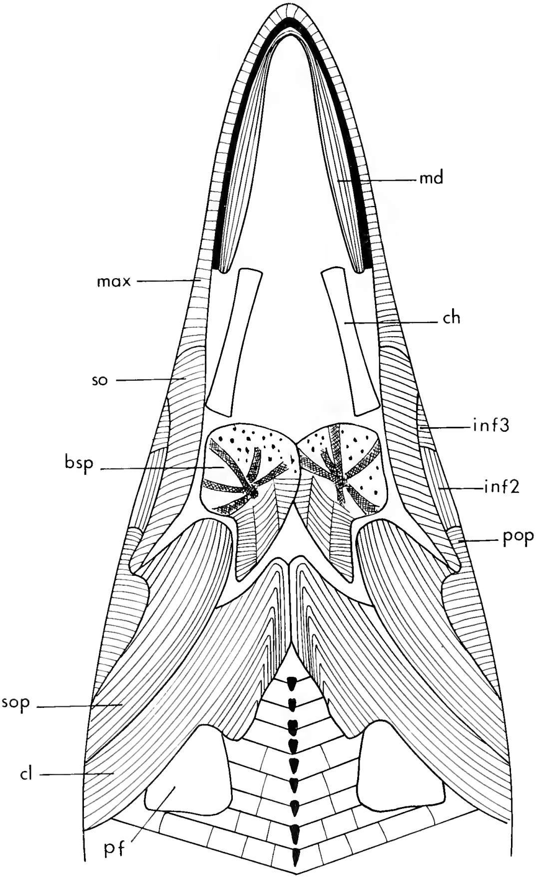
The opercular and the subopercular can be distinguished on all specimens (see text. fig. 5). The dorsal end of the opercular is quadrate in outline and it is slightly flexed and thickened in its anterodorsal corner where it articulates with the suspensorium. It slightly overlaps the subopercular along a very oblique and somewhat variable junction. In the largest specimen F10135 QM, the junction forms a deep V, whereas in others it is straight or has a slight V at its anteroventral extremity. The subopercular also is almost flat. Along its anterior edge it has a smooth strip which overlaps the suborbital, and at the upper end of this strip there is a thickened flexural notch that seems to articulate with the posterior prominence of the suborbital. The posterior edges of both bones overlap a recessed edge on the cleithrum.

The preoperculars are difficult bones to restore. They are almost always crumpled in appearance, and the posterior end of the parasphenoid with its various processes, as well as the superimposed ceratobranchials, always obscure the detail. However, we believe that two bones are present, separated by a straight oblique suture. The ventral edge of the lower bone is very thin and poorly preserved, but there is clear evidence on F58680 AM (counterpart) that it overlapped the posterior end of the suborbital, and it may also have overlapped infraorbital 2. A difficulty with the interpretation of these bones are preoperculars is that we are unable to recognize the preopercular lateral line on them. This may be the result of bad preservation, but such an explanation is unlikely because the dorsal part of preopercular 1 is frequently well enough displayed to show a canal if one were present. Apparently *Ecrinesomus* has no preopercular canal, though all three species of *Bobastrania* have the canal clearly developed. Schaeffer and Mangus (1976) explored the possibility that in *Ecrinesomus* these bones are suborbitals, but rejected that view in favour of a very guarded confirmation of their status as preoperculars. With this conclusion we are in agreement.

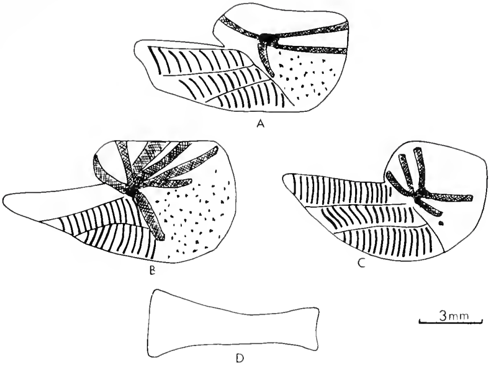


TEXT-FIG. 5. The bones of the cheek and lower opercular region separated to show their interrelationships. Stipple indicates overlapped area on the suborbital.

All specimens with the ventral edge of the head preserved have a characteristic club-shaped bone lying below the subopercular. It has a thick anterior body and a thickened anteromedial edge, but the bone is always preserved in such a way as to prevent its precise pattern of ossification being determined. It is clearly a dermal bone as is shown by the ornament, and consists of three arcuate segments, as shown in text-fig. 6, that seem to unite anteriorly to form one piece. The posterior edge also is weakly lobed in some specimens to correspond with the three segments. The bone would have



TEXT-FIG. 6. Ventral view of head and shoulder girdle. bsp, branchiostegal plate; ch, ceratohyal; cl, cleithrum; inf 2, 3 infraorbital; md, mandible; max, maxilla; pf, pectoral fenestra; pop, preoperculum; so, suborbital; sop, suboperculum.



TEXT-FIG. 7. A–C, three branchiostegal plates showing variation in outline and surface detail. Drawn from F58680, F58674, and F53871 AM respectively. D, outline of ceratohyal F58371 AM.

been paired, and in life would have abutted snugly against the suboperculum and the suborbital along its upper edge while overlapping its antimere medially. A bone in such a position would normally be regarded as a branchiostegal ray, but such rays were normally lath-like and functioned as a covering for a broad arch in the body around the flank of the gill chamber. The bone in *Ebenaqua* is single, covers the floor of the gill chamber, and negotiates change in body slope by hinging below the suborbital. It would seem most appropriate, therefore, to refer to this bone as a branchiostegal plate, and to note that it probably functioned as a second suboperculum (see text-fig. 7).

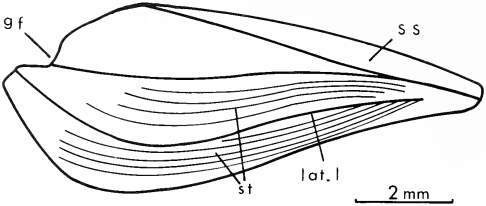
Mandible. Except for the anterior end, the mandible is usually preserved crushed against the inside of the maxilla. Interference between the longitudinal ornament on the two bones causes problems for the interpretation of the outline and the position of the lateral line canal. The best-preserved specimens are F58674 and F58694 (counterparts), F58680, F58683, and F58693 (counterparts) AM. In lateral view the mandible is lancet-shaped anteriorly with an abruptly terminated posterior (see text-fig. 8). Its biting edge is almost straight in lateral view, but its anterior tip is deflected inwards.

On the external surface the sutures are not clear, but there seem to be two divisions. The upper band, which is almost flat and carries a thickened oral edge, is presumably the dentary. The lower band is bulky, forming a subangular keel along most of its length, together with a number of subparallel striations that meet the dentary at an oblique angle. There seems to be a single ossification towards the posterior end of the bone giving rise to the thickenings. The lateral line canal cannot be distinguished with certainty, but it probably runs parallel with the above thickenings. Because this lower bone occurs back to the articulation in the position normally occupied by the angular, we propose to give it this name.

A fragment of the inner surface is seen on F53871 AM. It apparently was almost flat and smooth. Separate bones cannot be distinguished.

The glenoid fossa is a small depression, behind which is a short rounded projection covered by the angular. There is no indication of a coronoid process, and presumably there was a Meckelian cavity between the highest point of the dentary and the articulation.

Ornament of skull bones. The ornament of the skull bones consists primarily of a series of closely spaced approximately equidimensional striae that form various patterns—concentric, radial, or straight across the bone. Towards the dorsal edge of all bones the linear pattern breaks down and is



TEXT-FIG. 8. Reconstructed lateral view of mandible. Bones not clearly defined. gf, glenoid fossa; lat. l, lateral line; ss, smooth surface; st, striae.

replaced first by a regular series of pustules, and then by irregular pustules. Though there is variation in the pattern, the various bones have more or less consistent patterns and these are shown in text-fig. 9. Some peculiar variations are known. The maxilla normally has regular vertical striae across the whole bone, but on F10135 QM there is a marked discordance on the posterior quarter where a group of about a dozen striae are parallel with the posterior bone edge. On the opercular and subopercular the striae are invariably oriented dorso-ventrally, but on some, perhaps even most, individuals there is a series of oblique fine radial striae on the upper part of the subopercular. These radiate from a centre placed just behind the articulation with the suborbital. Similar transverse striae sometimes occur on the upper part of the opercular also. Both sets are well developed on F58680 AM. It should be noted that the dominant longitudinal striae are almost always finer on the subopercular than on the opercular. The distance from the dorsal edge, where the breakdown from striae to pustules occurs, varies from specimen to specimen, but particularly between specimens of different ages. For example, on the larger specimens about half the dermopterotic may be covered by pustules whereas on smaller ones its ornament is entirely linear.

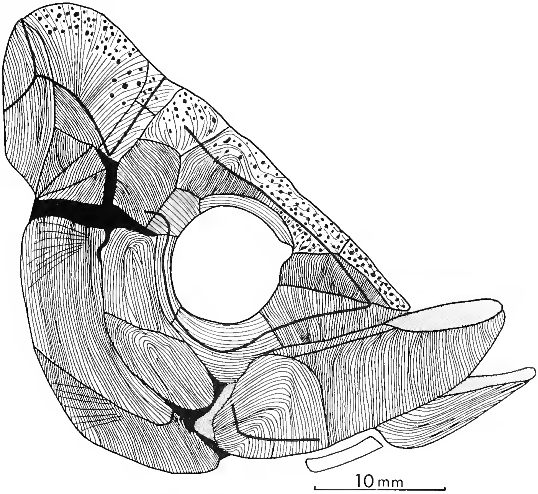
Shoulder girdle. The shoulder girdle consists of two bones, the cleithrum and the supracleithrum.

The cleithrum is by far the thickest bone in the skeleton, and extends from the mid-ventral line up to the level of the postspiraculars. Its external surface has a powerful ridge running down the bone separating a flattened or slightly concave posterior strip from a steep anterior branchial lamina. This ridge fades gradually towards the supracleithrum and more abruptly at the pectoral embayment. It flares around the lower edge of the pectoral embayment where it is separated from its antimere by four short rows of scales. The symphysis is formed of a short straight sector at the anterior edge of which is a slightly rounded knob. There is no unusual degree of fracturing of the bone towards the symphysis despite the fact that it all now lies in the one plane. This suggests that there was no sharp angular bend from the flank on to the ventral surface which, in the median line, may have been slightly keeled or rounded. The anterior edge of the cleithrum above the symphysis is slightly concave and must have been marginally covered by the branchiostegal plate.

The bone has a peculiar texture at present, consisting of cords of white kaolinite separated by films of black substance. The significance of this is not understoood, but it is probably a function of bone replacement. However, some of the internal structure is reflected by the ribbing on the surface, at least of the lateral surface of the bone, where the ornament is of similar dimensions to that of the opercular.

The supracleithrum, which is also ornamented like the adjacent skull bones with dorsoventrally arranged striae, is a much flatter bone. It is firmly sutured to the post-temporal and the posterior postspiracular.

There is no sign of an anocleithrum on any of our material. However, we note that because the cleithrum is so powerful, the crushing of the left and right sides together and the slight displacement of the two because of the strong ridging, produce marginal overlaps that could be misinterpreted as additional cleithral elements.



TEXT-FIG. 9. Pattern of ornament on the dermal bones of the skull. The diagram is intended to reflect the patterns commonly seen on the various bones in adult fishes, and it has been prepared from a number of specimens. The density of the lines and dots only approximates the density of the ridges and striae on the bones. The abrupt changes at bone boundaries and across lateral lines are overemphasized and are not seen on all specimens. Fine stipple indicates smooth bone; solid black indicates lacunae.

Palate. The only element that can be identified with certainty is the parasphenoid. This is a long narrow bone that extends from the level of the preoperculars almost as far as the level of the anterior end of the orbit. It is well ossified and is preserved on all specimens, lying across the lower quarter of the orbit. It bears no teeth, the surface being apparently quite smooth.

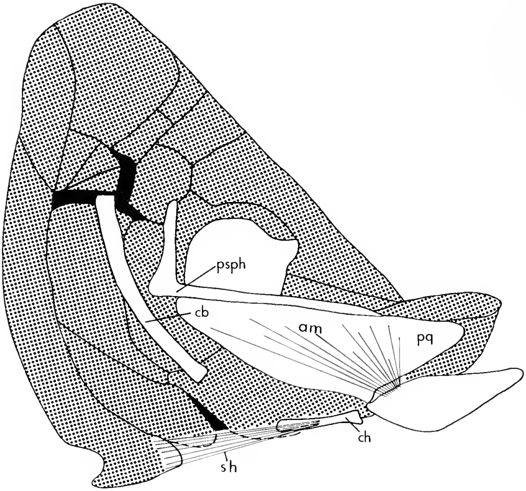
At the posterior end the parasphenoid is abruptly thickened where processes join it. On compression these processes rotate and shatter, making interpretation difficult. In particular, it is impossible to determine the length and attitude of the processes, though they must have been long and thin, arising abruptly from the main body. The centre of ossification is just anterior to the junction of the processes where the hyophysial pit must also be situated, though only doubtful traces of the pit can be observed.

There are two processes on each side, each being formed of a thickened rod flanked by much thinner flanges. Presumably the more posterior of the pair is the ascending process, and it would have stood up steeply. The anterior one may have been a dermal basipterygoid process, which in most genera is very short. Its apparent length is increased in this genus by the very slender stem of the parasphenoid. Moreover, the peculiar conformation of the mouth may have necessitated an unusually long basipterygoid process and a dermal cover for it. As Gardiner and Bartram (1977) have shown, the processes of the parasphenoid are very variable in palaeoniscoids, even in genera with similarly shaped heads. It would not be surprising if unusual forms like *Ebenaqua* showed peculiar structures.

The posterior extension of the parasphenoid behind the processes is very short, presumably indicating that it covered only the prechordal part of the basicranium. This is said by Gardiner (1973, p. 115) to be a primitive feature of actinopterygians.

It is noted that the posterior end of the parasphenoid shows no structure similar to the blade illustrated by Nielsen (1952, fig. 2) for *B. groenlandica*.

The palatoquadrate is quite unossified, but from what is known of the parasphenoid and the jaw articulation, the pterygoids must have formed a steeply inclined sheet lying obliquely to the suborbital and the maxilla as shown in text-fig. 10.



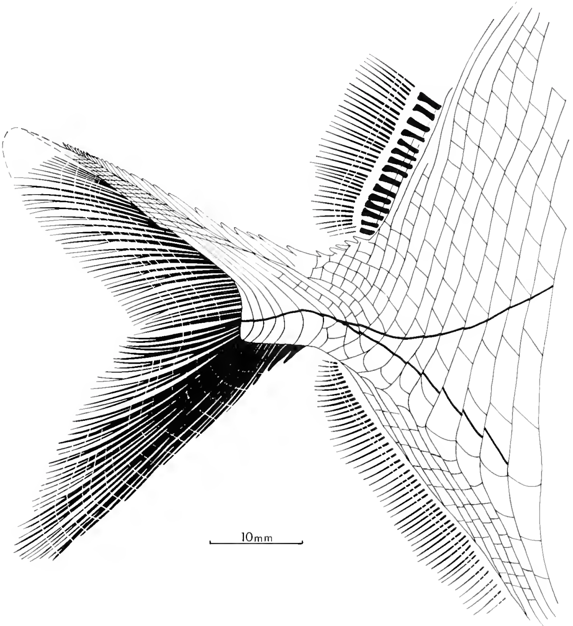
TEXT-FIG. 10. Cutaway diagram showing the dermal bones of the left side of the skull with the superimposed reconstructed parasphenoid (psph), ceratobranchial (cb), ceratohyal (ch), and palatoquadrate (pq). The shape of the palatoquadrate process is largely conjectural, and the shape of the palatoquadrate has been inferred from the preserved position of the mandible and the parasphenoid. The inferred positions of the adductor mandibulae (am) and the sternohyoideus muscles (sh) are shown.

Visceral arches. The hyomandibula was apparently unossified or only weakly ossified. The only element of the hyoid arch that can be recognized is the ceratohyal. It is a slightly ossified bone, usually crushed against its counterpart and thus has its shape obscured. It lies between the branchiostegal plate and the jaw articulation and it could be mistaken for another branchiostegal ray. However, its surface carries a few weak longitudinal lines quite unlike the dermal plates, and the cross-section of the bone is rod-like rather than plate-like. The best-preserved structures (F53871 and F58674 AM) are shaft-like and expand slightly towards their extremities. They are approximately half as long as the mandibles.

The ceratobranchials are very lightly ossified, but on several specimens they are strong enough to be impressed into the overlying operculum and preoperculum, obliquely down below the posterior end of the suborbital. This is their position as shown by Nielsen (1952, fig. 2) in *B. groenlandica*.

Squamation. The scale pattern of this species is quite distinctive. Although the flank scale rows are predominantly vertical, all specimens show a characteristic forward flexure of the rows in front of the apical angle.

The posterodorsal rows are very oblique to the body margin and the scales become progressively smaller and less ossified towards this margin. In addition, the individual scales in these rows become smaller towards the dorsal ends.



TEXT-FIG. 11. Enlargement of the posterior end of F58681 AM to show the scale and fin patterns, and the baseosts for part of the dorsal fin. The scales on the caudal peduncle are confused on this and other specimens, so that only the row outlines are shown. Those on the dorsal caudal lobe are very fine and confused so that only a generalized pattern is shown.

In the discussion that follows, the scale rows are counted along the lateral line from the first scale row behind the cleithrum. All the rows lying behind the row leading to the ventral angle (row 14 or 15) flex forwards as they approach the posteroventral margin. This flexure progressively increases on the more posterior rows back to about row 22 behind which they do not flex. Instead, the rows of fine ventral scales maintain an independent existence and meet the ends of the dorso-ventral rows abruptly (see text-fig. 11). The most distal three or four rows may meet the margin at each end. The scales in these latter rows are almost totally unossified.

There are seven to eight scale rows in front of the pelvic fin, sixteen to seventeen in front of the dorsal, and fourteen to fifteen in front of the anal. The caudal fin is at the end of a pronounced peduncle on which the scale rows are usually preserved in a confused state, and there is difficulty in distinguishing the first of the caudal rays in some specimens. However, there are twenty-nine to thirty-one rows in front of the caudal fin, though thirty-one to thirty-three scale rows are crossed by the lateral line before it terminates against the caudal fin.

The scale arrangement on the caudal peduncle and on the caudal lobe is also distinctive. Dorsoventral row 25 is the last of the complete rows to meet the ventral margin. Behind that there are five to six progressively shorter dorsoventral rows that are gradually and more or less regularly replaced by rows inclined along the length of the dorsal caudal lobe. On the peduncle the scales are short and occasionally slightly irregular in shape.

Scales extend the entire length of the caudal lobe, the number of rows towards the tip being gradually reduced first by elimination of those on the dorsal side, and then those on the ventral side as well. In addition, the scales become progressively smaller and form more elongated rhombs towards the caudal tip. On the crest of the caudal peduncle and the dorsal lobe, apparently extending right to its extremity, there is a row of overlapping ridge scales that diminish gradually in size and become progressively more overlapped distally. These number at least fifteen, but there are probably several more small uncountable ones on the caudal extremity.

Modified scales form the crest from the back of the skull to the dorsal apex. They are not regularly arranged or of uniform size, but on the best-preserved specimens they seem to alternate in position with the main scale rows. Each bears one or more spines, one being dominant if two or three are present. Similar scales with similar spines occur along the anteroventral margin. In front of the pelvic fin there is a modified scale with a rather stronger spine curved back under the fin base (Pl. 7, fig. 6).

Typical flank scales are rhomboid in form. They are flattened or slightly concave from top to bottom, but their anterior and posterior edges are bent sharply inwards, so that in section they are broadly mesa-shaped. The downturned edges meet only along their margins, leaving deep grooves separating the scale rows and imparting a strongly corrugated appearance to the surface. The amount of overlap between scales in successive rows is slight. The articulation between adjacent scales in the same rows has not been clearly observed, but several specimens (see Pl. 9, figs. 3, 6) show a regular pattern of cross-cutting lines suggesting that a long blade-like spike extends from the posterodorsal corner of a scale up under the scale above. This is very similar to the scales of *Bobasatrania* and *Platysomus*. Ornament on the flank scales consists of vertical striae which maintain their dimensions over the whole length. In structure the scales seem to be formed almost entirely of threads which produce the striae referred to above (see text-fig. 12). They show up similarly on the internal as well as the external surface, but internally they are bonded together by short, slight processes that produce a weak grid pattern.

The scales on the dorsum immediately behind the head are smaller and more irregularly shaped than those elsewhere. This seems to be the result of the flexure of the rows in response to the need to

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EXPLANATION OF PLATE 7

Ebenaqua ritchiei gen. et sp. nov.

Figs. 1–3. An almost complete small specimen, F58676 AM, showing the body form and the pelvic and anal fins.

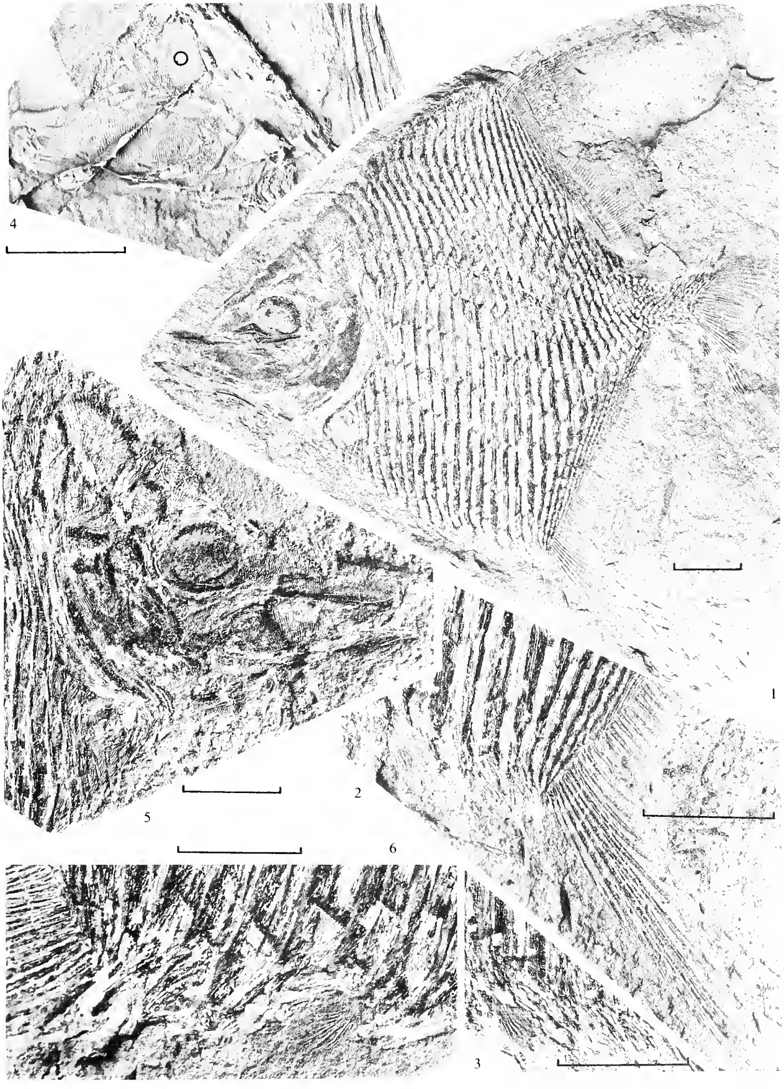
Fig. 4. Latex cast of part of the head of F53871 AM to show the ornament pattern on the bones of the maxillary and orbital regions, and the smooth convex area along the crest of the maxillary. Position of orbit marked by letter 'O'.

Fig. 5. Head of a well-preserved specimen F58694 AM. Note particularly the form of the jaw region, the ornament on the branchiostegal plate, the parasphenoid, and the row of scales below the pectoral fenestra.

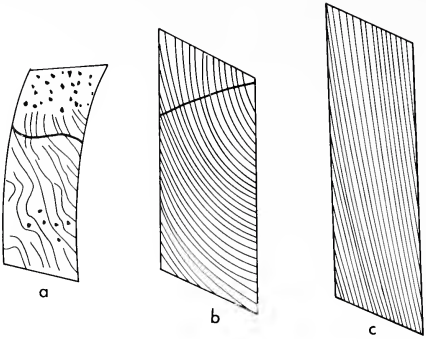
Fig. 6. Part of the ventral edge of F58681 AM to show the pelvic fin in its embayment, and the enlarged spines forming the margin on either side of it.

All scale bars are 10 mm long.

PLATE 7



CAMPBELL and PHUOC, Late Permian Actinopterygian fish



TEXT-FIG. 12. Diagrammatic representation of the shapes and ornament patterns of three scales taken about the mid-length of the body in (*a*) dorsal, (*b*) medial, and (*c*) ventral positions. Solid lines on (*a*) and (*b*) indicate lateral lines.

move the head sideways as a unit. There is also some slight modification of scale shape towards the anteroventral margin.

The ornament of the scales on the mid-flank is described above. Approaching the lateral line from below, the ornament pattern changes so that the striae run anteroventrally on the lower part of the scale and bend to run parallel with its margins on the upper part. Above the lateral line the whole scale is ornamented by striae that are oblique to the lower edges. On the uppermost scales the striae tend to become irregular, particularly on the shape specimens, and at the dorsal extremity they break up into rounded pustules.

The scales forming the rows behind the region of maximum depth conform to a similar pattern except that at the dorsal extremities there are no pustules, and the pattern in front of and on the caudal peduncle is quite distinctive (see text-figs. 10 and 11; Pl. 8, figs. 2, 7; Pl. 9, fig. 6).

The ridge scales on the caudal lobe are ornamented with very weak lines subparallel with their length.

EXPLANATION OF PLATE 8

Ebenaqua ritchiei gen. et sp. nov.

Figs. 1. Posterior part of F58683 AM. Note particularly the form of the dorsal fin and its lepidotrichs, and the way in which the scale rows are oriented anteroventrally to the caudal peduncle.

Figs. 2, 3. 2, posterior part of a latex cast, F53871 AM. Note the ornament pattern on the scales, the crest of ridge scales on the caudal lobe, and the lepidotrich pattern in the dorsal and caudal fins. 3, enlargement of the dorsal apex of the same specimen to show the spines on the ridge scales in front of the dorsal fin.

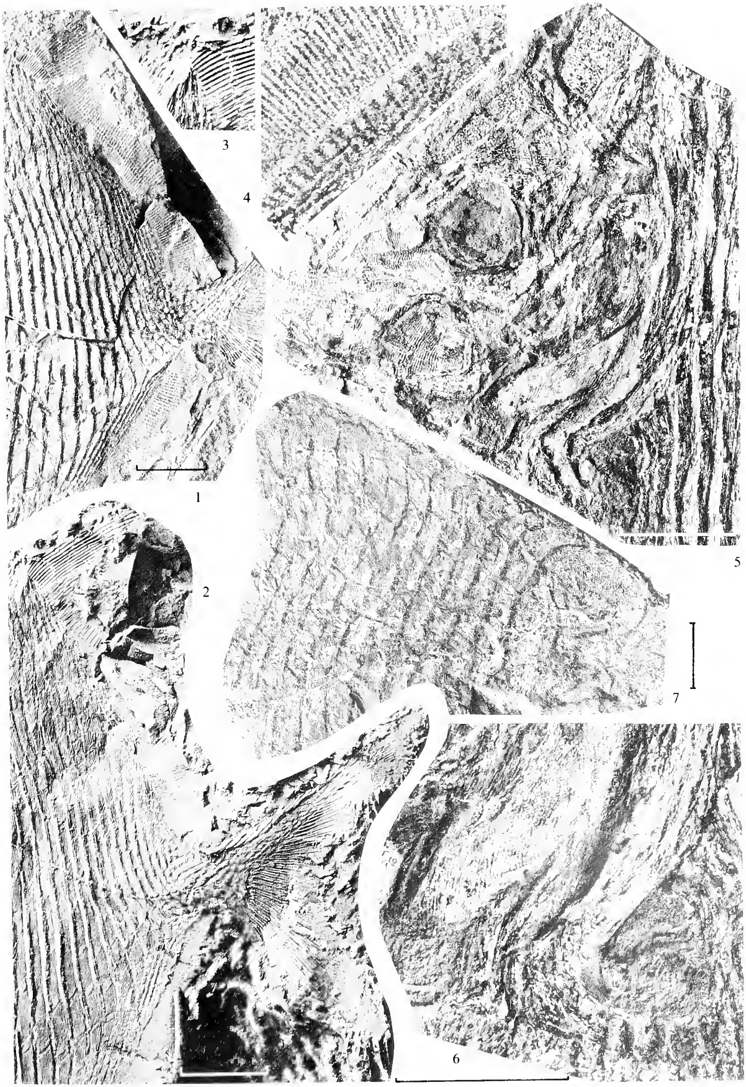
Fig. 4. Enlargement of part of the dorsal fin of F58681 AM (see Pl. 9, fig. 3) to show the baseosts.

Figs. 5, 6. 5, the head of the holotype showing almost all the bones. 6, enlargement to show the ornament on the suboperculum and the small basal part of the pectoral fin lying in the pectoral fenestra.

Fig. 7. A fragment, F58699 AM, to show the scale ornament pattern, the main lateral line canal with its crossbars, and the fragmentary irregular anterodorsal canal.

All scale bars are 10 mm long.

PLATE 8



CAMPBELL and PHUOC, Late Permian Actinopterygian fish

Lateral line canal. Everywhere the lateral line canal is in a bony sheath, and it opens to the surface through pores, some of which may be seen on F58684 AM. It usually stands out from the surface of the scales and is clearly visible except where it lies parallel with the striae of the surface ornament.

On the flanks the canal consistently follows the pattern shown on text-fig. 2. Its posterior end always lies at the junction between the ventral and dorsal caudal lobes (i.e. at the cleft in the caudal fin). The individual scale segments of the canal are usually straight and lie end to end, though in some specimens they are arcuate or even sigmoid on the first few scale rows. Given off from the body canal at irregular intervals are short dorsal tubules that are confined to the scale on which they originate. They usually occur only on the anterior half of the body, though on occasional specimens they occur further back also. Specimen F58684 AM has fourteen, which is the largest number observed on any one specimen. As many of the scales are incomplete, there could be more. On the largest specimens, F58699 AM and F10135 QM, there are occasional ventral projections matching the dorsal ones, and producing an arcuate crossbar effect similar to that observed in *Platysomus* and *Bobasatrania* by Westoll (1941).

There are two main subsidiary canals on the body. The anterodorsal one originates at the angular flexure of the canal on the supracleithrum, and can usually be traced to the upper edge of that plate, where it disappears. Irregularly on the first five or six scale rows there are discontinuous fragments of lateral line canal (see Pl. 8, fig. 7). These fragments are often curved and tend to be subparallel to the dorsal edge, so that there is some confusion between irregular ornament and the bone-sheathed lateral line canal. It is not possible to determine if these fragments were independently innervated or if they were connected by canals in the skin.

The posteroventral canal is much more regular and forms almost a straight line across eight or nine scale rows. In each row it transverses the scale that lies above the row inflexion. On some specimens the segments on successive scales lie end to end, but on others they are slightly curved and are offset. It divides from the main canal at scale row 23 or 24.

Fins. The pectoral fin is very small, consisting of approximately thirty rays only 5 mm long in a specimen 80 mm high. The possibility that the rays were much longer (like those of *Bobasatrania*) and have been obscured by the thick scales, has been considered, but there is no evidence to support it. The endoskeletal supports, seen in F58674 AM (counterpart) and F56881 AM, consist of a subtriangular plate with a broad median line from which about ten ridges radiate on each side (see text-fig. 13). From the free edge of this plate a fringe of short rays is given off all round (F53871 AM and F58674 AM counterpart). The rays are apparently unbranched, and articulations have not been observed (see also Pl. 8, figs. 5, 6).

The pelvic fin is situated in an embayment of the ventral edge. It, too, is very small, consisting of rays up to 4 mm long in a specimen 75 mm high. No endoskeletal supports are preserved, though on the two specimens with observable fins the rays are oriented so that the supports could be seen if they

EXPLANATION OF PLATE 9

Ebenaqua ritchiei gen. et sp. nov.

Figs. 1–2. 1, part of the head of the largest specimen F10135 QM. Note particularly the junction between the operculum and the suboperculum. 2, tail of same.

Fig. 3. An almost complete specimen F58681 AM with the rostrum and the anterodorsal edge destroyed. Note the overall scale pattern, the fins and the baseosts in the dorsal fin.

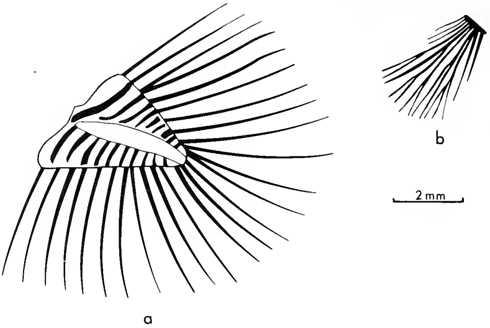
Figs. 4, 5. Two views of the head of F58676 AM in different lighting. Note the bone pattern of the head, the parasphenoid, the ceratohyal, the posterior articulation between the suborbital and the suboperculum, and the ornamented branchiostegal plate.

Fig. 6. The anterior end of the holotype. Note the jaws, the articulation between the suborbital and suboperculum, the branchiostegal plate, the lateral line system, and the row of spines on the ventromedian scales.

All scale bars are 10 mm long.

CAMPBELL and PHUOC, Late Permian Actinopterygian fish

had been ossified. The open embayment in the body outline is very distinctive, and means that the two fins must have been almost in contact during life. At the base of the fin there are nine or ten rays, the longest and strongest ones being in the middle, and those towards the margins being very weak indeed. The middle rays divide once, or possibly twice. No articulations have been observed.



TEXT-FIG. 13. Diagrams of (*a*) the pectoral and (*b*) the pelvic fins. In (*a*) the proximal structure is apparently a solid radially ridged structure as is shown on Pl. 8, fig. 6.

The dorsal and anal fins are similar in shape and structure. Each is markedly elongated towards its extremity and diminishes rapidly in length to produce a fringe of short rays that extends down on to the caudal peduncle. The fins begin immediately behind the dorsal and ventral angles respectively, the rays increasing rapidly in length to a maximum at ray 7 to 8. Only one or two rays and their bifurcations form this elongate sector, and the rapid reduction in ray length then occurs over the next five or six rays. The greatest ray length is approximately 32 mm in a specimen 72 mm high. The longest rays divide twice, but not in a regular fashion. The shorter rays are not bifurcated. At the caudal end the last eight to ten rays gradually decrease in length, producing a rounding off of the fin terminus. In specimens 75 mm high there are approximately seventy-five to eighty rays in both the dorsal and anal fins, through precise counts are not possible for both fins on any single specimen.

Each ray consists of a bony axis which has an angular edge on each side running the length of the ray—i.e. in transverse section the axis of each segment is almost square. Connecting adjacent axes there are clearly preserved membranes which were contiguous with (but perhaps not fused to) their neighbours. They split apart on compression, and in some specimens their edges are clear straight lines, suggesting that they were composed of strong tissue. This is supported by the presence of fine lineations on the membrane parallel with the length of the rays.

The proximal segments are somewhat longer on the long rays than the short ones. The long rays have twenty segments, or possibly more, but the shorter ones have only three or four. On rays of all types, the distal elements are very indistinct.

The caudal fin is heterocercal, equilobate, and posteriorly cleft. As in *Bobasatrania* the rays above and below the cleft are quite different in structure and in disposition. The cleft, of course, corresponds with the junction between the dorsal and ventral lobes. The rays in the dorsal lobe tend to be well separated at their bases and are joined by flanges like those on the median fins. Towards the caudal tip, as they become more oblique to the lobe, they become more closely spaced and the flanges are appropriately reduced. The rays on the dorsal lobe number approximately forty-five in the larger specimens, though counting of the very short rays at the caudal tip is not accurate. They usually bifurcate once, but occasionally twice. The lepidotrichs are very short and are slightly expanded at their junctions.

The rays on the ventral lobe are so crowded proximally that they are contiguous. They are also more heavily ossified than those on the dorsal lobe, and the degree of ossification increases slightly towards the ventral edge. The most ventral of the rays is very short and they gradually increase in length to the sixth or seventh, after which they gradually decrease towards the cleft. The shorter rays are undivided; those forming the longest part of the fin bifurcate only once towards their distal ends; those further towards the cleft bifurcate twice. Of course, the ossification decreases towards the distal extremities, the segments become less angular, and the membranes produce a webbed structure. So far as we can determine there are no unsegmented rays in this lobe. The proximal segments in the rays adjacent to the cleft are about 1·5–2·0 times as long as those in the equivalent dorsal lobe rays, and they are distinctly expanded at their junctions. There are fifteen to seventeen rays in the ventral lobe.

Axial skeleton. The vertebral column must have been completely unossified as no trace of it can be found. The best-preserved structures are the baseosts of the dorsal and anal fins. These are preserved on a number of specimens, but though there is ossification in the larger individuals, they appear mainly as dark stains on the rock in the smaller ones, apparently indicating that they were cartilaginous or weakly ossified. They are most clearly preserved where the scales are thinnest, and this is towards the caudal end of each fin. In these regions the crushed baseosts have a wide, flat, or slightly concave outer edge, are strongly waisted, and are expanded to a lesser extent at their inner ends. In each fin, ten baseosts support twenty-two to twenty-seven fin rays.

Axonosts are very indistinctly preserved. They are infrequently observed as compressions that deform the overlying scales, and are much weaker, when present, than those figured by Schaeffer and Mangus (1976, fig. 9) in *B. canadensis*. They are too vague to warrant description in detail, but they seem to be flat and sigmoid like those of *Bobasatrania*.

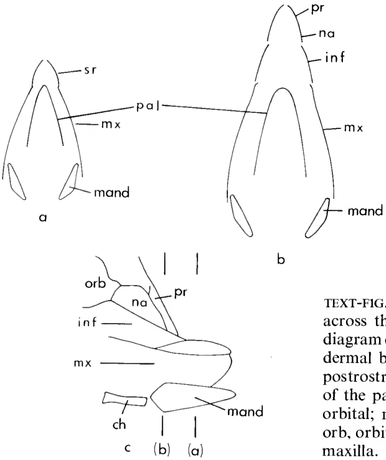
FUNCTIONAL INTERPRETATION

The environment. There is no doubt that the animal inhabited a freshwater coal swamp. The sediment is a grey shale that abounds with plant matter, and there is ample evidence from both the nature of the sediment and the distribution of the stratum that the water was quiet. There must have been large quantities of plant material in the water and although much of it had been broken down and degraded before burial, an abundance of finely divided plant tissue would have been available for feeding. Alternatively, soft invertebrates living in the mud of the bottom of the swamp would have provided suitable food. This is important because the other previously recognized members of the Order, *Bobasatrania* and *Ecrinesomus*, are both marine and have been interpreted as nibblers in coral reef environments, and *Platysomus gibbosus* is from the Kupferschiefer, a euxinic deposit.

Morphology. There are three main functions that may be investigated using the skeleton—viz. feeding, respiration, and locomotion. All these are, of course, closely interrelated, and hence it is necessary to produce a consistent interpretation of all these functions. We attempt to do this by an examination of the jaws, the buccal and branchial chambers, the body shape, and the fins. The method of analysis has been to establish the possible movements of the preserved elements, then to attempt the restoration of soft tissues, particularly the muscles, in the light of what is known of these structures in living primitive actinopterygians; and then finally to attempt a functional analysis. For the sake of continuity, the presentation below is integrated and does not follow this pattern.

(a) *The face and jaws.* In all specimens the maxilla is a large, flat, highly ornamented plate, surmounted by a smooth segment that is set at an angle to the plane of the ornamented plate. When the two sides of the fish are put together the maxillae have an apse-like form in anterior view. Unornamented bone in this fish occurs either where there is overlap or where the ossification is only slight. Because the upper sector of the rostrum cannot be involved in overlap it was probably slightly ossified, and it may have been encased in skin.

The mandible is situated in about the same position in all specimens. This seems to be the life position because if it is rotated about its articulation the tips of the mandible and maxilla would come into juxtaposition. The position of the quadrate is thus approximately fixed. It is known that the mandibles are slightly thickened at their tips and turn in slightly, but abruptly, towards the symphysis. It seems probable, therefore, that as the jaws were closed the maxillae would be rotated outwards slightly. This would have two main effects—the edges of the dentary and the maxilla would move past each other like a pair of scissors, and slight lateral expansion would be produced at the anterior end of the mouth to help counterbalance the volume change caused by vertical contraction.



TEXT-FIG. 14. (*a*), (*b*) diagrammatic vertical sections across the snout in the two positions indicated in diagram c, showing the mobile junctions between the dermal bones as gaps and immobile junctions (i.e. postrostral/nasal) as a continuous line. The position of the palate is inferred. ch, ceratohyal; inf, infraorbital; mand, mandible; max, maxilla; na, nasal; orb, orbit; pr, postrostral; sr, smooth rostral part of maxilla.

The size and strength of the jaws and adductor mandibulae (see below) indicate that the animal ate soft tissues, and these almost certainly included plants and/or small invertebrates. An inflow of water during the bite would then pull food tissues into the mouth while they were cut. This explains two unusual features of the jaw morphology—the depth of the maxilla and the straight edge of the dentary. The deeper the maxilla the greater the proportion of volume expansion of the oral cavity for any given angle of rotation (see text-fig. 14), and hence the production of a relatively greater suction. If the suction was weak, it would be an advantage for the upper edge of the dentary to be concave so as to hold the food in the bite, but this would limit the gape.

The infraorbitals overlap the maxilla and the suborbital. This loose junction did not allow rostrocaudal movement of these bones because the suborbital has an articulation with the suboperculum preventing such movement. Lateral rotation of the maxilla and the suborbital with the line of overlap as an axis would have been possible. In addition, the infraorbital/nasal suture is also open and would have permitted some lateral rotation. The vertical section through the preorbital region of the skull given in text-fig. 14 shows the possible movements of the various bones. For this to be accomplished there can have been no firm connection between the quadrate and the maxilla.

The design of the rostral region therefore seems to be that of an inverted C-spring with most of the resistance to the spreading of the maxilla being provided by skin on the top of the rostrum, supplemented by the strength of the median sutures in front of the orbits and by whatever rigidity existed in the bone overlaps and sutures.

A difficulty with this mechanism is the fact that we can find no evidence of a differentiated biting edge on either the maxilla or the dentary. There is no evidence of bone meeting bone in a biting action in any group of organisms, and hence one might expect dentine cutting edges on the above bones. The replacement of the skeletal tissue prevents testing this suggestion.

(b) *Adductor mandibulae*. There is no coronoid process, and the evidence is that there is an adductor pit situated just forward of the glenoid fossa. The adductor muscles, as is normal, would have taken origin on the outer face of the palatoquadrate. Lauder (1980*a*,*b*) has shown that in primitive modern actinopterygians fibres of the adductor mandibulae run behind and below the orbit, and to the hyomandibula. He postulates that in palaeoniscoids (1980*a*, fig. 18) there were three components of the adductor mandibulae. In *Ebenaqua*, however, there seem to be mechanical limits to such a scheme. It is unlikely that in such a small jaw a muscle would extend to the postorbital/hyomandibula region, especially as such a muscle would have no mechanical advantage when the jaw was open, and little advantage when it was closed. It may be that a posterior division of the adductor was lost in this group, but if present it must have been short and have taken its origin from the palatoquadrate below the orbit. The median and anterior divisions would have originated well forwards of the orbit. The arrangement would have been as shown in text-fig. 10. The muscles would have formed a rather thin sheet to fit in the confined space between the maxilla and the palatoquadrate. The palatoquadrate must have been cartilaginous or very poorly ossified, and so presumably was somewhat flexible. The contraction of the adductors would have pushed the quadrate outwards slightly and this would have at least maintained the lateral position of the maxilla, tending to maintain the volume of the front of the mouth during the bite.

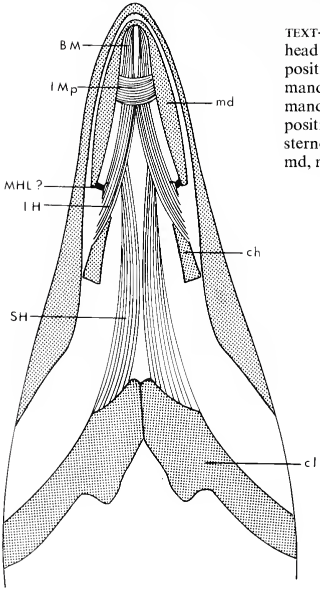
During the closing of the mouth the posterior intermandibularis muscles would have been relaxed, allowing full lateral expansion of the mandibular rami.

(c) *Abduction of the jaws*. For several reasons we believe that contraction of the epaxial and hypaxial musculature to produce tilting of the cranium and the shoulder girdle respectively, would have been of no consequence in *Ebenaqua*. The shape of the head and the forward position of the mouth would prevent movement of the cranium having any effect on the size of the gape. In any case the gape would have been small and the hyoid musculature would have been adequate to control it (see Lauder 1980*a*, 1982, for summary and references) (see text-fig. 15).

The ceratohyal part of the hyoid arch was strong and, as argued above, it was well separated from the hyomandibula, so that the epihyal and interhyal must have been long and cartilaginous, and hence very flexible. The sternohyoids would therefore have been able to produce considerable retraction of the hyoid bar, and some of this movement would have been mediated to the mandible via the tissues of the floor of the chamber. Lauder (1980*a*) has concluded that a mandibulohyoid ligament was primitive for actinopterygians, and that the sternohyoids functioned in retracting the mandible by the transmission of stress from the hyoid to the mandible via this ligament. It is possible that such a ligament existed in *Ebenaqua*, but it would be situated much further forward than in any of the forms discussed by Lauder. Even if such a mechanism existed, muscles between the hyoid arch and the mandible would also have had an important role, and in view of the distance between the ceratohyal and the mandible, muscles operating independently of the sternohyoids would seem to be necessary to provide the required delicate control over mandible movement. The geniohyoids operate in this way in higher fishes, but Lauder (1980*a*, p. 312) concluded that palaeoniscoids lacked these muscles. On the other hand, the interhyoideus muscles are part of the primitive actinopterygian hyoid musculature. Contraction of such muscles would not only have provided fine control on the opening of the mandible, but would also have exercised a control on the spread of the mandibular rami and thus on the volume of the buccal cavity. During this phase the intermandibularis posterior muscles would have been contracting, but presumably they did not cause the mandibular rami to move together. Rather, they exerted a control on the rate of spreading of the rami under the influence of the interhyoideus and sternohyoideus muscles.

In passing we note that in *Ebenaqua* there is no possibility of any connection between the action of the levator operculi and mandibular depression, which is said by Lauder to be a halecostome character.

Another important point relates to the absence of gulars, and the lack of a bony cover to the floor of the mouth and the gill chamber in front of the branchiostegal plate. Presumably this was covered



TEXT-FIG. 15. Diagrammatic ventral view of head and shoulder girdle to show the inferred positions of the main muscles. BM, branchiomandibularis; IH, interhyoideus; IMp, intermandibularis posterior; MHL?, possible position of mandibulohyoid ligament; SH, sternohyoideus; ch, ceratohyal; cl, cleithrum; md, mandible.

with loose skin, above which lay the usual intermandibularis and branchiomandibularis or interhyoideus muscles. If the space was covered by soft tissues it would be expected that they would play a passive role and this could be of significance. For example, if the floor of the mouth was covered with gular plates the volume of the buccal cavity would be increased by contraction of the interhyoideus muscles, but decreased when they relaxed and the jaws closed (Lauder 1980*a*, fig. 18). There would be no such control on volume of the buccal cavity in *Ebenaqua*, though with the soft floor in the mouth one would expect a less rapid decrease in volume as the jaws closed, and this would enhance the effect of the slight spread of the maxillae and suborbitals in controlling the rate of decrease of buccal volume as the jaws closed.

(d) *The posterior buccal and lower branchial cavities.* From an evolutionary point of view the shapes of these cavities have been produced largely by the forward movement of the jaws. The ceratobranchials extend around beneath the suborbital where the mouth and gills are able to occupy the full width of the head unimpeded by the jaw musculature. This is an important feature in an animal with such a narrow head. On the other hand, the dorsal part of the branchial chamber has been reduced slightly in comparision with that of other palaeoniscoids. The overall effect of the forward migration of the jaw has been to displace the main volume of the branchial chamber downwards and forwards.

Under these circumstances one might have expected to find a number of branchiostegal rays, but this is not so. Instead, a large subopercular and an unusual suborbital cover the flanks of the most voluminous part of the branchial chamber. The suborbital is flexibly fixed to the maxilla, which restricts its range of movement to a lateral rotation. Hence the only dermal plates able to move to permit egress of water from the gills are the operculars, suboperculars, and the branchiostegal plates.

It is important to appreciate that the last-mentioned plates give evidence of being compound, and each is formed of at least three branchiostegal rays. There must have been an advantage in forming such a plate to act as what is, in effect, a second suboperculum that could move laterally and also rotate around an axis along the ventral edge of the suborbital, thus widening and opening the chamber from the ventral mid-line of the animal.

Of considerable significance is the process on the posterior end of the suborbital. This articulates into a notch on the subopercular where there may have been a ligament attachment, and it is overlapped by the edge of the preopercular. It is clear, therefore, that lateral movement of the suborbital will result in movement of the whole opercular series of bones and the hyomandibula, which is assumed to have been attached to the preopercular in the usual way.

It is necessary also to reconstruct as much as possible of the hyoid arch. The hyomandibula is not preserved, but assuming the usual actinopterygian relationships between it and the dermal bones, and using Nielsen's work on *B. groenlandica* as a guide, inferences are possible. From the size and position of the preoperculars the hyomandibula would be expected to be large and vertically placed. Such a structure is found in *B. groenlandica*, but its posterior blade is larger than expected. Given the relative sizes of the preoperculars in this species and in *Ebenaqua*, an even broader hyomandibula with a more elongate opercular process could be inferred for the latter.

The ceratohyal is a long bone situated at a distance from the hyomandibula with which it must have been connected by a long cartilaginous epihyal and interhyal. The strength of the ceratohyal together with the powerful cleithrum extending around to its symphysis suggests that the sternohyoideus muscles were strong; what is more, the position of the ceratohyal with its head inside the median part of the ventral edge of the suborbital is ideal to produce maximum lateral movement of that bone on contraction of the sternohyoideus muscles.

(e) *Suspensorium and operculum*. It is necessary now to examine the possibility of interpreting the musculature that activates the suspensorium and the operculum. Many of these muscles originate on the walls of the neurocranium, and hence there is no possibility of reconstructing them; but some originate on the roofing bones and others around the posterodorsal edge of the orbit. A feature of *Ebenaqua* is the thickening of the dermal bones in the area where such muscles would have taken origin—the lower part of the dermopterotic, the dermosphenotic, the supraorbital, and the infraorbitals. This suggests that the muscles would have been powerful. The levator arcus palatini and the levator hyomandibulae would have originated on the dermopterotic and the dermosphenotic, and produced considerable vertical and the lateral expansion of the palate. Presumably they would contract at the same time as the sternohyoideus muscles and reinforce the expansion of the buccal and lower branchial chambers. They sometimes assist with the abduction of the operculum but such could not have been the situation in *Ebenaqua* because as has been shown below, expansion of the lower branchial chamber would have tended to close the operculum. Opening the operculum would then have become a function of the dilator operculi which would have taken origin on the dermosphenotic.

Now the problem becomes one of understanding the mechanism of the dilation and contraction of the branchial chamber, and the synchronization of these movements with the suction activity of the mouth. In attempting to solve this problem the posterior process on the suborbital seems to us to be of critical importance. As indicated above, lateral movement of that plate would lift the subopercular and the lower end of the preopercular, and hence the lower end of the hyomandibula. Note that although the subopercular would be moved laterally, its edge against the cleithrum would be held shut both because its hinge against the preopercular is also being moved laterally, and because the leverage is being applied in front of that hinge. A great deal therefore depends on the means for producing lateral movement in the suborbital.

Lateral movement at the base of the branchial chamber in actinopterygian fishes at all evolutionary grades is produced by contraction of the sternohyoideus muscles acting to draw the hyoid bar backwards and downwards. The bowed hyoid bar pushes laterally and ventrally on the overlying plates, usually the preoperculars and the branchiostegal rays (Alexander 1970, pp. 72–76 for summary). In *Ebenequa* the hyoid bar would push laterally against the lower part of the suborbital and downwards against the branchiostegal plate. The suborbital process would then lift the subopercular and the preopercular. Note that these movements would not cause the subopercular or the branchiostegal plates to rotate open. The effect of lifting the front of the subopercular would be to close its posterior edge more firmly against the cleithrum, and lifting the anteroventral corner of the operculum would produce the same effect on that bone. Consequently, the effect of dilating the suborbital would be to dilate the branchial chamber as a whole while keeping it firmly closed around its edges.

(f) *Biting/respiration cycle*. The sequence of biting and respiratory movements is extremely difficult to determine from skeletal considerations alone, as the work of Schaeffer and Rosen (1961) and Lauder (1979, 1980*a*, *b*, 1982) has shown. However, what is needed for *Ebenaqua* is the postulation of an internally consistent sequence of movements that would be possible given the proposed skeletal and muscle reconstruction. In proposing this sequence the only other control is what is known of the cycles in primitive modern fishes.

The following cycle of movements and effects seems to be possible given the bone/muscle arrangements postulated above.

1. The jaw begins to drop with relaxation of the adductor mandibulae and the contraction of the sternohyoideus and interhyoideus muscles. The operculum and the hyomandibula are abducted. Water moves through the mouth and into the lower part of the buccal cavity because, although the front of the mouth is laterally contracting a small amount due to the inward movement of the maxillae, it is vertically expanding with the jaw opening and this will probably maintain the volume of the cavity.

2. The further movement of water backwards in the mouth is then accomplished by increasing the volume of the buccal cavity as the hyoid arch pushes the suborbital laterally, thus pushing the opercular series outwards but not opening them, and by expansion of the roof of the mouth on contraction of the levator arcus palatini.

3. The jaw reaches maximum opening and the buccal and lower branchial chambers approach maximum expansion. The operculum remains abducted.

4. The jaw closes rapidly with fast adductor action and relaxation of the interhyoideus and levator arcus palatini muscles. The spreading of the maxillae compensates for the decrease in oral volume caused by the upward movement of the jaws, and at the same time the buccal and lower branchial chambers attain maximum expansion with the sternohyoideus muscles still contracted. A slight sucking of water into the front of the mouth during the completion of the bite holds the soft food in the mouth while it is cut by the scissors-like action of the jaws.

5. The buccal and lower branchial cavities collapse on relaxation of the sternohyoids. The operculum opens on contraction of the dilator operculi and the abduction of the hyomandibula. Because the mouth is closed, water is forced out between the operculum and suboperculum and the cleithrum, and ventrally between the branchiostegal plates. This completes the cycle.

Such a sequence maintains a water flow through the mouth and gill chambers without any reversals; it provides a pump for gill ventilation in a fish that moves slowly and feeds by browsing; it provides a suction in the mouth at the time of biting; and it does not require the action of any anatomical structures that are unknown in living primitive fishes.

The efficacy of the proposed sequence may be thought to depend too heavily on the fine relative timing of the movements—in particular the slight delay in the attainment of maximum expansion of the buccal and lower branchial chambers after the mandible has opened, and the still further delay in the abduction of the operculum. However, such delays have been established in modern fishes at all levels of evolutionary development (Ballantijn and Hughes 1965; Lauder 1979, 1980*a*, *b*, 1982).

Recently Lauder (1980*a*, p. 315) has criticized Hutchinson's suggestion (1973) that redfieldiiform fishes were suction feeders, mainly on the grounds that he had misinterpreted the effects of retraction of the pectoral girdle on pressures in the buccal cavity, but partly on the grounds that these fishes 'lack the morphological features identified here as correlates of a suction-feeding mechanism. The maxilla is fixed to the cheek, an interopercular bone is absent, and a single mechanism exists for mandibular depression.' Similar criticisms could be levelled at our interpretation of *Ebenaqua*, but they have validity only if suction is associated with one type of feeding and is produced by one mechanism.

What we are proposing is a modified set of mechanisms associated with a slow-moving, plant- or soft invertebrate-feeding fish, as opposed to the fast-moving predators studied by Lauder.

(g) *Fins and locomotion.* The striking features of the fins of *Ebenaqua* are: (*a*) the greatly reduced pectorals and pelvics that have become almost vestigial, and are placed well towards the ventral edge of the animal; (*b*) the symmetry of the dorsal and anal fins, not only in form and size, but also in the manner of subdivision of the rays; (*c*) the association of two or three rays with a single baseost, and the increased strength and marginal position of the baseosts towards the posterior ends of both the dorsal and anal fins; (*d*) the greater length and strength of the rays at the anterior ends of the dorsal and anal fins; (*e*) the symmetrical outline of the caudal fin; (*f*) the tendency of the fins to be preserved in similar orientations on most specimens indicating that they had a certain rigidity of ray orientation and were not collapsible.

The effect on movement produced by a heterocercal tail depends primarily on the relative area and flexibility of the dorsal and ventral fin ray lobes (Affleck 1950). In *Ebenequa* the dorsal lobe is long and slender, whereas the ventral lobe has a muscular scale-covered base that bears an array of thick densely clustered rays with long lepidotrichs. These rays together would have given the ventral lobe a rigidity comparable with that of the dorsal lobe. It is interesting to note, therefore, that the distribution of the weaker, more flexible rays with inter-ray membranes tends to be almost symmetrical around the median cleft. The caudal fin, though heterocercal, would have been approximately isobatic.

The swimming capacities of actinopterygians have been summarized recently by Webb (1982), who has emphasized the distinction between steady or time-independent locomotion, and unsteady or time-dependent (acceleration and turning) locomotion. Modern fishes with the general body form of *Ebenaqua*, with their large surface area/volume ratios and poor streamlining, are not adapted to even moderately fast steady locomotion. In addition, the scale rows on *Ebenaqua* stand out from the body producing strong corrugation. Though this is not of sufficient amplitude to penetrate the laminar boundary layer for expected movement velocities if the fish is treated as a rigid body, the thickness of the boundary layer decreases sharply with a flexing body and 'the mean drag of a flexing fish appears to be about 2 to 5 times greater than that of an equivalent non-flexing body' (Webb 1982). Under these circumstances the amplitude of the scale corrugation in *Ebenaqua*, estimated to be about 1 mm on the flanks of a fish 10 cm long, could become significant if the animal engaged in steady locomotion.

On the other hand, *Ebenaqua* has a large caudal fin and body area, long anal and dorsal fins, flexible body, and large muscle mass/body mass ratio, which are considered to be the morphological characters of unsteady movers. The effects of frictional drag are less significant for animals of this kind, inertial drag becoming dominant. Scale corrugation would therefore not be of consequence.

We conclude that *Ebenaqua* belonged to the class of unsteady locomotors, and because it has many of the optimal features of this class it probably had a well-developed capacity to accelerate and produce short darts either to escape predators or to grasp food.

The pectoral and pelvic fins are normally used for manœuvre, balance, and braking. The dorsal and anal fins serve several functions depending on the variety of movements the rays are able to accomplish. When extended they may act with the caudal fin to propel the animal, and in this position they also provide stability in a vertical plane and at the same time they may act as a rudder. In some holosteans and teleosts with long dorsal and anal fins, waves move along extended rays in either direction, and such fin movements provide control on both forward and backward movement, as well as on positive and negative pitch (Harris 1937, 1953; Gosline 1971).

If *Ebenaqua* is an unsteady swimmer, as has been inferred above, there would have been little need for the paired fins to act as brakes. Clearly they were too small, and placed far too low on the body, to be effective in this role in any case. They were also too small to function in any but the smallest equilibrium adjustments. The dorsal and anal fins must therefore have performed these roles. Holosteans and teleosts have flexible fins because of individual muscle control on each ray, but the conventional view is that the fins of primitive actinopterygians, of which *Acipenser* is a modern example, had 'fin muscles arranged like those of sharks and had the same range of fin movements as sharks' (Alexander 1970, p. 38). If this is true, the range of fin movements in *Ebenaqua* would presumably be too limited to produce the effects required by our analysis. However, no other control mechanism was available in that fish, and therefore we question the conventional view. This is not surprising as the number of living chondrosteans available for observation is very small, and there is no guarantee that they have fin structures representative of the whole group.

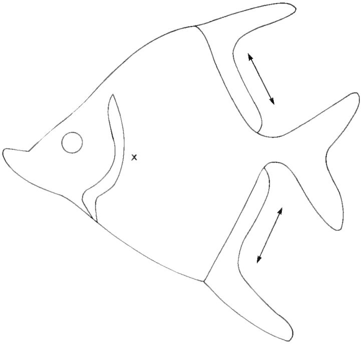
In this connection we note that the rays of both dorsal and anal fins become finer and shorter posteriorly, that there is a sudden reduction in ray length and strength after the first few rays, and that the baseosts are apparently strongest and closest to the rays on the posterior parts of the fins. These features suggest to us that both fins were more flexible toward the rear, the site of more powerful muscle insertion on the baseosts. The waves passing along the flexible part of the fin from front to back would decrease in wavelength and presumably provided finer control. The long, relatively less flexible rays towards the anterior extremity of each fin would prevent yawing.

We also note that the orientation of these fins would have promoted positive and negative pitch in an effective fashion. Both fins are set at approximately 60° to the horizontal axis of the fish, and assuming a centre of buoyancy as shown in text-fig. 16 and that the forces produced by undulations act along the length of the fin, these forces would exert a maximum pitching moment.

Waves passing uniformly along each fin from front to back would assist the forward motion produced by the tail. Waves passing uniformly in the reverse direction would act to brake the animal in a straight line or to provide forces to balance the propulsion effects of the respiratory currents and thus allow it to hover in the water. Reverse waves passing at different rates along the two fins would produce braking and either positive and negative pitch (for summary in modern fishes see Lindsey 1978).

This raises the question of buoyancy. Some workers such as Romer (1966) have assumed that chondrosteans were negatively buoyant, and that therefore they had to move at moderate speeds to remain off the bottom. This seems to us to be inherently improbable because many of them were predaceous and had downward driving heterocercal tails, but the pectoral fins were not appropriately placed or shaped to provide lift. Species with these characteristics must have had neutral or positive buoyancy.

Harris (1937, 1953) has shown that asymmetrical undulations caused by movement of the rays at different speeds on opposite sides of the sagittal plane; may produce forces at a high angle to that plane. Large median fins normally produce stability against yaw and roll, but in *Ebenaqua* it may be that they served this function by remaining unflexed when the fish was moving in a straight line, but could induce yaw and roll as required, by wave formation. We believe that they did act in this way because there seem to be no other mechanisms available to produce yaw and roll.



TEXT-FIG. 16. Outline of *Ebenaqua ritchiei* showing directions of movement resulting from the action of the dorsal and anal fins. Note that with the centre of buoyancy placed approximately in the position x on the longitudinal axis, these fins exert maximum torque.

Consequently, we conclude: the animal was a slow mover, capable of short bursts of acceleration; that it had neutral buoyancy; that in the absence of effective pectoral and pelvic fins, the dorsal and anal fins must have been able to brake, pitch, yaw and roll the animal; that to do this requires a capacity to produce waves moving in either direction in each fin; that the arrangement of length and strength of the rays is such as to make these waves possible; that although there are at least two rays to each baseost, this cannot be regarded as inhibiting effective wave formation despite the evidence from living chondrosteans; and that there is no evidence for collapsible dorsal and anal fins.

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APPENDIX

'*Platysomus gibbosus*' Agassiz

Plate 10, figs. 1–4; text-fig. 17

Agassiz (1835) nominated five species as members of his new genus, all from the Late Permian in Germany or England. Four of these were placed in synonymy by Woodward (1891) without discussion, and discussed under the specific name *Platysomus gibbosus* (Blainville). The species omitted was *P. macrurus* Agassiz which he had assigned to *Globulodus* Munster, 1842. No systematic review of the remaining species has been attempted, though Schaumberg (1977) continues to use the name *P. striatus* Agassiz, and has figured details of the skull roof, body form, and scales as though the species is distinguishable.

Professor Goujet has sent us photographs of some of Agassiz's figured specimens now housed in the Institute de Paleontologie, Museum National d'Histoire Naturelle, Paris, but these specimens are too poorly preserved to permit interpretations to be made, at least without direct reference to the specimens themselves.

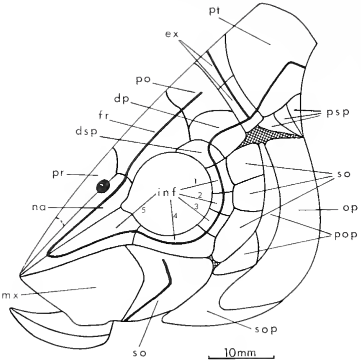
In the absence of a complete analysis of this group, we wish to provide a description of certain Kupferschiefer specimens that are of the *P. gibbosus* type mainly to point out that their relationships are quite different from those currently accepted.

The specimens are: 841-1 Geologisch Paläontologisches Institut und Museum der Universität, Göttingen, from Ilmenau; and 3216–3218 Geological Museum, Copenhagen, from Wolfsberg, Richeldorfer Gebirge.

The Göttingen specimen is preserved as an external impression in a concretion, and hence has some relief. This permits the bone outlines to be traced more easily than on the flattened specimens. The surface detail also is well preserved. The Copenhagen specimens are almost completely flattened in a slightly calcareous siltstone. The bone can be removed with dilute hydrochloric acid causing little damage to the matrix, and this has been done for one head, 3217, with good results.

Emphasis is placed on details of cranial morphology because these indicate the relationships of the species most clearly. Only the main points of postcranial morphology are mentioned. A more complete description, and a discussion of the taxonomy of this species, will await work on the abundant material in European museums.

Description. The post-temporal is large, and rather rounded in outline medially. The lateral line canal has an angular bend at its radiation centre, which is below its topographic centre. The two extrascapulars are long and narrow, the median being smaller than the lateral. The parietal and dermopterotic are present but their lateral-line connections are not clear, and the shape of the dermopterotic is apparently different in the two specimens in



TEXT-FIG. 17. Reconstruction of the head of '*Platysomus gibbosus*' based largely on specimen 841-1 Geologisch-Paläontologisches Institut und Museum, Göttingen.

which it is preserved. The best estimates of outlines and canals are given in text-fig. 17. The frontal is a long bone, and seems to reach to the upper edge of the eye where it forms an inflected flange. The post-rostral and the nasal are both long and splinter-like, their anterior edges being obscured on all our specimens. The anterior naris is well preserved, and lies on the junction between these bones.

Between the rostrum and the dermosphenotic are five infraorbitals, the most anterior one of which is very long. Infraorbitals 4 and 5 have a loose overlapping contact with the maxilla and the bone behind it. The lateral line canal can be distinguished running around the complete set, and sends off short tubules towards the eye on the three bones in the post-orbital position. The canal on to the dermosphenotic is not clear, and text-fig. 17 shows the best estimate of its position. Behind the infraorbitals there are three bones that can only be suborbitals. The upper two are almost square, but the third is elongate and runs ventral to meet the end of the bone behind the maxilla that in *Ebenaqua* we have referred to as a suborbital. As can be seen from the text-figure, it is in series with the suborbitals, and we refer to it in this species as the anterior suborbital. Its suture against the maxilla is convex backwards, unlike that of *Ebenaqua*. The Göttingen specimen shows that the suture is of the overlapping type, and runs concordantly with the ornament so that it is normally difficult to observe. Moreover, it is possible that in adults these bones tend to become fused. The lateral line on this bone is clear. It enters the bone obliquely from the overlying skin, runs ventrally to the ossification centre, and then turns abruptly to run a course to the anteroventral corner.

The maxilla is large and edentulous, and along its ventral edge there is a curved, lenticular expansion that probably added to the slicing effect of the bite.

There are clearly two preoperculars forming a thin boomerang-shaped outline and making contact with the posterior extremity of the anterior suborbital. Apart from the fact that they touch we can add nothing to the relationship between these bones.

On the Göttingen specimen three postspiraculars can be distinguished. The region is badly broken, but there is little doubt that the anterior edge of the middle one is strongly curved. The operculum is a long, narrow,

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EXPLANATION OF PLATE 10

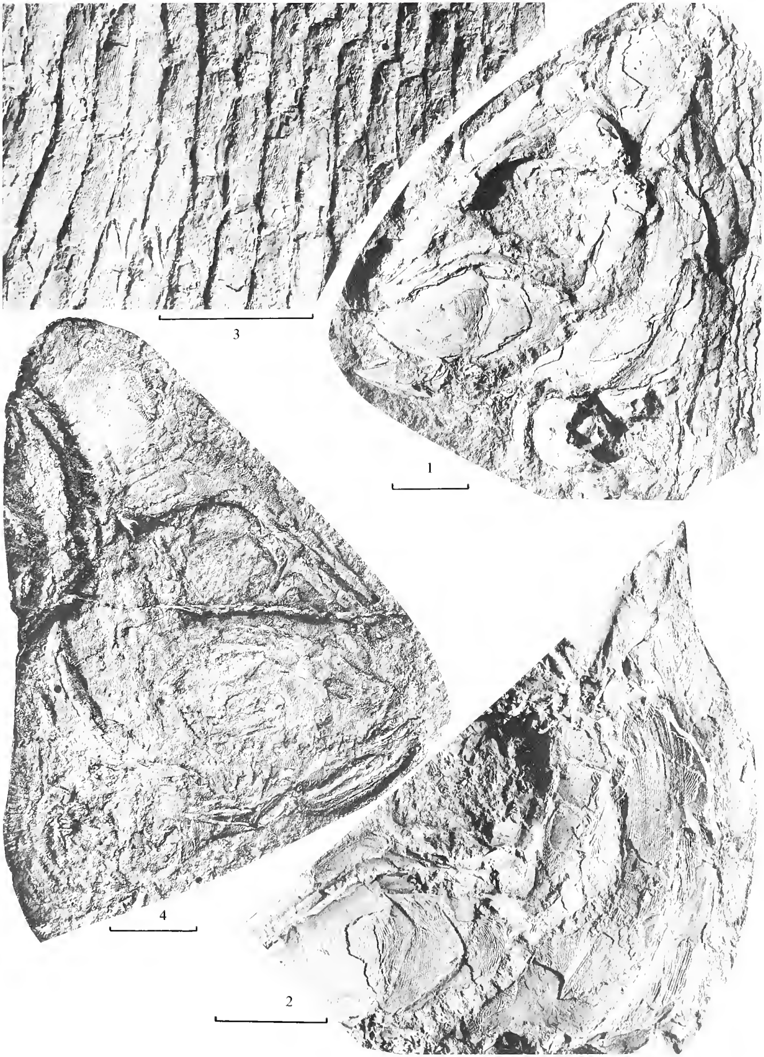
'*Platysomus gibbosus*' Agassiz

Figs. 1–3. Latex cast of specimen 841-1 Geol. Pal. Inst. und Mus. der Univ., Göttingen, from Ilmenau. 1, 2, photographed in different lights to show details of the opercular and suborbital regions. 3, shows the detail of the scales on the anteromedian part of the flank. Note the peg and socket arrangement on the lower left.

Fig. 4. Latex cast of specimen 3217 Geological Museum, Copenhagen, to show details of the ornament pattern on the head bones, the overall size of the mandible, and the branchiostegal rays.

All scale bars are 10 mm long.

PLATE 10



CAMPBELL and PHUOC, Late Permian Actinopterygian fish

approximately parallel-sided bone that extends well round to a point beneath the posterior end of the anterior suborbital. It overlaps, in a deep rounded V, the much smaller suboperculum, which extends around below the anterior suborbital.

Preservation of the bones below the suboperculum is not good, but 3217 in the Copenhagen collection seems to have a broad plate made of about five posteriorly joined branchiostegal elements that are free at their anterior ends, producing a deeply serrated edge. There is probably also at least one free branchiostegal ray.

The cleithrum and supracleithrum are strong bones. Ventrally there is a deep embayment in the cleithrum for the pectoral fin.

The mandible is lancet-like in outline but in section it is narrow dorsally and abruptly expanded ventrally below a keel. The articulation lay beneath the posteroventral end of the maxilla. The individual bones cannot be distinguished but the lateral line is well developed, and runs the full length of the jaw below the keel.

The ornament of the dermal bones is very similar to that of *Ebenaqua*, consisting predominantly of striae on the lower bones of the head, but breaking up into nodes on the upper ones. The operculum is very distinctively ornamented; in addition to the vertical striae that run approximately parallel to its edge, there are finer oblique lines that abruptly strengthen and hook around as they cross the mid-length of the bone forming a pronounced series of invaginated U's.

The body scales and their ornament are also of the same type as *Ebenaqua* and *Bobasatrania*, with evidence of articulation by long blade-like pegs and shallow furrows between scales in the same vertical rows. Posteroventrally the scale rows turn abruptly and run obliquely to the margin. In this they appear to be less regular and more oblique than those of *Ebenaqua*.

The dorsal and anal fins are both situated well behind the deepest part of the body, and the anterior rays in each are the longest. The dorsal fin is short and may have as few as thirty rays, the precise number not being determinable on our material. The anal fin is much longer, extending almost to the caudal peduncle, where the rays form a very short fringe only about 2 mm long. There are approximately seventy to eighty rays in the fin. The dorsal lobe of the caudal fin continues to the extremity. It is long and acute, being 35 mm long in a fish of 125 mm total length. Its crest carries twelve to fifteen strongly overlapping ridge scales. The caudal fin has the same type of construction as *Ebenaqua* and *Bobasatrania* with strong closely packed ventral rays and thin, more widely spaced dorsal ones. It is deeply cleft.

Copenhagen specimen 3218 has the pelvic fin preserved. It is small, being approximately 5 mm long, and consists of sixteen to twenty rays attached to a paddle-like base. It is situated low on the flank about half-way along the posteroventral margin. The pectoral fin is a larger structure consisting of possibly as many as thirty powerful primary rays extending back along the body. Their posterior extent is not shown on our material, but they must extend back some distance, possibly in the manner of *Bobasatrania*.

Remarks. Despite the defects in the available material, enough is known to highlight the remarkable similarity between this species and the Bobasatraniformes. Though not mentioned above, there are other features that seem to add to these similarities, such as the position and shape of both the axonosts and baseosts. Unfortunately, they are not well-enough preserved in our material to warrant description.

Attention is drawn to the fin pattern. The pelvic fin is quite unlike that of *Ebenaqua* in both form and position, and *Bobastrania* seems to have lost its pelvic fins. Both dorsal and anal fins are much shorter and weaker in '*P. gibbosus*' than in the above genera, whereas the pectoral fin is much stronger than that of *Ebenaqua* and at least as strong as that of *Bobasatrania*. From a functional point of view, '*P. gibbosus*' was clearly a scissors-type feeder that depended for on its pectoral and pelvic fins for locomotory control more than did *Ebenaqua* and *Bobastrania*. It also has unreduced suborbitals, a relatively undeveloped snout, and a complex branchiostegal arrangement. In all these features, '*P. gibbosus*' is the most primitive-known member of the Bobasatraniformes.

REFERENCES

AFFLECK, R. J. 1950. Some points in the function, development and evolution of the tail in fishes. *Proc. zool. Soc. Lond.* **120,** 349–368.

AGASSIZ, L. 1833–1844. *Recherches sur les poissons fossiles*, 5 vols., 1420 pp., 396 pls., with supplement. Neuchâtel.

ALEXANDER, R. MCN. 1970. *Functional design in fishes*. Hutchinson, London, 160 pp.

BALLANTIJN, C. M. and HUGHES, G. M. 1965. The muscular basis of respiratory pumps in the trout. *J. exp. Biol.* **43,** 349–362.

GARDINER, B. G. 1963. Certain Palaeoniscoid fishes and the evolution of the snout in actinopterygians. *Bull. Br. Mus. nat. Hist.* (*Geol.*), **8** (6), 255–325, pls. 1–2.

GARDINER, B. G. 1967*a*. Further notes on the Palaeoniscoid fishes with a classification of the Chondrostei. Ibid. **14** (5), 145–206, pls. 1–3.

——1967*b*. The significance of the preopercular in actinopterygian evolution. *J. Linn. Soc.* (*Zool.*), **47,** 197–209.

——1973. Interrelationships of teleostomes. *In* GREENWOOD, P. H., MILES, R. S. and PATTERSON, C. (eds.). *Interrelationships of fishes*, 105–135. Academic Press, London.

——and BARTRAM, A. W. H. 1977. The homologies of ventral cranial fissures in osteichthyans. *In* ANDREWS, S. M., MILES, R. S. and WALKER, A. D. (eds.). *Problems in vertebrate evolution*, 227–245. Ibid.

GOSLINE, W. A. 1971. *Functional morphology and classification of Teleostean fishes.* University of Hawaii Press, 208 pp.

GRAHAM-SMITH, W. 1978. On the lateral lines and dermal bones in the parietal region of some crossopterygian and dipnoan fishes. *Phil. Trans. R. Soc. Lond.* (B) **282** (986), 41–105.

HARRIS, J. E. 1937. The mechanical significance of the position and movements of the paired fins in the Teleostei. *Publ. Carnegie Inst. Washington*, **475,** 171–189.

——1953. Fin patterns and mode of life in fishes. *In* MARSHALL, S. M. and ORR, A. P. (eds.). *Essays in marine biology*, 17–28. Edinburgh.

HUTCHINSON, P. 1973. A revision of the Redfieldiiform and Perleidiform fishes from the Triassic of Bekker's Kraal (South Africa) and Brookvale (New South Wales). *Bull. Br. Mus. nat. Hist.* (*Geol.*), **22** (3), 236–354.

JESSEN, H. 1968. *Moythomasia nitida* Gross und *M.* cf. *striata* Gross, devonische Palaeonisciden aus dem oberen Plattenkalk der Bergisch-Gladbach-Paffrather Mulde (Rheinisches Schiefergebirge). *Palaeontographica*, **128A,** 87–114, pls. 11–17.

KEMP, E. M., BALME, B. E., HELBY, R. J., KYLE, R. A., PLAYFORD, G. and PRICE, P. L. 1977. Carboniferous and Permian palynostratigraphy in Australia and Antarctica: a review. *B.M.R. J. Aust. Geol. Geophys.* **2** (3), 177–208.

LAUDER, G. V. 1979. Feeding mechanics in primitive teleosts and in the halecomorph fish *Amia calva*. *J. Zool. Lond.* **187,** 43–578.

——1980*a*. Evolution of the feeding mechanism in primitive actinopterygian fishes: a functional anatomical analysis of *Polypterus*, *Lepisosteus* and *Amia*. *J. Morph.* **163,** 283–317.

——1980*b*. On the evolution of the jaw adductor musculature in primitive gnathostome fishes. *Breviora Mus. comp. Zool. Harvard*, **460,** 1–10.

——1982. The evolution of the feeding mechanism in Actinopterygian fishes. *Amer. Zool.* **22** (2), 275–285.

LEHMAN, J. P. 1956. Compléments a l'étude des genus *Ecrinesomus* et *Bobasatrania* de l'Éotrias de Madagascar. *Ann. Paléont.* **42,** 67–94, pls. 1–9.

LINDSEY, C. S. 1978. Form, function and locomotory habits in fish. *In* HOAR, W. S. and RANDALL, D. J. (eds.). *Fish physiology, vol. 7, Locomotion*, 1–100. Academic Press, New York.

MOY-THOMAS, J. A. and DYNE, M. BRADLEY, 1938. Actinopterygian fishes from the Lower Carboniferous of Glencartholm, Eskdale, Dumfriesshire. *Trans. R. Soc. Edinb.* **59,** 437–480.

——and MILES, R. S. 1971. *Palaeozoic fishes.* Chapman and Hall, London, 259 pp.

NIELSEN, E. 1952. A preliminary note on *Bobasatrania groenlandica*. *Meddr. Dansk geol. Forening*, **12** (2), 197–204.

PATTERSON, C. 1973. Interrelationships of holosteans. *In* GREENWOOD, P. H., MILES, R. S. and PATTERSON, C. (eds.). *Interrelationships of fishes*, 233–305. Academic Press, London.

ROMER, A. S. 1966. *Vertebrate paleontology.* University of Chicago Press.

SCHAEFFER, B. and MANGUS, M. 1976. A lower Triassic fish assemblage from British Columbia. *Bull. Amer. Mus. nat. Hist.* **156,** 515–564.

——and ROSEN, D. E. 1961. Major adaptive levels in the evolution of the actinopterygian feeding mechanism. *Amer. Zool.* **1,** 187–204.

SCHAUMBERG, G. 1977. Der Richelsdorfer Kupferschiefer und seiner Fossilien, III. Die tierischen Fossilien des Kupferschiefers. 2. Vertebraten. *Aufschluß*, **28,** 297–352.

STAINES, H. R. E. 1972. Blackwater Coalfield: correlation of seams in the Rangal Coal Measures, Mackenzie River to Sirius Creek. *Rept. geol. Surv. Queensland*, **70,** 1–11.

——1975. Coal exploration, south central Bowen Basin. *Rept. geol. Surv. Queensland*, **89,** 1–18.

STENSIÖ, E. A. 1932. Triassic fishes from East Greenland collected by the Danish expeditions in 1929–1931. *Meddr. Gronland*, **83** (3), 1–305, pls. 1–38.

TRAQUAIR, R. H. 1879. On the structure and affinities of the Platysomidae. *Trans. R. Soc. Edinb.* **29,** 343–391.

WEBB, P. W. 1982. Locomotor patterns in the evolution of actinopterygian fishes. *Amer. Zool.* **22** (2), 329–342.

WESTOLL, T. S. 1941. The Permian fishes *Dorypterus* and *Lekanichthys*. *Proc. zool. Soc. Lond.* **111,** 39–58.

——1944. The Haplolepidae, a new family of Late Carboniferous bony fishes. A study in taxonomy and evolution. *Bull. Amer. Mus. nat. Hist.* **83,** 1–122.

WHITE, E. I. 1932. On a new Triassic fish from north-east Madagascar. *Ann. Mag. nat. Hist.* ser. 10, **10,** 80–83.

WOODWARD, A. S. 1891. *Catalogue of the fossil fishes in the British Museum* (*Natural History*), ii. xliv + 567 pp., 16 pls. London: Brit. Mus. (Nat. Hist.).

—— 1939. The affinities of the pycnodont ganoid fishes. *Ann. Mag. nat. Hist.* ser. 11, **4,** 607–610.

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LATE CAMBRIAN TRILOBITES FROM THE NAJERILLA FORMATION, NORTH-EASTERN SPAIN

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ABSTRACT. Six late Cambrian trilobite taxa are described from the Najerilla Formation of the Mansilla district, Sierra de la Demanda, Logroño Province, northern Spain. *Maladioidella colcheni* sp. nov., *Langyashania felixi* sp. nov., an undetermined aphelaspidine genus and species, and an undetermined genus and species probably referable to Leiostegiidae, constitute the fauna of the basal member of the Najerilla Formation; and a younger assemblage comprising an undetermined solenopleuracean genus and species resembling *Lajishanaspis* Chu, 1979, and a pagodiine which may represent *Pagodia* (*Wittekindtia*) occurs at the top of member 2 of this formation. Although the available material is inadequate for the confident determination and description of all but two of the six taxa, it is important to document these assemblages because they belong to a late Cambrian biofacies from which trilobites have not been described or illustrated previously in the Mediterranean region. Earlier determinations given for some of these trilobites are unsatisfactory and biochronologically misleading. This Mediterranean biofacies has little in common with the well-known Acado-Baltic biofacies of northern Europe, but may have greater relationship with contemporaneous assemblages in central Asia and northern China.

RESUMEN. Se estudian varias sucesiones estratigráficas en los alrededores de Mansilla (Logroño) y se define formalmente la Formación Najerilla (Cámbrico superior—¿Tremadociense?). De esta formación se describen seis taxones de Trilobites, cuya conservación y el número de ejemplares recolectado, sólo permite determinar con precisión dos de ellos. En el miembro inferior se encuentran: *Maladioidella colcheni* sp. nov., *Langyashania felixi* sp. nov., un Aphelaspidino gen. et sp. indet., y otra especie y género indeterminado referible a un Leiostegido. En el techo del miembro 2, aparece un Solenopleuráceo gen. et sp. indet. aff. *Lajishanaspis* y un Pagodiino que probablemente se trate de *Pagodia* (*Wittekindtia*). Estas asociaciones representan un importante documento para conocer las biofacies mediterráneas del Cámbrico superior, cuyos Trilobites no habían sido ilustrados ni descritos; consecuencia de lo cual, esta primera determinación no ha dado todo el rendimiento apetecido para algunos de los taxones estudiados, de modo que su biocronología no queda bien establecida del todo. Las biofacies mediterráneas tienen poco en común con las mejor conocidas biofacies acadobálticas del norte, pero sí tienen una más estrecha relación con las asociaciones que coexisten en Asia Central y norte de China.

THE trilobites described in this paper are from the Mansilla district along the southern margin of the Sierra de la Demanda, an upland region which straddles the Burgos-Logroño provincial boundaries in north-eastern Spain (text-fig. 1). The geology of this area has been described in detail by Colchen (1974). Essentially, the Sierra de la Demanda massif is composed of Precambrian, Cambrian, Ordovician, and Carboniferous rocks, which, although separated from the Iberian Mountain Ranges to the south-east by Mesozoic cover, must represent a prolongation of the western Asturian-Leonese Zone as defined by Lotze (1945).

The existence of Cambrian rocks in the Sierra de la Demanda was first recognized by Schriel (1930) who quoted the occurrence of inarticulate brachiopods, and correlated the lithostratigraphic sequence with the Lingula Flags of Wales. Sos (1936) and Olagüe (1936) documented further brachiopod discoveries, and these were restudied by Hernández-Sampelayo (1942, 1949, 1950), who also reported the first trilobites, referred to *Olenellus*, and trace fossils, referred to *Cruziana*. Subsequently, middle Cambrian trilobites from the Mansilla district have been described and/or recorded by Sdzuy (1958) and Josopait and Schmitz (1971); late Cambrian brachiopods have been described by Colchen and Havliček (1968); and the problematical echinoderm *Oryctoconus* has

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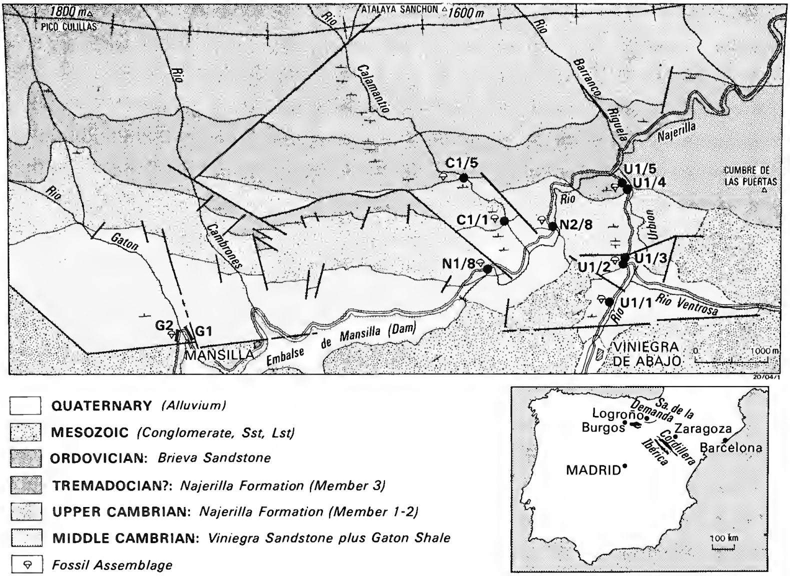
been described by Colchen and Ubaghs (1969). Colchen (1967, 1974) has also reported the occurrence of late Cambrian trilobites and early Ordovician articulate brachiopods, as yet undescribed. Seilacher (1970) has described *Cruziana barbata* from the early Cambrian part of the sequence below the Bunte Jalón-Schichten. Useful summaries of previous biostratigraphic work in the Sierra de la Demanda have been published by Colchen (1974) and Schmitz and Walter (1974). The material described herein is from sections originally investigated by Colchen (1964, 1967, 1974) and briefly also described by Calatayud, Garcia-Ruiz, and Pérez-Lorente (1980), and was mainly found by Liñán and Palacios during the course of re-mapping the Mansilla district (Palacios 1979). The material is housed in the collections of the Department of Palaeontology, University of Zaragoza.



TEXT-FIG. 1. Geological map of the Mansilla district, Logroño Province, showing locations of collecting sites.

Although poorly preserved, this material is important. It is the first Spanish late Cambrian trilobite fauna to be described, and also represents the first documentation of the late Cambrian trilobite faunas of the Mediterranean region. The relationships of our faunas have considerable significance for the study of late Cambrian biogeography. Interestingly, they have little in common with the well-known Acado-Baltic late Cambrian faunas of northern Europe, but, as suggested by Colchen's original generic determinations of *Chuangia* and *Prochuangia*, there is close relationship with the faunas of central and eastern Asia.

In this paper, Liñán and Palacios were responsible for collecting the material and the introductory and stratigraphic passages; and Shergold is responsible for the sections on the age and relationships of the fauna and its systematic description.

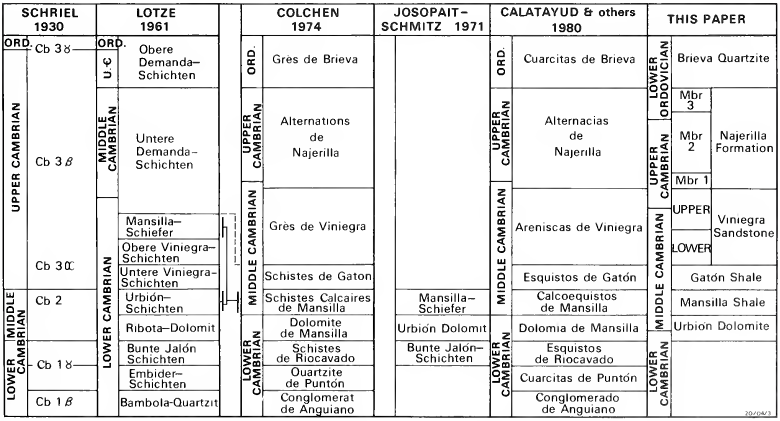
STRATIGRAPHY

Stratigraphic summary

Following the recognition of Cambrian rocks in the Sierra de la Demanda by Schriel (1930), the lithostratigraphy has been developed by Lotze (1958, 1961, 1966) and Josopait and Schmitz (1971). Most of the terminology used herein, however, is based on the International Stratigraphic Guide (Hedberg 1976) (text-fig. 2). Brief notes are given for the stratigraphic units of the Mansilla district shown in text-fig. 3 to place the faunas of the Najerilla Formation in stratigraphic context and to document the presently known biochronology. Although quite heavily faulted and folded, the sequence in the Mansilla district is thought to be complete.

Urbión Dolomite (Josopait and Schmitz 1971). This formation comprises some 70 m of light-brown dolomite, massively bedded in its lower part, fining and becoming microlaminated upwards due to alternating micaceous and non-micaceous laminae. No fossils have been reported, but an early to middle Cambrian age can be inferred from the regional stratigraphic context and by correlation with the Ateca district to the south-east.

Mansilla Shale (Colchen 1974). This formation is composed of 39 m of green calcareous shale containing calcareous modules several centimetres in diameter. The upper part of the Mansilla Shale is sandy and less calcareous. The fauna contains trilobites, trilobitomorphs, brachiopods, echinoderms, and hyolithids, from which Josopait and Schmitz (1971, based on determinations by Sdzuy), Liñán (1979), and Palacios (in press) have reported *Badulesia tenera* (Hart), *Conocoryphe* (*Conocoryphe*) *heberti* Munier-Chalmas and Bergeron, *Conocoryphe* (*Parabailiella*) *languedocensis* Thoral, *Ctenocephalus* (*Hartella*) *antiquus* Thoral, *Ellipsocephalus*? sp. indet., *Paradoxides* (*Eccaparadoxides*) *mediterraneus*? Pompeckj, *Paradoxides* (*Eccaparadoxides*) *rouvillei* Miquel, *Paradoxides* sp., *Pardailhania hispida* (Thoral), *Pardailhania* cf. *hispanica* Sdzuy, *Peronopsis* sp., *Solenopleuropsis* cf. *ribeiroi* (de Verneuil and Barrande), *Solenopleuropsis* sp., *Riojaia perezi* Liñán, and *Decacystis* sp. This faunal assemblage indicates the presence of the *Badulesia*, *Pardailhania*, and *Solenopleuropsis* Substages of Sdzuy (1971, 1972) which are correlated with the *Paradoxides paradoxissimus* Stage of the Swedish Middle Cambrian.



TEXT-FIG. 2. Development of lithostratigraphic terminology in the Sierra de la Demanda.

Gaton Shale (Colchen 1974). This name is applied to the succeeding 200 m alternation of grey shale and sandstone. A massively bedded sandstone occurs at the base of the formation, but succeeding sandy layers are thinly bedded. Graded bedding, ripple marks, and ball and pillow structures characterize this unit, from which only ichnofossils are known: *Monocraterion* sp., *Planolites reticulatus* Osgood, and *Planolites* sp. A late *Paradoxides paradoxissimus* or post *P. paradoxissimus* middle Cambrian age is inferred by superposition.

Viniegra Sandstone (Colchen 1974). This formation includes 300 m of light-coloured sandstone, occurring in layers several metres thick, intercalated with thin grey shales and lenticular layers of bluish limestone. Ripple marks, flaser bedding and cross-lamination, slumping, and flute-casting have been observed. Brachiopods, trilobites, hyolithids and ichnofossils occur, the last including *Bergaueria* sp., *Cruziana* sp., *Diplichnites* sp., *Monocraterion* sp., *Planolites striatus* Hall, *Rusophycus didymus* Salter, and *Rusophycus* sp. Sdzuy (1958) described *Solenopleurina demanda* from a roadside exposure in this formation just to the north of the village of Viniegra de Abajo. A late middle Cambrian or even initial late Cambrian age is suggested by superposition.

Najerilla Formation (Colchen 1974, and see below). This is a thick unit, 700 m, of alternating sandstone and blue-grey decalcified shale. Fossiliferous layers occur near the base and top (text-figs. 3, 4). Brachiopods (Colchen and Havlíček 1968), echinoderms (Colchen and Ubaghs 1969), ichnofossils (Seilacher 1970), and trilobites (herein) have been described, and indicate that the base of the formation has a late Cambrian age, and the top is perhaps Tremadocian. The internal stratigraphy of this unit is described more fully below.

Brieva Sandstone (Colchen 1974). The Cambrian–Tremadoc sequence in the Mansilla district is capped by thick-bedded greyish quartz sandstone with interbedded shale and rare lenticular limestone, in excess of 440 m thick. An early Ordovician age is contemplated on the basis of trace fossils and brachiopods (see Colchen 1974).

The Najerilla Formation

The Najerilla Formation is based on the informal term Najerilla Alternations (Colchen 1974). 'Lower Beds of la Demanda' (Lotze 1961) is an earlier synonym (text-fig. 2). The Najerilla Formation is characterized by an alternation of sandstone and blue-grey shale, the latter containing intercalated lenticular limestone layers. It is distributed over some 500 km^2, occupying nearly all of the central part of the Sierra de la Demanda. The formation lies between massive sandstones or quartzites at the top of the Viniegra Sandstone and base of the Brieva Sandstone (text-fig. 3). The type section of the Najerilla Formation is located on the western bank of the river Calamantío. A supplementary (paratype) section is located along the valley of the river Urbión, by the side of the road which runs from Viniegra de Abajo to La Venta de Viniegra. At the type section, the formation strikes east–west, and beds dip to the north at 30–65°. Accurate assessments of thickness are complicated by the presence of several small-scale faults and folds. Nevertheless, three members, aggregating an estimated 660 m, can be recognized on the river Calamantío section.

Member 1 comprises alternating grey-brown shale and red calcareous sandstone, the latter predominating towards the base of the member. Sedimentary structures include current and wave ripples and slumping. The thickness is estimated at 85 m. Member 2 is recognized by the disappearance of calcareous sandstone and the introduction of blue-grey shale containing abundant organic matter. Some of the intercalated sandstones have thicknesses of several metres. Calcareous layers and nodules reappear in the upper part of this member, which has an estimated thickness of 290 m. Member 3 commences with a thick quartzite layer, about 100 m thick, and is followed by an alternation of blue-grey shale and quartz-feldspar sandstone, totalling some 270 m.

Along the river Urbión, there is also a general east–west strike and northerly dip. The same three members can be recognized, but member 1 is thinner here, having an estimated thickness of only 65 m, and there are fewer bioturbated layers. In member 2, which is correspondingly thick at 350 m, the sandy intervals have thickened at the expense of the shales. Member 3 is now

200 m thick, and in it the thickness of the sandstone layers is reduced. More trilobites and brachiopods have been found on the Urbión section than on the type section.

FAUNA OF THE NAJERILLA FORMATION: AGE AND RELATIONSHIPS

Six trilobite taxa, probably representing four superfamilies, are segregated into two regionally discrete faunal horizons, as noted earlier by Colchen (1967, 1968, 1974). His horizons F1–3 are equivalent to our collected localities U1/2–3 and N1/4–8 on the Rio Urbión and Rio Najerilla sections respectively, and his F4 is equivalent to our U1/4 and C1/5, the latter on the Rio Calamantío section.

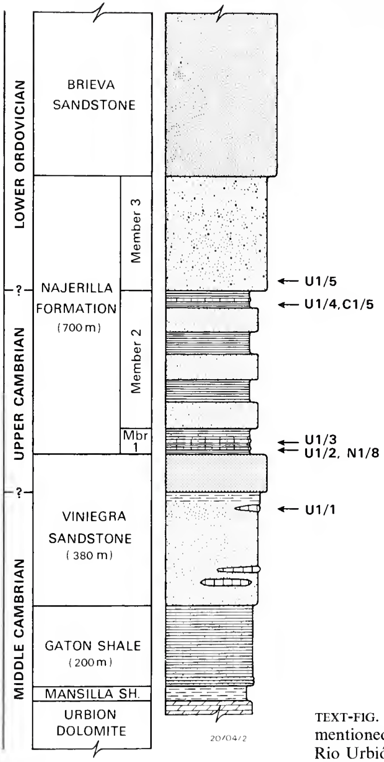
So far, the earlier fauna, from U1/2–3, N1/4–8, comprises four taxa, as follows: Aphelaspidine genus et species undetermined; leiostegiid? genus et species undetermined; *Maladioidella colcheni* sp. nov. (Pterocephaliidae); *Langyashania felixi* sp. nov. (Shirakiellidae). The younger fauna, from U1/4 and C1/5, has yielded only two taxa: pagodiine genus et species undetermined (possibly *Pagodia* (*Wittekindtia*) sp. undet.); solenopleuracean? genus et species undetermined aff. *Lajishanaspis* sp. undet. The two faunas are separated by a 400 m thick alternation of siltstone and quartzite layers (text-fig. 3) in which only brachiopods (Colchen and Havlíček 1968) and ichnofossils, *Cruziana*, *Rusophycus*, and *Planolites* spp. have been found.

The taxonomic philosophy employed here is a compromise between open nomenclature determinations and the creation of new taxa. Taxa have been left under open nomenclature where they are either inadequately preserved (solenopleuracean?), or numerically deficient (pagodiine, leiostegiid?, aphelaspidine). *Langyashania felixi* and *Maladioidella colcheni*, are sufficiently abundant in our collections, that they can be formally named as new taxa.

Colchen (1967, 1974) has referred previously to *Langyashania* under the name *Agraulos longicephalus* (Hicks), and to the pagodiine as *Chuangia* (of the *Ch. batia* (Walcott) group). The description of cranidia referred to *Prochuangia* (Colchen 1967, p. 1688) fits the genus *Maladioidella* of this account. Pygidia as described by Colchen (loc. cit., with a pair of marginal spines) have not been discovered in our collections.

Material recently collected by Palacios (1979) and Liñán is from thin (up to 25 cm thick) decalcified layers and laminae within the lowest siltstone unit of the Najerilla Formation (text-fig. 3); and from similar layers among more indurated siltstone containing decalcified nodules and lenses in the uppermost siltstone unit of this formation. Much of the material is poorly preserved and represented as fragile ferruginized moulds. Other material, occurring as scattered debris in compact micaceous siltstone is more robust, but not much better preserved. All material has been deformed to some extent: it has been flattened as well as sagittally and transversely compressed. Accordingly, foreshortened and elongated morphs of the same taxon, which may look quite different, have been recognized within material assigned to the aphelaspidine, the leiostegiid?, *Maladioidella* and *Langyashania*.

The late Cambrian faunal stratigraphy of the Mediterranean region as a whole, which extends at least from Spain to Turkey, is very poorly known. In this province, only brachiopods and ichnofossils have been described from upper Cambrian rocks. Although trilobites other than those described here have been noted, particularly from elsewhere in Spain (see Sdzuy 1972 for summary; Josopait 1972; Wolf 1980*a*) and Turkey (Haude 1972), they remain undescribed. There is therefore no biostratigraphic context in which to place the newly described faunas. Since they cannot be related to antecedent or descendant assemblages, there is no phylogenetic continuity, and biofacies relationships cannot satisfactorily be evaluated. Agnostid trilobites and wide-ranging polymeroids like *Irvingella* have not been described from the Mediterranean late Cambrian, with the result that an accurate dating for the faunas from the Sierra de la Demanda is also not yet possible. The quest for conodonts, which are as important as trilobites for correlation in the late Cambrian and Tremadocian, has been delayed, particularly in Spain, by the nature of the rock sequences—silts, sands, and quartzites. Microflora has been obtained from Cambrian–Ordovician transition beds in the Ateca–Daroca area, some 130 km to the south-east of the Sierra de la Demanda



TEXT-FIG. 3. Stratigraphic relationship of samples mentioned in this paper. The scale is based on the Rio Urbión section.

(Wolf 1980*b*), and it may eventually prove possible to use acritarchs to support macrofaunal correlations.

Taxonomic difficulties lead directly to other problems concerning the age and relationships of the two Sierra de la Demanda assemblages, particularly the earlier one. In the stratigraphic summary we have attempted to summarize the known Cambrian biostratigraphy of the Mansilla district based on information given in Lotze (1958, 1966), Lotze and Sdzuy (1958, 1972), Colchen (1964, 1967, 1968, 1974), Colchen and Havliček (1968), Colchen and Ubaghs (1969), Seilacher (1970), and Josopait and Schmitz (1971). While the middle Cambrian assemblages are well known, and can be fairly readily related to the Mediterranean middle Cambrian biofacies previously described from Spain by Sdzuy (1968, 1971, 1972), only inferences can be made at this stage regarding the correlation of our late Cambrian assemblages. Contemporaneous rock sequences are known in the Ateca district, and in these the middle Cambrian faunas can be confidently recognized (Josopait and Schmitz 1971). It is more difficult to recognize the late Cambrian assemblages: the pagodiine from our younger assemblage may correlate with the *Tinaspis* (Sdzuy *in* Josopait 1972; = *Pagodia* (*Wittekindtia*) *in* Wolf 1980*a*) recorded from the Valconchán Formation; and, from the earlier assemblage, our *Maladioidella* may represent Sdzuy's (op. cit.) *Taenicephalus?* sp., and our aphelaspidine may be his *Taenora?* sp. (Shergold, in Sdzuy and Shergold, in prep.). Whereas these faunas are separated by some 400 m of strata in the Sierra de la Demanda, in the Ateca district they are in juxtaposition (see Josopait 1972, fig. 3).

1. The earlier late Cambrian fauna: this fauna cannot be placed accurately biochronologically for the above-stated reasons. Its co-occurrence with the articulate brachiopod *Billingsella* cf. *linguaeformis* Nikitin (see Colchen and Havliček 1968) suggests a late Dresbachian or younger age on the North American late Cambrian biochronological scale. *Maladioidella* ranges throughout the later two-thirds of Cambrian time, being first recorded apparently post-dating the recurrence of *Irvingella* in the *Eochuangia* Zone (late Changshanian) of South Korea, the *Wentsuia iota*/*Rhaptagnostus apsis* Assemblage-zone of northern Australia, and *Cedarellus felix* Zone of the northern Siberian Platform. It is last reported in the early Payntonian of northern Australia. *Langyashania* occurs in the middle part of the Langyashan Formation in Anhui Province, eastern China, where it is associated with *Rhaptagnostus* and *Prochuangia* species *inter alia*. Its range is not known, but if the Korean species *Megagraulos breviscapus* can be referred to it, then in South Korea at least it also occurs in the *Eochuangia* Zone (late Changshanian). The association of *Maladioidella*, *Langyashania*, and the aphelaspidine which resembles forms from the *Irvingella* Zone of central Kazakhstan, tends to suggest an early Franconian (*Elvinia*/*Conaspis* Zones equivalents), rather than a late Franconian or Trempealeauan age on the North American late Cambrian biochronological scale.

No elements of the Acado-Baltic biogeographic province can be confidently recognized in the Mansilla faunas. If anything, the trilobites, like the billingsellid brachiopod, demonstrate greater relationships with some elements from the faunas of central Kazakhstan described by Ivshin (1956, 1962), and with eastern China (Lu and Zhu 1980). The aphelaspidine appears more similar to forms actually described as *Aphelaspis* by Ivshin (1956; *in* Nikitin 1956) from the Kujanda Yarus (late Dresbachian to early Franconian) than to late Dresbachian faunas described by either Palmer (1954, 1960, 1962, 1965) or Rasetti (1965) from North America; *Maladioidella*, originally described from north-eastern China by Endo, has a wide peri-Gondwanaland distribution from Turkey to northern Australia (Shergold and Sdzuy, in prep.); the shirakiellid *Langyashania* is known from eastern China and Korea; and the undetermined leiostegiid? may also relate to similar morphologies found in Kazakhstan (*Tatulaspis*) and the Sayan–Altai Basin of southern Siberia (e.g. *Chuangiopsis*?). Hence, although Colchen's (1964, 1967) determinations of Asian trilobite genera in the Sierra de la Demanda are not entirely correct, the early Franconian Mediterranean biofacies may well have had a Tethyan distribution similar to that of the early Tremadocian.

2. The younger late Cambrian fauna: different kinds of problems occur in assessing the relationships of this younger assemblage because it cannot be determined with confidence. The cranidium of the pagodiine could represent more than one late Cambrian genus (e.g. *Pagodia* (*Pagodia*), *Pagodia* (*Oreadella*), *Eochuangia*), or more than one early Ordovician taxon (*Pagodia* (*Wittekindia*), *Szechuanella*). However, in the Sierra de la Demanda, this pagodiine is found in association with questionable echinodermal debris described by Colchen and Ubaghs (1969) as *Oryctoconus lobatus*. Such material occurs elsewhere in northern Spain, notably in the Valconchán Formation of the Ateca–Daroca region (Wolf 1980*a*), where it co-occurs with a pagodiine which is indistinguishable from *Pagodia* (*Wittekindtia*), a Tremadocian taxon dated by conodonts originally described from Afghanistan (Wolfart 1970). Thus, the pagodiine cranidium from the Sierra de la Demanda may belong to *Wittekindtia*. In the Ateca district, the Valconchán Formation was deposited close to the transition from late Cambrian to early Ordovician time (Wolf 1980*a*, 1980*b*; Sdzuy and Shergold, in prep.). The dating depends largely on the age of the overlying biotas of the Borrachón Formation. Wolf (1980*b*) found that the acritarch assemblages of the Borrachón differed from those of the Valconchán Formation. Similarly, the trilobites he listed (1980*a*) are different, those from the Borrachón Formation constituting an early Tremadocian olenid/asaphid

biofacies similar to that already known in central Mexico (Robison and Pantoja-Alor 1968), Argentina (Harrington and Leanza 1957), and Bolivia (Pribyl and Vaňek 1980), which may represent the shelly equivalents of the Acado-Baltic olenid/graptolite facies. This American biofacies is rather distinct from that commonly encountered elsewhere in southern and central Europe (southern France, Bavaria, Bohemia), which is characterized by the frequent association of such forms as *Niobella*, *Proteuloma*, *Onchonotellus*, and *Macropyge*, and can be traced into central Turkey, southern Kazakhstan, Afghanistan, southern Siberia, and northern China according to Shergold and Sdzuy (in prep.).

The age of *Pagodia* (*Wittekindtia*) in Spain therefore poses a chronological problem: it has a Tremadocian age based on conodonts in Afghanistan where a Eurasian biofacies prevails, and yet it predates an Acado-Baltic cum South American biofacies demonstrably of initial Tremadocian age, also on the basis of conodonts. The dilemma can be solved if it is assumed that *P.* (*Wittekindtia*) initially occurs in the late Cambrian. It seems that a terminal Cambrian age must be accepted in the Ateca district. By association with *Oryctoconus*, a similar age is correlated to the Sierra de la Demanda. Unfortunately, the pygidium of *Wittekindtia*, which is characterized by a pair of anterolateral ventrally directed articulating spines, and which would settle the issue of correlation, has not been confirmed there. Support for a probably terminal Cambrian age for the pagodiine in the Sierra de la Demanda comes from eastern China where sequences containing *Pagodia* (*Pagodia*) *major* Lu and Zhu (1980) and saukiid trilobites overlie the Langyashan Formation whose middle part contains *Langyashania*.

SYSTEMATIC DESCRIPTIONS

The terminology used in the ensuing taxonomic descriptions and discussions is based on that defined by Harrington, Moore and Stubblefield (*in* Moore 1959, pp. 117–126), with additions and modifications as suggested by Öpik (1961, 1963, 1967) and Shergold (1972, 1975). The eye indices are defined by Struve (1958).

Symbols used for measured parameters herein are:

Lc	maximum cranidial length (sag.)
Lb	length (sag.) of cranidial or pygidial borders
G	maximum glabellar length (sag.)
Gn	maximum glabellar length plus occipital ring (sag.)
A	maximum length (exsag.) of palpebral lobe
Lp_1	maximum pygidial length (sag.) including the articulating half-ring
Lp_2	maximum pygidial length (sag.) excluding the articulating half-ring
Wp	maximum pygidial width (tr.)
A:G	large eye index
A:Gn	small eye index

Superfamily OLENACEA Burmeister, 1843
Family PTEROCEPHALIIDAE Kobayashi, 1935
Subfamily APHELASPIDINAE Palmer, 1960

Aphelaspidine genus et species undetermined

Plate 12, figs. 8–11

Material. Five cranidia and cranidial fragments (N1/8/4, N/1/8/5a, N1/8/7–8, U1/2/15) measuring between 4·5 and 9·0 mm (four specimens) are matched with two pygidia (U1/2/95–96) with lengths (Lp_1) of 6·0 and 7·5 mm respectively.

Occurrence. Member 1 of the Najerilla Formation; Rio Urbión section, horizons U1/2, U1/3; Rio Najerilla section, horizons N1/8.

Description. The cranidium is elongate (sag.), flat in anterior profile, and with low to moderate convexity (sag.) in lateral aspect. The glabella is long (sag.), 55–61% of the cranidial length (sag.) (G : Lc) for three measured specimens, 69–72% if the occipital ring is included (Gn : Lc); anteriorly truncate; anteriorly tapering; moderately convex (sag.) in lateral profile; and with a hint of preoccipital glabellar furrows. The occipital ring is as wide as the preoccipital glabellar width (tr.), and also has low convexity (laterally). The palpebral lobes attain 44–50% of the glabellar length (G), and have mid-points opposite or just behind the middle of the glabella (G). The width (tr.) of the palpebral areas is about 0·3 that of the glabella opposite the mid-points of the palpebral lobes. Ocular ridges are effaced. The preocular sections of the facial sutures enclose a relatively long (sag.) preglabellar area, up to one-third the cranidial length (sag.), which comprises a gently convex (sag.) preglabellar field, a sharp and narrow anterior cranidial marginal furrow, and a narrow (sag.) upturned anterior cranidial border, 10–12% of the cranidial length (Lc). The postocular sections of the facial suture enclose blade-like posterolateral limbs.

Two pygidia are associated with the cranidial fragments, and because they resemble those associated with aphelaspidine cranidia in Kazakhstan, are referred to the same species. These pygidia are subtrapezoidal, with lengths (Lp_1) about 50% of the maximum width (Wp), and have steeply inclined articulating facets which emphasize their shape. The axis, with three segments and a terminal piece, is long (sag.), reaching to the posterior pygidial margin. There are two pleural segments defined by pleural furrows. The anteriormost pleural furrows extend almost to the anterolateral margin, but end blindly a short distance in front of the articulating facets. The second pair of pleural furrows merge distally into the posterolateral marginal furrow which is a shallow flange limited in its extent between the end of the axis and the distal ends of the second pleural furrows. The pleural zone behind the second pleural segment slopes steeply into this marginal furrow and has a strongly triangular shape. The pygidial border is also restricted by the length of the axis and is defined only adjacent to the marginal furrow.

Discussion. Our material differs from the typical *Aphelaspis* Resser, 1935 in its palpebral morphology: its ocular ridges are not prominent, but its palpebral lobes are posteriorly situated. Among *Aphelaspis* species, only *A. haguei* (Hall and Whitfield) appears to have comparably situated palpebral lobes (see Palmer 1965, p. 59, pl. 9, figs. 19–26). Glabellar and preglabellar morphology resembles such species as *A. longispina* Palmer (1965, p. 60, pl. 9, figs. 13, 15–17).

Aphelaspidine undetermined has a simple reflected anterior cranidial border which distinguishes it from several pterocephaliine genera otherwise sharing cranidial resemblance, e.g. species of *Cernuolimbus* Palmer and *Listroia* Palmer (see Palmer 1960, 1962, 1965). The absence of a preglabellar boss precludes classification with forms such as *Kujandaspis* Ivshin or *Ketyna* Rozova. In *Amorphella* Rozova (see *A. modesta* Rozova, 1968, pl. 7, figs. 6–14) there is also a tendency to produce a preglabellar swelling, otherwise this genus is cranidially similar. *Lochmanaspis* Ivshin (1962, pl. 20, figs. 1–5) is essentially similar, but has a pitted anterior cranidial marginal furrow, more like that of *Lakella* Kobayashi (1962, p. 79). Some species of *Kaninia* Walcott and Resser are also cranidially similar judging from their original illustrations (see *K. lata* Walcott and Resser, 1924, pl. 1, fig. 22; *K. quadrata* Lazarenko, 1960—see Lazarenko and Nikiforov 1968, pl. 15, figs. 1–3) but the palpebral lobes appear to be situated further to the rear of the cranidium. Most closely related, however, appear to be species from Kazakhstan referred to *Aphelaspis* by Ivshin (1956), particularly *A. nobilis* Ivshin (1956, pl. 3, figs. 1–12, 13; pl. 4, figs. 16–17). The holotype cranidium of that species, however, has a mesially interrupted anterior cranidial marginal furrow, and more anteriorly situated palpebral lobes.

The associated pygidia very strongly resemble those from central Kazakhstan illustrated by Ivshin (1956, pl. 4, figs. 19–23) as *Aphelaspis* sp. There is also resemblance to others from Tennessee referred to *Dytremacephalus angulatus* by Rasetti (1965, pl. 21, figs. 6–8), but in those the marginal furrow merges with the first pleural furrows rather than the second. The pygidium assigned to *Kaninia quadrata* by Lazarenko (*in* Lazarenko and Nikiforov 1968, pl. 15, fig. 4) has a similar triangular shape, flat flange-like borders, and a posteriorly extended axis. That assigned to *Kaninia*? sp. 2 (Rozova 1968, pl. 9, fig. 16) has a shorter axis. Similarly the pygidium of *Amorphella modesta* Rozova (see Rozova 1968, pl. 7, fig. 14), although triangular and having flat borders, also has a short axis. The pygidium assigned to *Pesaia* by Walcott and Resser also has an appropriate shape, an axis extending to the posterior border, and comparable borders. In *P. exsculpta* (see Walcott and Resser 1924, pl. 2, figs. 18–19), the anterior and lateral pygidial margins are drawn into a lateral point similar to that seen here on Pl. 11, fig. 10, but the borders are thicker, and together with the pleural exoskeletal surface, heavily striated with terrace lines.

Genus MALADIOIDELLA Endo, 1937

Type species. Maladioidella splendens Endo (*in* Endo and Resser 1937, pp. 346–347, pl. 69, figs. 13–18), late Changshanian, Daizan Formation, Paichiashan Hill, Chinchiachengtzu, Liaoning, China; by original designation.

Other species. Other species of *Maladioidella* have been listed by Shergold (1975, p. 152; 1980, p. 51). To these should possibly be added *Saratogia latefrons* King (1937, pp. 10–12, pl. 2, fig. 3*a–c*), from north-central Iran. This species was nominated as the type of *Iranella* by Hupé (1953), but it has been regarded subsequently by Kobayashi (1967, p. 493) and Wolfart and Kürsten (1974, p. 218) as a species of *Maladioidella.* In addition, *Cedarellus felix* Lazarenko (1966, pp. 48–49, pl. 3, figs. 1–9), from the *Irvingella* Zone of Yakutia, may represent an *en grande tenue* species of *Maladioidella*; cranidia, which Lake (1931, p. 131, pl. 16, figs. 10–15) referred to *Conocephalina abdita* (Salter 1866) may represent a deformed species of *Maladioidella* occurring in Wales; and it may be possible to regard such taxa as *Elrathiella taira* Kobayashi (1962, p. 50, pl. 4, figs. 3–4) and *Megagraulos medius* Kobayashi (1962, p. 66, pl. 2, figs. 2–3) from the *Eochuangia* Zone of South Korea as a deformed effaced species of *Maladioidella.*

Discussion. The type material of *Maladioidella* has been rediagnosed, redescribed and reillustrated by Lu and Zhu (1980, pl. 2, figs. 5–7; pl. 3, figs. 1–2; pl. 4, fig. 1). If *Iranella* Hupé, 1953, and *Cedarellus* Lazarenko, 1966, are accepted as synonyms of *Maladioidella* then the concept of the genus must be expanded to include species, with both more strongly developed dorsal furrows and those in which they are largely effaced. Effacement apart, cranidia of all their genera are morphologically similar, *Maladioidella sensu* Endo (1937) and *Cedarellus* also have similar pygidia.

Maladioidella has been classified (Shergold 1975, 1980) within the Family Idahoiidae Lochman because the construction of the cranidium and librigena was considered more typical of Idahoiidae than Pterocephaliidae with which it was previously classified. Furthermore, the pygidium described by Shergold (1980) for *M. doylei* could not be accommodated in the latter. This pygidium is quite distinct from those assigned by Endo (1937) to *M. splendens* and by Lazarenko (1966) to *Cedarellus felix*, and in retrospect probably does not belong to *Maladioidella.* Accordingly, reclassification with Aphelaspidinae (Pterocephaliidae, Olenacea) must be considered from a number of lines of evidence. (1) There is some resemblance between cranidia of *Maladioidella* and those of some short-eyed aphelaspidine pterocephaliids such as *Litocephalus* Resser, *Olenaspella* Wilson, *Eugonocare* Whitehouse, *Aphelaspidella* Rasetti, some species of *Aphelaspis*, and pterocephaliines like *Cernuolimbus* Palmer. Attention is drawn particularly to such species as *Aphelaspidella macropyge* Rasetti (1965, p. 96, pl. 11, figs. 1, 2, 7, 8), *Aphelaspis camiro* (Walcott) *sensu* Rasetti (1965, p. 83, pl. 12, figs. 1–17), *A. bridgei* Rasetti (1965, p. 77, pl. 13, figs. 1–7), and *A. laxa* Resser *sensu* Rasetti (1965, p. 80, pl. 13, figs. 8–15). The more effaced forms of *Maladioidella* quite closely resemble the aphelaspidine *Taenora*, as previously noted by Palmer (1960, p. 80). (2) The hypostoma

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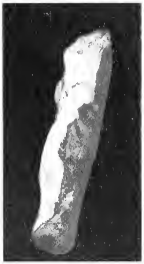
EXPLANATION OF PLATE 11

Figs. 1–13. *Maladioidella colcheni* sp. nov. 1, U1/2/62, internal mould of laterally compressed cranidium, length 25 mm; ×2. 2, U1/2/12b, lateral view of internal cranidial mould; ×2. 3, U1/2/93, internal mould of obliquely distorted cranidium, estimated length 8 mm; ×3·5. 4, U1/2/7, holotype, internal mould of cranidium; length 26·5 mm; ×1·5. 5, U1/2/55, internal mould of hypostoma; ×1·5. 6, U1/2/100B, internal mould of librigena, ×3, associated with undetermined aphelaspidine cranidium (U1/2/100A). 7, U1/2/8b, latex replica of cranidial mould, ×1·5. 8, U1/2/57, internal mould of cranidium slightly obliquely compressed; length 14 mm; ×3. 9, U1/2/11, internal mould of pygidium, estimated length (Lp_2) 6·5 mm; ×2·5. 10, U1/2/19, lateral view of pygidium, estimated length (Lp_2) 12·25 mm; ×1·5. 11, U1/2/19, as above, dorsal view, ×1·5. 12, U1/2/81, internal mould of pygidium, length (Lp_2) 7·5 mm; ×3·5. 13, U1/2/73, internal mould of pygidium, length (Lp_2), 9·5 mm; ×2·5.

PLATE 11


1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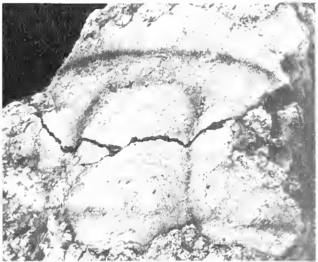
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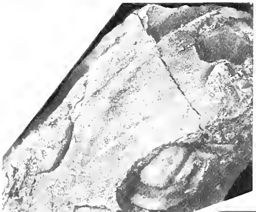
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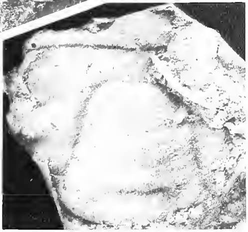
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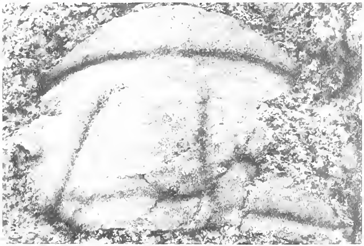
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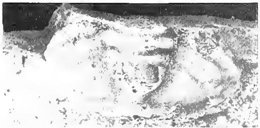
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12


13

SHERGOLD, LIÑÁN and PALIACOS, Spanish Cambrian trilobites illustrated here in association with *M. colcheni* very closely resembles those assigned by Rasetti to *A. camiro* (Walcott) (Rasetti 1965, pl. 12, figs. 11, 15), *A. rotundata* Rasetti (op. cit., pl. 14, fig. 4), and *A. tarda* Rasetti (op. cit., pl. 20, fig. 9). Palmer (1960, pl. 11, figs. 4, 8) has illustrated other similar hypostomata and suggested that they may belong to the pterocephaliine *Cernuolimbus* with which cranidial resemblance is noted above. (3) Pygidia assigned to *M. splendens* by Endo (1937) have a pterocephaliine shape, similar, but shorter to those of species of *Signocheilus* as illustrated by Palmer (1965). Pygidia assigned to *Cedarellus felix* Lazarenko also have this shape. Those associated with cranidia of *M. colcheni* figured here more closely resemble the specimen from Kazakhstan which Ivshin (1956) has placed in species of *Aphelaspis*, particularly *A. nobilis* Ivshin (1956, pl. 3, fig. 13), but cranidia of *A. nobilis* (loc cit., figs. 1–12) have a tendency to form a preglabellar boss which distinguishes them immediately. An overall balance of characteristics, therefore, seems to favour classification with Pterocephaliidae rather than Idahoiidae, and this classification is adopted here.

Maladioidella colcheni sp. nov.

Plate 11, figs. 1–13

1967 *Prochuangia* (*pars*, cranidium only); Colchen 1967, p. 1688 (listed).
1974 *Prochuangia* (*pars*, cranidium only); Colchen 1974, p. 180 (listed).

Name. This species is named for Dr. Michel Colchen who originally found late Cambrian trilobites in the Mansilla district, Sierra de la Demanda.

Types. Holotype, cranidium, University of Zaragoza Palaeontological Collections U1/2/7; paratype cranidia, same collection U1/2/8, 12, 15b, 19, 57, 62, 83, 93, 98; paratype librigenae, U1/2/5, 14, 17, 55, 73, 90, 92; paratype hypostomata, N1/8/5d, N1/8/1b, U1/2/100b; paratype pygidia, N1/8/9, 12, U1/2/11, 19, 20, 21, 50, 61, 70, 71, 73, 75, 76, 81, 82, 88, 90, 97, 100c.

Material. This is the most abundant taxon in the present collections. There are ten measurable cranidia and fragments of many others, twenty-one pygidia, eleven librigenal fragments, and three appropriately sized hypostomata may also belong to this taxon. Cranidia are rather large but generally incomplete; measurable specimens have estimated lengths (Lc) between 5·5 and 26·5 mm, and associated pygidia measure between 4·0 and 14·0mm.

Occurrence. Rio Urbión section, U1/2, U1/3; Rio Najerilla section, N1/8; member 1 of the Najerilla Formation.

Diagnosis. A semi-effaced species of *Maladioidella* with the following cranidial characteristics: truncato-conical glabella with effaced furrows; small palpebral lobes, relatively wide spaced, situated a short distance in advance of the middle of the glabella (G); a relatively short (sag.) preglabellar area, about half the glabellar length (G).

Description. The cranidium of *Maladioidella colcheni* sp. nov. has a subrectangular glabella which tapers gently forwards, has effaced furrows, and is sometimes laterally constricted and anteriorly truncate. For ten measured specimens, the glabella (G) varies between 50 and 80% of the cranidial length (sag.), 64 and 73% if the occipital ring is included (Gn : Lc). The glabella has a very low lateral profile. The occipital furrow generally reaches the axial furrows abaxially, and defines an occipital ring which is transversely slightly wider than the preoccipital glabellar width. *M. colcheni* has small (exsag.) palpebral lobes whose mid-points lie slightly in advance of the middle of the glabella (G.). They are quite wide-spaced: the palpebral areas are a little over half the glabellar width (tr.) at the level of the middle of the palpebral lobes. Faint, gently oblique, duplicated ocular ridges are seen on some specimens. The preocular sections of the facial suture diverge widely and define a wide (tr.) preglabellar area, one-half to one-third as long (sag.) as wide (tr.). The preglabellar field and anterior cranidial border are of approximately equal width (sag.), but the former slopes gently forwards, and the latter is often flat or gently reflected. The border occupies 16–21% of the cranidial length (sag.). The anterior cranidial marginal furrow is sinuous to varying degrees depending largely on deformation, and is not pitted. The postocular sections of the facial suture are also widely divergent, and these enclose transversely extensive posterolateral limbs which are broadly triangular. They bear posterior marginal furrows which terminate at the distal extremities of the posterolateral limbs, and do not continue on to the librigenae. The assigned librigenae are broad and flat, with an anterior prong and a short genal spine. The lateral marginal furrows are shallow depressions, but the posterior ones are effaced completely.

Three hypostomata may also belong to *M. colcheni*: the largest has a length (sag.) of 9·5 mm. These hypostomata are long (sag.) and relatively narrow (tr.) (the width of two measurable specimens is between 66 and 68% of the length), and they have narrow lateral and posterior borders. The anterior border is an upturned edge, whereas the remaining borders are distinctly thickened, the lateral ones almost parallel-sided, and the posterior one truncate. The median body is long (sag.) and ovoid, highly but narrowly convex (tr.), and possesses a well-defined posterior lobe. The maculae are small and inconspicuous.

The pygidium, assigned on both abundance and association, is subtrapezoidal, but is generally deformed. The axis has three well-defined segments and a terminal piece, and a short (sag.) post-axial ridge carries its course to the posterior marginal furrow. There are three complementary pleural segments, each marked by wide (exsag.) pleural furrows. The border is evenly narrow, and the marginal furrow represents the break in convexity between the pleural zone and border except anterolaterally where it merges with the first pleural furrow distally.

Superfamily SOLENOPLEURACEA Angelin, 1854
Family INCERTAE SEDIS
Solenopleuracean? genus et species undetermined
aff. *Lajishanaspis* Chu, 1979 sp. undet.

Plate 12, figs. 12–13

Material. A single cranidial fragment (U1/4/1), with glabellar length (G) of 3·75 mm.

Occurrence. Member 2 of the Najerilla Formation; Rio Urbión section, horizon U1/4.

Discussion. It is not possible to accurately classify the cranidial fragment at our disposal since little is known of the palpebral lobes or preglabellar area. It has an ovoid, laterally expanded, convex (tr., sag.) glabella with three pairs of transverse gently curved furrows; a narrow (sag.) occipital ring; and vestiges perhaps of palpebral lobes which appear to lie close to the glabella. The preglabellar area may exclude a preglabellar field.

The glabellar shape is reminiscent of some olenaceans (olenids), solenopleuraceans (lonchocephalids, onchonotellids), and catillicephalaceans (catillicephalids). Catillicephalidae, as conceived by Rasetti (*in* Moore 1959), most typically seem to have a forwards expanding glabella extending to the anterior cranidial margin and excluding a preglabellar area. Öpik (1967) included *Onchonotellus* Lermontova, 1956 in this family, but this genus has a shorter (sag.), more ovoid glabella, and a distinct anterior cranidial border. Lu (*in* Lu *et al.* 1965) created the Family Onchonotellidae to accommodate this genus and classified it among Solenopleuracea, and this assignment is preferred here, thus preserving Rasetti's concept of Catillicephalidae. Generally in *Onchonotellus* the glabellar furrows are faint, but they are observed on some otherwise generically indistinguishable taxa, e.g. *Onchonotellus privus* Rozova (1968, pl. 1, figs. 1–9; Lazarenko 1966, pl. 8, figs. 1–3), and *O. trisulcatus* Ivshin (1962, pl. 7, figs. 13–15). Species of *Seletella* Ivshin, 1962 and *Seletoides* Ivshin, 1962 also have swollen glabellae, but these lack furrows and the frontal lobe is distinctly pointed. *Galeaspis* Ivshin, 1962 also lacks glabellar furrows, but is highly granulose. A virtually identical cranidial fragment described from the late Cambrian of Qinghai by Chu (*in* Chu, Lin and Zhang 1979, pp. 101–102, pl. 40, figs. 9–12) as *Lajishanaspis subsphaericusa* gen. et sp. nov., and assigned to the Family Catillicephalidae (Solenopleuracea). In our opinion this Chinese cranidium can be no more confidently determined than that figured under open nomenclature here.

Typically, lonchocephalids have an occipital spine, but some genera included in the Family Lonchocephalidae do not. The glabellar shape and segmentation of the Spanish cranidium resembles those specimens from Maryland which Rasetti (1961, pp. 117–118, pl. 24, figs. 23–25) described as *Quebecaspis conifrons* Rasetti, and similar ones from Alaska which Palmer (1968, p. 95, pl. 9, figs. 8–10) described as *Quebecaspis conifrons*? Rasetti. These forms have a late Dresbachian or early Franconian age in North America.

Some olenaceans also have a glabellar shape similar to the Spanish fragment, e.g. species of

Peltura and *Westergaardia* in the late Cambrian of Scandinavia (Henningsmoen 1957), and some species of *Bienvillia* from North and Central America (see *B. grandis* Robison and Pantoja-Alor, 1968, pl. 100, fig. 16). In general, these olenaceans can be distinguished by their small, anteriorly situated palpebral lobes. Although insufficient information is available, it would appear that the Spanish specimen has palpebral lobes situated at least opposite the glabellar mid-point, and perhaps even behind this.

On the balance of its characteristics, the present material appears to have most similarity with Solenopleuracea, but because it is not possible to classify it satisfactorily, we can only regard it as a queried and undetermined solenopleuracean with affinity with *Lajishanaspis* Chu.

Superfamily LEIOSTEGIACEA Bradley, 1925
Family LEIOSTEGIIDAE Bradley, 1925
Subfamily PAGODIINAE Kobayashi, 1935
Pagodiine genus et species undetermined
aff. *Pagodia* (*Wittekindtia*)? Wolfart, 1970

Plate 12, figs. 14–15

1967 '*Chuangia*, en particulier au groupe *Chuangia batia* (Walcott)'; Colchen 1967, p. 1688 (listed).
1974 '*Chuangia*, en particulier au groupe de *Chuangia batia*'; Colchen 1974, p. 180 (listed).

Material. A single cranidium (C1/5/1), known from internal and external moulds, with length (Lc) of 8·5 mm; and a single pygidium (C1/5/2) of doubtful association, 6·0 mm long (Lp_2).

Occurrence. Member 2 of the Najerilla Formation, Rio Calamantío section, horizon C1/5.

Discussion. The inadequate nature of this material prevents a comprehensive description. The cranidium is slightly compressed sagittally, and the pygidium is vertically compressed.

The cranidium is characteristically pagodiine, having a glabella which extends to the anterior cranidial marginal furrow and an upturned cranidial border. The glabella (G), occupying some 76% of the cranidial length (sag.), tapers very gently forwards, is bluntly rounded anteriorly, and bears vestiges of at least two pairs of apparently transverse furrows. There is a faint lateral constriction at the level of the median furrows, and anterolaterally the axial furrows are bridged by a diverticulum which connects the anterolateral corners of the glabella to the preocular areas. Both features are seen in other pagodiines. The palpebral lobes, which are situated behind the mid-point of the glabella, are also similar to those seen in other pagodiines.

The associated pygidium has an entire rounded margin. The axis is composed of four segments and a terminal piece, but only a single pleural segment is visible. It appears to have a distinct marginal furrow and border, a feature not commonly found in Pagodiinae, and more typical of Leiostegiinae such as *Leiostegium* Raymond *sensu* Walcott (1925). The adventrally directed anterolateral articulating spines, which would permit classification with *Pagodia* (*Wittekindtia*) have not been observed.

Cranidially, this Spanish pagodiine could be referred to a number of genera. It is, however, insufficiently effaced for classification with *Chuangia* Walcott, the glabella is insufficiently conical for inclusion in *Lotosoides* Shergold, and the anterior border is upturned and not flat as in *Iranochuangia* Kobayashi. Accordingly, it could belong to *Prochuangia* Kobayashi, *Eochuangia* Kobayashi, *Szechuanella* Lu, or one of the subgenera of *Pagodia* Walcott (see Shergold 1980, p. 68, table 2 for listed pagodiine cranidial characteristics). More material is required to confirm the pygidial association.

The material is therefore insufficient to assign a genus with confidence. However, deductive rather than objective reasoning suggests the possibility of classification with *Pagodia* (*Wittekindtia*) Wolfart. Our material is associated with pelmatozoan debris which has been described as *Oryctoconus lobatus* by Colchen and Ubaghs (1969). Similar debris, also determined as *Oryctoconus* (e.g. Wolf 1980*a*), occurs to the south-east of the Sierra de la Demanda, between Ateca and Daroca in both the eastern and western Iberian Mountain Chains. In this area, *Pagodia* (*Wittekindtia*)

(= *Tinaspis*? of Josopait 1971) occurs with *Oryctoconus* close to the Cambrian–Tremadoc boundary at several localities in the Valconchán Formation (Wolf 1980*a*; Sdzuy and Shergold, in prep.). We acknowledge, however, that such material as has been referred to *Oryctoconus* may have a long stratigraphic range, and that the pagodiine we have described here may eventually prove to be other than *Wittekindtia*. For instance, material from eastern China, described as *Pagodia* (*Pagodia*) *major* by Lu and Zhu (1980, p. 18, pl. 5, figs. 10–12), apparently occupies a similar stratigraphic position with regards the occurrence of *Langyashania*. *P.* (*P.*) *major* has a similar cranidium to the Spanish *Pagodia* (*Wittekindtia*), but as in that species the possession of a pygidial articulating spine cannot be confirmed. Thus there is a possibility that the specimens from Mansilla could also represent *Pagodia* (*Pagodia*).

Leiostegiid genus et species undetermined

Plate 12, figs. 4–7

Material. This taxon is known only from four cranidial fragments (N1/8/12, U1/2/9, 27, 80), with estimated lengths (Lc) between 9·0 and 19·0 mm.

Occurrence. Member 1 of the Lower Najerilla Formation; Rio Urbión section, horizon, U1/2; Rio Najerilla section, horizon N1/8.

Description. This undetermined leiostegiid genus has an elongate cranidium with low convexity, both in anterior and lateral profiles. Characteristically, our material has a relatively long (sag.) (G : Lc 60–64%) anteriorly tapering, pear-shaped glabella which bears traces of three pairs of glabellar furrows. The preoccipital furrows are gently curved and posterosagittally directed; the median lateral ones are shorter (tr.), more gently curved; and the anterolateral ones are very short (tr.), and more or less transverse. The occipital furrow is curved anteriorly, reaches the axial furrows, and defines a crescentic occipital ring which has about the same transverse width as the preoccipital lobes. The palpebral lobes are inadequately known; they seem to be posteriorly sited, with their anterior tips opposite the middle or rear of the median lateral glabellar lobes, but the position of their posterior tips cannot be confirmed. They are connected by faint ocular ridges to the frontal glabellar lobe. The intraocular width (tr.) is appreciable, the width (tr.) of each palpebral area being at least 50% of the preoccipital glabellar width. The preocular areas are gently convex (exsag.); they curve around the anterolateral corners of the glabella, and merge into the preglabellar band—a depressed diverticulum in the floor of the preglabellar furrow. Caeca apparently pass forwards from this band near the anterolateral corners of the glabella, and pits lying in the anterior cranidial marginal furrow indicate the presence of others passing from the preocular areas into the anterior cranidial border. The anterior cranidial border is wide (sag.), occupying over 20% of the cranidial length (Lc) on the two measured specimens, and in profile slopes gently forwards. It is separated from the preocular areas and the parafrontal band by a well-defined anterior cranidial marginal furrow. Nothing is known of the posterolateral limbs.

Discussion. An interesting combination of cranidial characteristics poses classificatory problems for our material. Basically, this genus has the glabellar shape typical of Housiinae (Pterocephaliidae) combined with a preglabellar and preocular structure reminiscent of Mansuyiinae (Leiostegiidae). The posteriorly sited palpebral lobes tip the balance of diagnostic characteristics towards classification with Leiostegiidae.

The pear-shaped glabella, with only faint traces of glabellar furrows is found in three distinct groups of late Dresbachian and early Franconian trilobites. It is particularly characteristic of Housiinae (Pterocephaliidae) and is well expressed in *Housia* Walcott, *Prehousia* Palmer, and *Parahousia* Palmer (see Palmer 1954, 1960, 1965). These genera have variably long (sag.) preglabellar fields, but are united in having small (exsag.) palpebral lobes anteriorly situated and close to the axial furrows. Housiinae are typically distributed at the margins of the North American craton during the late Dresbachian. Contemporaneous, presently unsatisfactorily classified, relatives in Kazakhstan, referred by Ivshin (1956) to *Olentella*, *Kujandina*, and *Tatulaspis*, also have a pear-shaped glabella and variable preglabellar field. They have small palpebral lobes which are not as far advanced as in Housiinae, and which are more widely spaced (tr.). The Spanish specimens resemble *Tatulaspis* Ivshin most because it has the shortest (sag.) preglabellar field (see Ivshin 1956, pl. 9, figs. 1–4).

Also contemporaneous are various Pagodiinae (Leiostegiidae) which inhabited the fringes of the Siberian, North Chinese, and North American cratons. *Chuangia frequens* (Dames) has an appropriate glabella which extends to the anterior cranidial marginal furrow, but its anterior border, as in the majority of leiostegiids is reflected rather than depressed as in the Spanish specimens (see Schrank 1974, pl. 1, fig. 8). *Iranochuangia persica* (King) does have a depressed border, and indeed similar preglabellar structure altogether, but its glabella is more or less straight-sided, gently tapering forwards (see King 1937, pl. 2, fig. 4*a*). *Bernicella minuta* Frederickson (1949, pl. 68, figs. 14–16), from Oklahoma, is a more obvious pagodiine with a pear-shaped glabella. Species of *Chuangiopsis* Sivov (1955), an enigmatic southern Siberian genus of uncertain classificatory position, may also be related to the undetermined Spanish leiostegiid.

The structure of the preglabellar and preocular areas is reminiscent of younger leiostegiids assigned to the Subfamily Mansuyiinae (Shergold 1980), as are the posteriorly sited palpebral lobes (cf. *Peichiashania rectangularis* (Endo) *in* Endo and Resser 1937, pl. 68, fig. 21). Mansuyiinae such as *Peichiashania*, however, have a relatively long (sag.) concave preglabellar area, and reflected, rather than depressed, anterior cranidial border.

The Spanish leiostegiid probably represents a new generic taxon, but before this can be named it is necessary to confirm the extent of the palpebral lobes and the posterolateral limbs. Our current material is inadequate for this purpose.

Family SHIRAKIELLIDAE Hupé, 1953

Genus LANGYASHANIA Lu and Zhu, 1980

Type species. Langyashania distincta Lu and Zhu (1980, p. 17, pl. 5, figs. 2–4; pl. 6, fig. 12?). Late Cambrian, middle Langyashan Formation, Chuxian–Quanjiao region, eastern Anhui Province, China; by original designation.

Other species. Langyashania transversa Lu and Zhu (1980, p. 17, pl. 5, figs. 5–8), locality and age as above. Some Late Cambrian species assigned to *Megagraulos* by Kobayashi (1962), e.g. *M. breviscapus* Kobayashi (1962, p. 66, pl. 2, fig. 1) from the *Eochuangia* Zone of South Korea, but not *M. medius* (op. cit., pl. 2, figs. 2–3, = ?*Maladioidella*) from the same locality.

Discussion. Shirakiellidae are late Cambrian agrauloid trilobites with anteriorly situated palpebral lobes, preglabellar fossulae, and truncatoconical glabella with effaced furrows. The family, comprising the genera *Shirakiella* Kobayashi, 1935, *Neoshirakiella* Sun and Xiang, 1980, and *Langyashania* Lu and Zhu, 1980, has a Changshanian and Fengshanian age in South Korea (Kobayashi 1935, 1962), south-western China (Sun and Xiang 1980), and eastern China (Lu and Zhu 1980). *Langyashania* differs from species of *Shirakiella*, as conceived by Kobayashi (1935, 1960)

EXPLANATION OF PLATE 12

Figs. 1–3. *Langyashania felixi* sp. nov. 1, U1/2/24, holotype, internal mould of cranidium, length 12·5 mm; ×3. 2, U1/26, internal mould of cranidium, length 11·75 mm; ×3. 3, U1/2/24, lateral view of holotype, ×3.

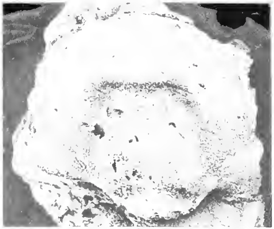
Figs. 4–7. Leiostegiid? gen. et sp. undet. 4, U1/2/27, internal mould of cranidium, length 19 mm, showing trace of granulose prosopon, ×2. 5, U1/2/27, as above, latex replica, ×2. 6, U1/2/80, sagitally compressed internal cranidial mould, indicating convexity (sag.) and glabellar furrows, estimated length 18·5 mm; ×2. 7, U1/2/27, lateral view, ×2.

Figs. 8–11. Aphelaspidine gen. et sp. undet. 8, U1/2/15, internal mould of cranidium, length 9 mm; ×3·5. 9, U1/2/100A, latex replica of cranidial mould, ×5. 10, U1/2/95, internal mould of pygidium, length (Lp_1) 7·5 mm; ×4.5. 11, U1/2/96, internal mould of pygidium, length (Lp_1) 6 mm; ×4·5.

Figs. 12–13. Solenopleuracean? gen. et. sp. undet. aff. *Lajishanaspis* sp. 12, U1/4/1, internal mould of cranidial fragment, ×5. 13, U1/4/1, as above, lateral view, ×5.

Figs. 14–15. Pagodiine gen. et sp. undet., aff. *Pagodia* (*Wittekindtia*) sp. 14, C1/5/1, latex replica of cranidial internal mould, estimated length 8·5 mm; ×3. 15, C1/5/2, latex replica of pygidial internal mould, estimated length (Lp_2) 6 mm; ×3.

PLATE 12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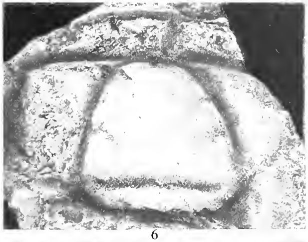
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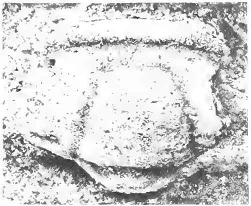
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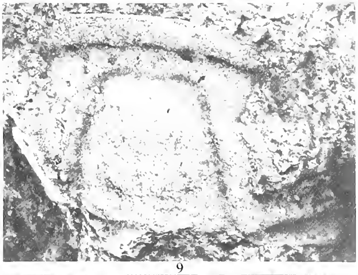
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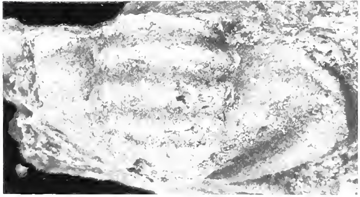
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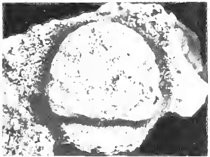
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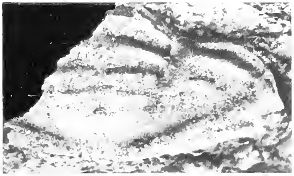
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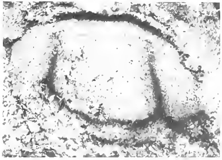
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non Lu *et al.* (1965), by having more widely spaced palpebral lobes and a proportionately wider (tr) preglabellar area. *Neoshirakiella*, not readily interpretable from its illustrations, appears to have an anteriorly more rounded glabella, and may also have palpebral lobes lying closer to the axial furrows.

The cranidia at hand are those of an agrauloid trilobite, having effaced glabellar and anterior cranidial marginal furrows, and thus a gently convex (sag.), composite preglabellar area, as in *Agraulos* Hawle and Corda, 1847, an early paradoxididian middle Cambrian genus from Europe and maritime eastern North America with which they have been previously identified. They are referred to *Langyashania* on the combined glabellar, palpebral, and preglabellar morphology, and degree of effacement of their dorsal furrows. There are no pygidia among the Spanish collections which resemble those assigned to *Langyashania* by Lu and Zhu (1980, pls. 5–6).

Langyashania felixi sp. nov.

Plate 12, figs. 1–3

1967 *Agraulos longicephalus* (Hicks); Colchen 1967, p. 1687 (listed).
1974 *Agraulos longicephalus* (Hicks); Colchen 1974, p. 179 (listed).

Name. This species is named for Dr. Félix Pérez-Lorente, University College of Logroño, in appreciation of his assistance in collecting this material.

Types. Holotype, cranidium, University of Zaragoza Palaeontological Collection U1/2/24; paratypes, same collection, N1/8/1a, N1/8/6, N1/8/10, U1/2/23, 25, 26, 72a–b, U1/3/1, 6, 9, 12b.

Material. This taxon is based on fourteen quantifiable cranidia, all internal or external moulds, ranging in length (Lc) between 5·25 and 12·50 mm.

Occurrence. Rio Najerilla section, horizon N1/8; Rio Urbión section, horizons U1/2, U1/3; from within member 1 of the Najerilla Formation.

Diagnosis. A transverse species of *Langyashania* with relatively small, wide spaced, anteriorly situated palpebral lobes, and comparatively flat dorso-ventral profile.

Description. Langyashania felixi has an anteriorly broadly rounded cranidium which is mostly effaced. It has low convexity (tr., sag.) when viewed both laterally and anteriorly. The glabella is subrectangular, anteriorly truncate, slightly tapering forwards, 43–57% of the cranidial length, 61–76% if the occipital ring is included. Glabellar furrows are effaced. Axial furrows are deeply incised only in front of the glabella, where a pair of shallow pits is situated near the anterolateral corners of the glabella. On some specimens, these cause indentations along the posterior edge of the preglabellar field. The occipital furrow is anteriorly bowed, and does not reach the axial furrows laterally, apparently defining a crescentic occipital ring. A pair of diverticula, issuing from the abaxial extremities of the occipital ring, merges into the postocular fixigenae, and the posterior cranidial margin appears to pass underneath the occipital ring. An occipital node is faintly discernible. The palpebral lobes are faintly defined, small (A:Gn 27–37%), sited anterior to the middle of the glabella (G), and distant from the axial furrows. The transverse width of the palpebral areas is approximately two-thirds that of the glabella opposite the mid-points of the palpebral lobes. Faint ocular ridges are present on some specimens. The preocular sections of the facial suture are not widely divergent, and meet in a wide arch sagitally. They enclose a preglabellar area, 24–42% of the cranidial length (sag.) which has a gentle anterior convexity (sag.). Preocular areas are not differentiated, but occasionally it is possible to observe a faint anterior cranidial marginal furrow dividing an anterior border from an equally wide (sag.) preglabellar field. The postocular facial sutures diverge appreciably and enclose triangular posterolateral limbs which bear mostly shallow posterior marginal furrows. The anterior edge of these furrows appears to be formed by the diverticula which originate from the occipital ring noted above.

Discussion. Langyashania felixi has lower dorso-ventral relief than other species assigned to this genus. It has wider spaced palpebral lobes than either *L. distincta* or *L. transversa* from Anhui. In this last characteristic it more closely resembles the cranidium referred by Kobayashi (1962, p. 66, pl. 2, fig. 1) to *Megagraulos breviscapus* Kobayashi from the *Eochuangia* Zone of South Korea. This species differs from the type species of *Megagraulos*, *M. coreanicus* Kobayashi, 1935, which has more posteriorly situated palpebral lobes, and a non-interrupted transverse occipital furrow. *M. breviscapus* appears to have a narrower preglabellar area than *L. felixi*. It may represent another species of *Langyashania*.

Colchen (1967) has drawn attention to specimens of *Agraulos longicephalus* (Hicks), illustrated by Sdzuy (1961, pl. 23, figs. 7–17), which are associated with middle Cambrian genera such as *Paradoxides*, *Solenopleuropsis*, and *Pardailhania inter alia* in the Murero-Schichten of the Ateca district (Aragon) and Bres (Asturia), and concluded that these are no different from the form occurring on the Rio Urbión section. Accordingly, Colchen (1967, 1974) referred to the presence of *Agraulos longicephalus* at the base of his lithological Unit XI (faunal horizons F1 and F2), i.e. at the base of the Najerilla Formation of this paper, on the hillside above the intersection of roads from Viniegra de Abajo and Ventrosa de Viniegra, about 0·75 km north of the former (text-fig. 1). Following Lotze (1961), he assigned this part of the sequence to the middle Cambrian. Since Colchen's horizon F3, with *Billingsella* cf. *linguaeformis* Nikitin (Colchen and Havliček 1968), is the same as our locality U1/3 on this section, we feel that the horizon with *Agraulos* must probably be the same as our locality U1/2. The faunas described here from U1/2 and U1/3 are essentially the same, so that it seems that *A. longicephalus* (Hicks) *sensu* Colchen refers to *Langyashania felixi* sp. nov. Although similar, *Agraulos* and *Langyashania* can be distinguished. The latter has a more anteriorly truncate glabella with more totally effaced furrows; occipital furrow not reaching the axial furrows laterally and defining a crescentic rather than transversely annulate occipital ring; a pair of shallow pits in the preglabellar furrow at the anterolateral corners of the glabella; and preocular areas which are confluent with the preglabellar area.

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REFERENCES

CALATAYUD, P., GARCIA-RUIZ, J. M. and PÉREZ-LORENTE, F. 1980. *Itinerario geológico y geomorfológico por el Valle del Najerilla.* Inst. Estud. riojanos, 37 pp. Serv. Cultura de la Excma Diputacion Provincial Logroño.

CHU, CHAO-LING, LIN, HUAN-LING and ZHANG, ZHI-HENG, 1979. Trilobita. *In Atlas of palaeontology of northwestern China.* Qinghai, part 2. 219 pp., 82 pls. Geological Press, Beijing.

COLCHEN, M. 1964. Successions lithologiques et niveaux repères dans Paléozoïque antécarbonifère de la Sierra de la Demanda (Burgos–Logroño, Espagne). *C.R. Acad. Sci. Paris*, **259**, 4758–4761.

—— 1967. Sur la présence du Cambrien supérieur à *Prochuangia* et à *Chuangia* dans la Sierra de la Demanda (Logroño, Espagne). Ibid. **264** (ser. D), 1687–1690.

—— 1968. Le Cambrien et ses limites dans la Sierra de la Demanda (Burgos–Logroño, Espagne). *C.R. somm. Soc. géol. Fr., fasc.* **6,** 180.

—— 1974. Géologie de la Sierra de la Demanda, Burgos–Logroño (Espagne). *Mem. Inst. geol. min. España,* **85** (2. vols.), 436 pp., pl., figs.

—— and HAVLIČEK, V. 1968. Le niveau à *Billingsella* cf. *lingulaeformis* Nikitin, du Cambrien de la Sierra de la Demanda (Logroño, Espagne). *Bull. Soc. géol. Fr.* 7ᵉ sér. **10,** 133–137, pls.

—— and UBAGHS, G. P. 1969. Sur les restes d'Échinodermes (?) du Cambro-Ordovicien de la Sierra de la Demanda (Burgos–Logroño, Espagne). Ibid. **11,** 649–654, text-pl. 1.

ENDO, R. 1937. Introduction; Stratigraphic Geology: and Addenda to Parts I and II. *In* ENDO, R. and RESSER, C. E., *Bull. Manchur. Sci. Mus.* **1,** 1–102, 302–365, pls. 58–73.

—— and RESSER, C. E. 1937. The Sinian and Cambrian formations and fossils of Southern Manchukuo. Ibid., 474 pp., pls. 14–73.

HARRINGTON, H. J. and LEANZA, A. F. 1957. Ordovician trilobites of Argentina. *Spec. Publ. Univ. Kansas Dept. Geol.* **1,** 276 pp., 104 figs.

HARRINGTON, H. J., MOORE, R. C. and STUBBLEFIELD, C. J. 1959. Morphologic terms applied to trilobites. *In* MOORE, R. C. (ed.). *Trilobita*, 117–126. University of Kansas Press.

HAUDE, H. 1972. Stratigraphie und Tektonik des südlichen Sultan Dağ (SW-Anatolien). *Z. Dtsch. Geol. Ges.* **123,** 411–421.

HAWLE, I. and CORDA, A. J. C. 1847. Prodrom einer Monographie der böhmischen Trilobiten. *Abhandl. K. Böhm. Gesell. Wiss.* **5,** 176 pp. 7 pls.

HEDBERG, H. (ed.), 1976. *A guide to stratigraphic classification, terminology, and procedure*, xvii + 200 pp. John Wiley & Sons, New York.

HENNINGSMOEN, G. 1957. The trilobite family Olenidae. *Skr. Norske Vidensk. (Oslo), mat.-naturv. Kl.* **1,** 303 pp., 31 pls.

HERNÁNDEZ-SAMPELAYO, P. 1942. Yacimientos paleontológicos en la Demanda. *Not. y Com. Inst. Geol. Min. Espana*, **10,** 13.

—— 1949. Criaderos de mineral de hierro de la Sierra de la Demanda (Burgos y Logroño). *Revta Acad. Ciencias Exactas. Fisicas y Naturales*, *Madrid*, 9, 51 pp.

—— 1950. Nuevas especies silurianas de la Sierra de la Demanda. *Mem. Inst. Geol. Min. España, Libro jubilar*, **1,** 145–171.

HUPÉ, P. 1953. Classification des trilobites. *Ann. Paléont.* **39,** 61–168, figs. 1–92.

IVSHIN, N. K. 1956. *Upper Cambrian trilobites of Kazakhstan, 1.* Trudy Inst. geol. Nauk, Akad. Nauk Kazakh. SSR, Alma-Ata, 98 pp., 9 pls. [In Russian.]

—— 1962. *Upper Cambrian trilobites of Kazakhstan, 2.* Ibid., 412 pp., 21 pls. [In Russian.]

JOSOPAIT, V. 1971. Geologische Untersuchungen im Kambrium und Tremadoc südlich von Ateca (Westliche Iberische Ketten, NE-Spanien). *Inaugural-Dissertation Westfalische Wilhelms-Universität Münster*, 115 pp. (unpubl.).

—— 1972. Das Kambrium und das Tremadoc von Ateca (Westliche Iberische Ketten, NE-Spanien). *Münster. Forsch. Geol. Paläont.* **23,** 121 pp., 26 figs., 3 pls.

—— and SCHMITZ, U. 1971. Beitrag zur Stratigraphie im Unter- und Mittelkambrium der Sierra de la Demanda (NE-Spanien). Ibid. **19,** 85–99, pl. 1.

KING, W. B. R. 1937. Cambrian trilobites from Iran (Persia). *Mem. geol. Surv. India, Palaeont. indica*, N.S., **22** (5). 22 pp., 2 pls.

KOBAYASHI, T. 1935. The Cambro-Ordovician formations and faunas of South Chosen. Palaeontology, part III. Cambrian faunas of South Chosen with special study on the Cambrian trilobite genera and families. *J. Fac. Sci. Imp. Univ. Tokyo*, ser. 2, **4** (2), 49–344, pls. 1–25.

—— 1960. The Cambro-Ordovician formations . . ., part VII, Palaeontology VI. Supplement to the Cambrian faunas of the Tsuibon Zone with notes on some trilobites genera and families. Ibid. **12** (2), 329–420, pls. xix–xxi.

—— 1962. The Cambro-Ordovician formations . . ., part IX. Palaeontology, VIII. The Machari fauna. Ibid. **14** (1), 1–152, pls. 1–12.

—— 1967. The Cambro-Ordovician formations . . ., part X, section C. The Cambrian of eastern Asia and other parts of the Continent. Ibid. **16** (3), 381–534.

LAKE, P. 1931. A monograph of the British Cambrian trilobites. *Palaeontogr. Soc. London*, pp. 149–172, pls. 19–22.

LAZARENKO, N. P. 1966. Biostragraphy and some new trilobites from the Upper Cambrian of the Olenek Uplift and Kharaulakh Mountains. *Uchen. Zap. Paleont. Biostratigr., nauchno-issled. Inst. Geol. Arktiki.* **11,** 33–78, pls. 1–8. [In Russian.]

—— and NIKIFOROV, N. I. 1968. Trilobite complexes from Upper Cambrian deposits on the River Kulyumbe (northwestern Siberian Platform). Ibid. **23,** 20–80, pls. 1–15 [In Russian.]

LERMONTOVA, E. V. 1956. *See* NIKITIN, I. F. 1956.

LIÑÁN, E. 1979. *Riojaia perezi*, un nuevo trilobitoideo del Cámbrico medio de la Sierra de la Demanda (Espana). *Estudios geol.* **34,** 319–321.

LOTZE, F. 1945. Zur Gliederung der Variszichen der Iberischen Meseta. *Dtsch. Geotekt. Forsch.* **5,** 78–90.

—— 1958. Zur Stratigraphie des spanischen Kambriums. *Geologie*, **7** (3–6), 727–750.

—— 1961. Teil 1: Stratigraphie. *In* LOTZE, F. and SDZUY, K., q.v., pp. 285–498.

—— 1966. Kambrium Spaniens. *Zbl. Geol. Paläont.* **1,** 1966 (6), 1206–1227.

—— and SDZUY, K. 1961*a*. Das Kambrium Spaniens. Teil 1: Stratigraphie. *Abh. Akad. Wiss. Lit. math.-naturw. Kl.* **1961** (6), 285–498.

—— —— 1961*b*. Das Kambrium Spaniens. Teil 2: Trilobiten, 1. Ibid. **1961** (7), 501–594, 15 pls.

LOTZE, F. and SDZUY, K. 1961*c*. Das Kambrium Spaniens. Teil 2: Trilobiten, 2. Ibid. **1961** (8), 597–693, pls. 16–34.

LU YENHAO, CHANG WENTANG, CHU CHAOLING, CHIEN YIYUAN and HSIANG LEEWEN, 1965. *Chinese fossils of all groups. Trilobita*, **1**, 362 pp., 66 pls.; **2**, 363–766, pls 76–135, Science Publ. Co. Peking. [In Chinese.]

LU YANHAO, and ZHU ZHAOLING, 1980. Cambrian trilobites from Chuxian-Quanjiao region, Anhui. *Mem. Inst. Geol. Palaeont. Nanjing*, **16**, 1–25 [Chinese], 25–30 [English], pls. 1–6.

MOORE, R. C. (ed.), 1959. *Treatise on Invertebrate Paleontology*. Part O, Arthropoda, **1**, xix + 560 pp. Geol. Soc. Amer. and Kansas Univ., Press.

NELSON, C. A. 1951. Cambrian trilobites from the St. Croix Valley. *J. Paleont.* **25** (6), 765–784, pls. 106–110.

NIKITIN, I. F. 1956. Cambrian and Lower Ordovician brachiopods from northeastern central Kazakhstan. *Trudy Inst. geol. Nauk. Akad. Nauk. Kazakh. SSR, Alma-Ata*, 143 pp., 15 pls. [In Russian.]

OLAGÜE, O. 1936. Nota sobre la estratigrafía del Jurásico en la Rioja. *Bol. R. Soc. Española Hist. Nat.* **36** (2), 101–123.

ÖPIK, A. A. 1961. The geology and palaeontology of the headwaters of the Burke River, Queensland. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.* **53**, 249 pp., 24 pls.

—— 1963. Early Upper Cambrian fossils from Queensland. Ibid. **64**, 133 pp., 9 pls.

—— 1967. The Mindyallan fauna from northwestern Queensland. Ibid. **74;** vol. 1, 404 pp.; vol. 2, 166 pp., 67 pls.

PALACIOS, T. 1979. El Cámbrico entre Viniegra de Abajo y Mansilla. Tesis de Licenc. Univ. de Zaragoza, 86 pp., 8 figs., 15 pls. (Mem. inéd.).

—— (in press). Nuevos datos bioestratigráficos sobre el Paleozoico inferior de la Sierra de la Demanda (Logroño). *Estudios geol.*

PALMER, A. R. 1954. The faunas of the Riley Formation in Central Texas. *J. Paleont.* **28** (6), 709–786, pls. 76–92.

—— 1955. Upper Cambrian Agnostidae of the Eureka district, Nevada. Ibid. **29** (1), 86–101, pls. 19–20.

—— 1960. Trilobites from the Upper Cambrian Dunderberg Shale, Eureka district, Nevada. *Prof. pap. U.S. geol. Surv.* **334-C**, 109 pp., 11 pls.

—— 1962. *Glyptagnostus* and associated trilobites in the United States. Ibid. **374-F**, 49 pp., 6 pls.

—— 1965. Tilobites of the late Cambrian pterocephaliid biomere in the Great Basin, United States. Ibid. **493**, 105 pp., 23 pls.

—— 1968. Cambrian trilobites from east-central Alaska. Ibid., **559-B**, 115 pp., 13 pls.

PŘIBYL, A. and VANĚK, J. 1980. Ordovician trilobites of Bolivia. *Rozpr. Českoslov. akad. věd, Rada matemat. přírod. věd*, **90** (2), 90 pp., 26 pls.

RAMSAY, A. C. 1866. The geology of North Wales. *Mem. geol. Surv. G.B.* **3**, viii + 381 pp.

RASETTI, F. 1959. *See* MOORE, R. C. (ed.), 1959.

—— 1965. Upper Cambrian trilobite faunas of northeastern Tennessee. *Smithson. misc. Collns.* **148** (3), 127 pp., 21 pls.

RAYMOND, P. E. 1913. Notes on some old and new trilobites in the Victoria Memorial Museum. *Bull. geol. Surv. Canada, Victoria Mem. Mus.* **1**, 33–39, pls. 3–4.

ROBISON, R. A. and PANTOJA-ALOR, J. 1968. Tremadocian trilobites from the Nochixtlán region, Oaxaca, Mexico. *J. Paleont.* **42** (3), 767–800, pls. 97–104.

ROZOVA, A. V. 1968. Biostratigraphy and Upper Cambrian and Lower Ordovician trilobites from the northwest Siberian Platform. *Trudy Inst. Geol. Geofiz., Akad. Nauk SSSR Sib. Otdel. Novosibirsk*, **36**, 196 pp., 27 pls. [In Russian.]

SALTER, J. W. 1866. On the fossils of North Wales. Appendix, *In* RAMSAY, A. C., q.v., pp. 239–363, pls. 1–26.

SCHMITZ, U. and WALTER, R. 1974. Das Kambrium und das Tremadoc der Iberischen Halbinsel. Bericht über neuere Untersuchungen (1965–1972). Teil 1: NE-Spanien, Zentral-Spanien, S-Spanien. *Zbl. Geol. Paläont. Teil 1*, **1974** (1–2), 72–124.

SCHRANK, E. 1974. Kambrische Trilobiten der China-Kollektion v. Richthofen. Teil 1: Die *Chuangia*-Zone von Saimaki. *Z. geol. Wiss.* Berlin, **2** (5), 617–643, pls. 1–5.

SCHRIEL, W. 1930. Die Sierra de la Demanda und die Montes Obarones. *Abh. Ges. Wiss. Göttingen, math.-phys. Kl., N.F.*, **16** (2), 105 pp., 27 figs., 9 pls.

SDZUY, K. 1958. Neue Trilobiten aus dem Mittelkambrium von Spanien. *Senckenbergiana lethaea*, **39** (3–4), 235–253, pls. 1–2.

—— 1961. Teil II: Trilobiten. *In* LOTZE, F. and SDZUY, K., q.v., pp. 285–693, pls. 1–34.

—— 1968. Trilobites del Cámbrico medio de Asturias. *Trab. Geol.* **1**, 77–133, pls. 1–10.

—— 1971. La subdivisión bioestratigráfica y la correlación del Cámbrico medio. *Publ. 1, Congr. hispano-luso-americ. Geol. económ.* **2** (1), 769–782.

—— 1972. Das Kambrium der acadobaltischen Faunenprovinz. *Zbl. Geol. Paläont. Teil II*, **1972** (1–2), 1–91.

SDZUY, K. and SHERGOLD, J. H. (in prep.). Cambrian trilobites from the Ateca district, Iberian Mountain Ranges, north-eastern Spain. *Senckenbergiana lethaea.*

SEILACHER, A. 1970. *Cruziana* stratigraphy of 'non-fossiliferous' Palaeozoic sandstones. *In* CRIMES, T. P. (ed.), *Trace Fossils. Geol. J. Spec. Issue*, **3**, 447–476, pl. 1.

SHERGOLD, J. H. 1972. Late Upper Cambrian trilobites from the Gola Beds, western Queensland. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.* **112,** 126 pp., 19 pls.

—— 1975. Late Cambrian and early Ordovician trilobites from the Burke River Structural Belt, western Queensland, Australia. Ibid. **153,** 251 pp., 58 pls.

—— 1980. Late Cambrian trilobites from the Chatsworth Limestone, western Queensland. Ibid. **186,** 111 pp., 35 pls.

—— and SDZUY, K. (in prep.). Cambrian and initial Tremadocian trilobites from Sultan Dağ, central Turkey. *Beih. Geol. Jb.*

SOS, V. 1936. Sobre unos moldes de Braquiópodos paleozoicos de la Sierra de Cameros. *Bol. Soc. españ. Hist. nat.* **36** (2), 124–126, 1 fig.

STRUVE, W. 1958. Beiträge zur Kenntnis der Phacopacea (Trilobita). 1. Die Zeliszkellinae. *Senck. leth.* **39,** 165–220, 4 pls.

SUN YUNZHU and XIANG LIWEN, 1980. Late Upper Cambrian trilobite fauna from western Yunnan. *Bull. Chinese Acad. geol. Sci.* ser. 1, **1** (1), 1–17, pls. i–iv. [In Chinese, English summary.]

WALCOTT, C. D. 1925. Cambrian and Ozarkian trilobites. *Smithson. mis. Collns*, **75** (3), 61–146, pls. 15–24.

—— and RESSER, C. E. 1924. Trilobites from the Ozarkian Sandstones of the island of Novaya Zemlya. *In*, *Report of the Scientific Results of the Norwegian Expedition to Novaya Zemlya 1921*, **24,** 3–14, pls. i–ii. Soc. Arts Sci. Kristiania.

WOLF, R. 1980*a*. The lower and upper boundary of the Ordovician System of some selected regions (Celtiberia, Eastern Sierra Morena) in Spain. Part 1: The Lower Ordovician sequence of Celtiberia. *N. Jb. Geol. Palaont., Abh.* **160** (1), 118–137.

—— 1980*b*. Lithology and acritarchs of the Lower Ordovician formations of Celtiberia (NE Spain), with stratigraphic and palaeoenvironmental implications. *Dissertation, Naturwiss. Fac. III (Erdwiss.), Julius-Maximilians-Universität Würzburg*, 236 pp. (unpubl.).

WOLFART, R. 1970. Fauna, Stratigraphie und Paläogeographie des Ordoviziums in Afghanistan. *Beih. Geol. Jb.* **89,** 125 pp., 21 pls.

—— and KÜRSTEN, M. 1974. Stratigraphie und Paläogeographie des Kambriums im mittleren Süd-Asien (Iran bis Nord-Indien). *Geol. Jb.* **8,** 185–234, pl. 28.

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NEOSELACHIAN SHARKS' TEETH FROM THE LOWER CARBONIFEROUS OF BRITAIN AND THE LOWER PERMIAN OF THE U.S.A.

by CHRISTOPHER J. DUFFIN *and* DAVID J. WARD

ABSTRACT. Isolated teeth of *Anachronistes fordi* gen. et sp. nov. are recorded from the Upper Carboniferous Limestone, Lower Carboniferous of Derbyshire, England, and Clwyd, North Wales. The teeth are assigned to the Family Anachronistidae fam. nov. of uncertain position within the neoselachian sharks. A further unnamed tooth belonging to the genus is recorded from the Lower Permian of Nevada, U.S.A. The teeth of *Anachronistes* are neoselachian since they possess a conical central cusp, well-developed lateral blades and basal flange, V-shaped basal root face and hemiaulacorhize vascularization. The teeth of *Anachronistes* lack enameloid. The teeth are most closely comparable to those of *Squatina* and *Orectolobus*, and belong to a bottom feeder. The teeth extend the record of the neoselachian sharks from the Lower Norian (Upper Triassic) back into the Dinantian (Lower Carboniferous). Two types of monognathic gradient heterodonty are distinguished: linear gradient heterodonty in which there is gradual reduction in coronal profile commissurally; and non-linear gradient heterodonty, where coronal profile reduction occurs both mesially and distally from a central high tooth row.

SHARK remains are known from deposits of Lower Devonian to Recent age. Articulated skeletons are rare in the fossil record, with the exception of certain lithologies, such as black and oil shales (for example, the Lower Carboniferous shales of Mazon Creek in Illinois, U.S.A., the Lower Carboniferous of Glencartholm, Scotland, and the Lower Jurassic of north-west Europe) and very fine-grained limestones (for example, the Upper Jurassic of the Solnhofen-Eichstätt area in southern Germany, the Upper Cretaceous of the Hakel and Hajula regions of the Lebanon, and the Monte Bolca limestone from the Italian Eocene).

More commonly, fossil shark remains comprise the isolated mineralized hard parts of the skeleton (Applegate 1967). Of these, teeth, dorsal fin spines, and dermal denticles are the most common, although calcified vertebrae, jaw cartilages, and occasional specialized dermal structures such as clasper spines and cephalic spines are also known. From the point of view of shark taxonomy, teeth, dorsal fin spines, and calcified vertebrae have proved the most useful, and are the most intensively studied.

Three successive levels of organization were recognized by Schaeffer (1967) in living and fossil sharks. These were designated the cladodont, hybodont, and modern shark levels. Various authors have since incorporated Schaeffer's levels of organization into a taxonomic framework for the sharks (Blot 1969; Compagno 1973, 1977; Maisey 1975; Duffin 1980). There are now generally taken to be four cohorts within the Elasmobranchii: the cladodontiforms which include cladoselachians, various cladodont groups, and xenacanths; the hybodontiforms which include the hybodonts, tristychiids, and related genera; the ctenacanthiforms which include the ctenacanthids; the neoselachiforms which include all living sharks and rays plus the palaeospinacids, orthacodontids, and anacoracids.

The definition of the neoselachian condition is based mainly upon skeletal characters (Compagno 1973, 1977; Reif 1977), amongst the most important of which are the possession of calcified vertebrae, subterminal hyostylic jaws, U-shaped scapulocoracoid, and only one or two basal segments between the enlarged pelvic basipterygium and the clasper shaft cartilage in adult males. Dorsal fin spines, when present, lack posterior ornament, and possess an at least partly lamellar trunk which meets the mantle at a sharply defined junction (Maisey 1975).

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There has been some debate over the recognition of neoselachian teeth (see Duffin 1981 for a review). Reif (1973, 1977, 1978, 1980) prefers the use of enameloid ultrastructure. In most neoselachian sharks the enameloid is triple layered; a basal layer of tangled apatite fibres is overlain by a middle layer of parallel fibre bundles, which in turn is overlain by a surface layer of shiny enameloid. The teeth of ctenacanths and hybodonts possess only a single crystallite enameloid, within which the apatite crystallites are randomly oriented. Root morphology and vascularization are also important taxonomic criteria. Casier (1947*a–c*) concluded that whilst hybodonts and ctenacanths possess a simple root with many entrant vascular foramina of no particular spatial organization, the vascularization of neoselachian teeth is reduced, often to a single medio-internal vascular canal flanked by a series of lateral vascular canals. The basal face of the root in neoselachian sharks teeth is usually a modified V-shape (Duffin 1980).

At the present time the oldest known neoselachian shark is *Reifia minuta* Duffin (1980), which is represented by isolated teeth from the Lower Norian (Upper Triassic) of southern Germany. From this time onward, neoselachian remains occur sporadically through the stratigraphic column.

The cohort Neoselachii are divided into four suborders (Compagno 1973), all of which are represented in the Jurassic: the Squalomorphii are represented by *Squalus* in the Cretaceous (Herman 1975), hexanchoids ('*Notidanus*') in the Tithonian of southern Germany (Schweizer 1964), and possibly by *Pseudodalatias barnstonensis* Sykes (1971) in the British Rhaetic and the Rhaetian of the Lombardy Alps (Sykes 1974; Reif 1978; Duffin 1978; Tintori 1980); the Squatinomorphii are represented by possibly four species of *Squatina* from the Tithonian of Solnhofen (Dinkel 1920; Schweizer 1964); the Batoidea are represented by *Spathobatis bugesiacus* Thiollière (1849), *Belemnobatis sismondae* Thiollière (1854), and *Asterodermus platypterus* Agassiz (1843) from the Tithonian of Germany and France; all four families of the Galeomorphii are represented—Heterodontiformes by *Heterodontus falcifer* (Wagner 1857) from Solnhofen, Carcharhiniformes by *Palaeoscyllium formosum* Wagner (1857) from Solnhofen, Lamniformes by *Palaeocarcharias stromeri* de Beaumont (1960) from Solnhofen, and Orectolobiformes by *Crossorhinus jurassicus* Woodward (1918), *Phorcynis catulina* Thiollière (1854), and *Corysodon cerinensis* Saint-Seine (1949) from the Lower Tithonian of Solnhofen and France.

Duffin (1981) has reviewed the pre-Jurassic record of the neoselachians. There is no neoselachian known in pre-Norian deposits at the present time.

The fact that the major taxonomic categories of the neoselachian sharks were in existence during the Jurassic, and in some cases during the Upper Triassic, implies the existence of neoselachian sharks before the Upper Trias. The lack of fossil evidence of neoselachian sharks in Lower Triassic and Permian strata is probably due to the absence of suitable marine deposits. It is reasonable, therefore, to look to the Carboniferous for evidence of early neoselachian history.

The object of this paper is to describe new selachian teeth from the British Lower Carboniferous and the Permian of the U.S.A., and to discuss their affinity to the neoselachians.

METHODS

The teeth described in this paper come from three sites: Steeplehouse Quarry, Wirksworth, Derbyshire; Quarry dump at Esclusham Mountain, near Minera, Clwyd, North Wales; Ward Mountain, Pine County, Nevada, U.S.A.

The teeth from Steeplehouse Quarry were collected from bulk samples made between 1972 and 1979. Both the limestone and shale partings were sampled. The limestone was dissolved in a 5% solution of formic acid buffered with calcium orthophosphate, and yielded a rich phosphatic residue. The shale was disaggregated by repeated drying, soaking in paraffin oil (kerosene), and then further soaking in boiling water. The shale yielded a less concentrated phosphatic residue.

The Permian tooth from Ward Mountain was sorted from disaggregated residues prepared from thinly bedded limestones and calcareous sandstones for microfossil study.

The teeth from Esclusham Mountain, North Wales, were dissolved by acid preparation from four small hand specimens of limestone that displayed visible petalodont tooth plates and other vertebrate debris.

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES
Subclass ELASMOBRANCHII
Cohort NEOSELACHII
Superorder and Order incertae sedis
Family ANACHRONISTIDAE nov.

Familial diagnosis. Known only on the basis of small (1 to 2 mm long) isolated teeth. The crown possesses a lingually inclined central cusp. The crown base possesses well-developed lateral blades, and a basal flange is developed, underlain by a basal groove at the crown/root junction. The root possesses a downward-projecting labial buttress beneath the basal flange of the crown. A central pit is developed lingual to the labial buttress. The remainder of the root is lingually extended and moderately deep. The basal face is arcuate in basal view; the two lateral wings are directed labially. The root vascularization comprises a single median internal canal which is usually roofed by the basal face of the root. The root is hemiaulacorhizoid.

Genus ANACHRONISTES gen. nov.

Type species. Anachronistes fordi sp. nov.

Derivation of name. The generic name is derived from Anachronismos (Greek—out of time) and refers to the early position of these teeth in the stratigraphic record.

Generic diagnosis. As for Family.

Anachronistes fordi sp. nov.

Plate 13, figs 1–10; Plate 14, figs 1–7, 9; text-figs. 2A, 3D

Derivation of name. The specific name is dedicated to Dr. Trevor D. Ford of Leicester University, since it was his work (Ford 1964, 1980) which led us to sample the fish-bed at Steeplehouse Quarry.

Diagnosis. As for the genus.

Holotype. British Museum (Natural History), Department of Palaeontology number P.60670. An isolated, almost perfect tooth (Pl. 13, figs. 6, 7, 9, 10), from Steeplehouse Quarry, Derbyshire.

Other material. Thirty-five isolated teeth from Steeplehouse Quarry (BM(NH), P.60671, Pl. 13, fig. 1, Pl. 14, fig. 3; P.60673, Pl. 13, fig. 3, Pl. 14, figs. 5, 6; P.60674, Pl. 13, figs. 4, 5, 8; P.60675, Pl. 13, fig. 2; P.60690, Pl. 14, fig. 4; P.60697, Pl. 14, figs. 1, 2; P.60676 to P.60689, P.60691 to P.60696, and P.60698 to P.60705). One isolated tooth from Esclusham Mountain (P.60672, Pl. 14, figs. 7, 9). The teeth are very friable.

Type locality. Steeplehouse Quarry (disused), Wirksworth, Derbyshire, U.K., Grid reference SK 288554.

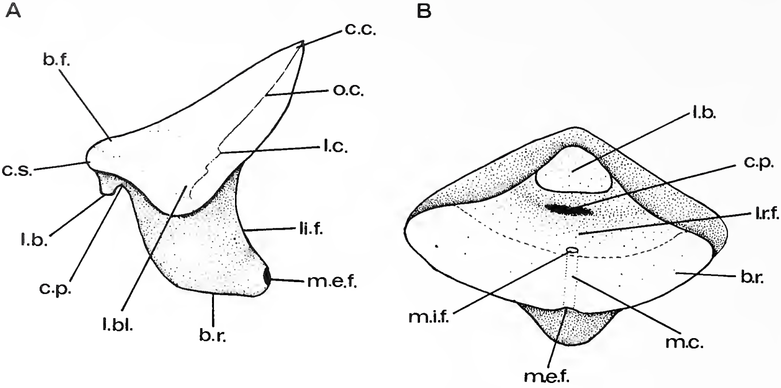
Age. Cawdor Limestones, P_1 sub-zone, Upper Viséan, Dinantian, Lower Carboniferous.

Lithology. Interbedded crinoidal limestone and black shale bands.

Other localities. Quarry tip at Esclusham Mountain, south-west of Minera, Clwyd, North Wales. Grid reference SJ 253503. The original location of the limestone debris yielding teeth of *Anachronistes* is unknown. The age of local deposits is presumed to be Asbian to Brigantian, Viséan, Dinantian, Lower Carboniferous (Dr. B. Rosen pers. comm.).

Description of the Holotype. The tooth is small, measuring 1·9 mm mesio-distally, 1·56 mm high, and 1·5 mm labio-lingually from basal flange to cusp apex. The tooth is fairly well preserved, sustains some polish due to post-mortem transport, and is cracked.

The crown is well developed, its most prominent feature being a lingually directed central cusp (c.c. in text-fig. 1, which gives a guide to the descriptive terminology used in the text). The apical angle of the central cusp is approximately 45° (Pl. 13, fig. 6). The cutting edge of the crown is formed by a moderately developed occlusal



TEXT-FIG. 1. Diagrammatic representation of a typical tooth of *Anachronistes* in A, lateral view; B, basal view, in order to show descriptive terminology. Abbreviations: b.f., basal flange; c.c., central cusp; o.c., occlusal crest; l.c., lateral cusplet; c.s., crown shoulder; l.bl., lateral blade; l.b., labial buttress of the root; c.p., central pit housing prominent vascular foramen; b.r., basal face of the root; li.f., lingual face of the root; l.r.f., labial face of the root; m.c., median vascular canal; m.i.f., medio-internal foramen; m.e.f., medio-external foramen.

crest (o.c.) running the length of the crown mesio-distally. The occlusal crest passes through the apex of the central cusp. The central cusp is flanked on either side by a well-developed lateral blade (l.bl.) which is triangular in shape. The labial shoulder of the crown (c.s.) is substantially inflated to form a basal flange (b.f.) (Pl. 13, fig. 6). The labial face of the crown is comparatively short at the mesial and distal extremities of the crown, and is roughly rhomboidal in occlusal view (Pl. 13, fig. 9). The lingual face of the crown is moderately deep, sloping labially toward the crown/root junction. The lingual face of the crown is somewhat inflated centrally, toward the base of the central cusp. No lateral or accessory cusplets are developed. Both labial and lingual faces of the crown lack ornament. Just above the crown/root junction on the lingual face, at the base of the central cusp, there is a very small wear facet (Pl. 13, fig. 10).

The junction between the crown and the root is not well marked in this specimen. The labial basal flange of the crown substantially overlaps the crown/root junction (Pl. 13, fig. 6), whereas the crown/root transition is much smoother on the lingual side (Pl. 13, fig. 10). The mesial and distal extremities of the crown extend well beyond the crown/root junction (Pl. 13, figs. 9, 10).

The root has a roughly triangular attachment to the crown, the longest side of this figure being the lingual root border. The labial protrusion of the basal flange of the crown over the crown/root junction gives the root the appearance of having been lingually displaced in basal view. The bulk of the root projects lingually from the crown/root junction (Pl. 13, fig. 6). On the labial side, a short (labio-lingually), labial root buttress (l.b.) base is

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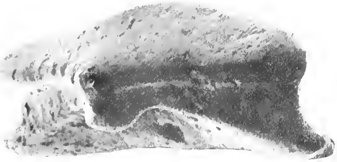
EXPLANATION OF PLATE 13

Figs. 1–10. *Anachronistes fordi* from the Lower Carboniferous of Derbyshire, England. 1, P.60671 in oblique labial view, × 30. 2, P.60675 in labial view, × 35. 3, P.60673 in lateral view showing labial flange, × 50. 4, P.60674 in labial view, × 35. 5, P.60674 in labio-basal view, × 35. 6, P.60670 (Holotype) in lateral view, × 35. 7, P.60670 in oblique lingual view, note the conical central cusp, well-developed lateral blades, and labial flange, × 30. 8, P.60674 in lateral view, × 40. 9, P.60670 in labial view, note the conical central cusp, well-developed lateral blades, and labial flange, × 35. 10, P.60670 in lingual view, × 35.



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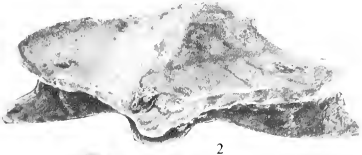

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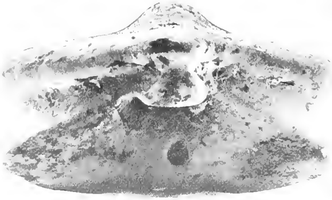

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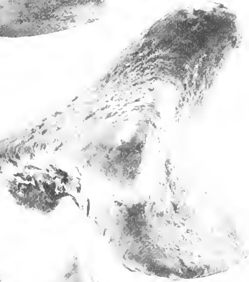

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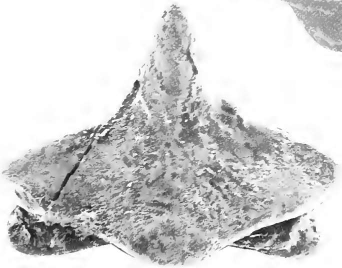

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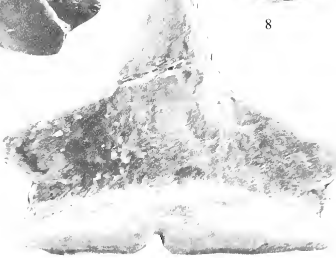

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DUFFIN and WARD, *Anachronistes fordi*

located beneath the labial basal flange at the base of the central cusp. This labial projection of the root is non-foraminate and triangular in basal view. It is separated from the remainder of the root by a deep central pit (c.p.), which appears to expose the crown/root junction internally. From the central pit, the remainder of the labial root face descends steeply toward the basal face. Mesially and distally, the root becomes increasingly longer, such that the mesio-lateral and disto-lateral root faces converge in their ascent to the crown/root junction (Pl. 13, fig. 10). The basal face of the root is mildly arcuate and flat.

The vascularization of the root comprises a large median internal vascular canal (m.c.) situated central to the basal root face, and running labio-lingually, opening by a medio-internal foramen (m.i.f.) and medio-external foramen (m.e.f.) along the labio-basal and linguo-basal borders of the root respectively (Pl. 13, fig. 10). The medio-external foramen is accommodated in a notch on the linguo-basal border of the root.

Variation. The teeth in the sample vary from 1 to 2 mm in length (mesio-distally) (P.60695 is 2 mm long). The morphological features which are most variable within the sample, are degree of lingual inclination and distal inclination of the central cusp, prominence of the basal flange, the development of a longitudinal crest on the labial crown shoulder, root vascularization, and overall tooth shape.

The longer, more slender teeth in the sample tend to be those with low coronal profiles. Those teeth with large upright central cusps are often quite deep labio-lingually. Many of the teeth in the sample have heavily eroded central cusps (e.g. P.60671, Pl. 13, fig. 1; Pl. 14, fig. 3) in relation to little worn roots, due largely to ante-mortem wear rather than post-mortem abrasion. Those teeth with well-preserved central cusps often show considerable lingual and distal central cusp inclination (Pl. 14, fig. 9). With progressive lingual inclination of the central cusp, there tends to be a parallel increase in distal inclination of the cusp (see, for example, P.60679, P.60684, P.60688, P.60691, P.60700). Some teeth do show considerable lingual inclination with little distal inclination of the central cusp (P.60676). The basal flange at the labial base of the crown may be prominent in teeth with a high, upright central cusp (P.60670, P.60671), and in teeth with high central cusp inclination (P.60680). The increasing lingual and distal inclination of the central cusp with lowering of the crown profile seems to represent gradient monognathic heterodonty. The development of a strong longitudinal crest along the labial crown shoulder occurs in a few specimens (P.60674, P.60672, Pl. 14, figs. 8, 9).

In the root, the median internal canal may be unroofed in certain cases, although this is probably due to tooth abrasion and transport. P.60696 is unique in that it possesses multiple vascular foramina in the area of the central pit (six foramina lateral to the pit on the single preserved side). Several teeth (P.60675, P.60683, P.60686, P.60687) show one or two lateral foramina along the linguo-basal root border. The lateral vascular canals do not usually exit on the labial root face.

P.60705 has very strong lateral rami developed at the base of the labial root buttress and lateral to the central pit.

Anachronistes sp.

Plate 14, figs. 8, 10

Material. One complete tooth (Pl. 14, figs. 8, 10); Los Angeles County Museum (LACM) catalogue number 119970.

Locality. Ward Mountain, White Pine County, Nevada, U.S.A. Los Angeles County Museum locality 4536.

Lithology. Thinly bedded limestone and calcareous sandstone.

Age. Arcturus Formation, probably *Parafusulina* zone, Leonardian Stage, Early Permian.

EXPLANATION OF PLATE 14

Figs. 1–7, 9. *Anachronistes fordi* from the Lower Carboniferous of England. 1, P.60697 in oblique basal view, × 35. 2, P.60697 in basal view, × 30. 3, P.60671 in lateral view showing labial flange, × 50. 4, P.60690 in basal view, showing medial pit and hemiaulacorhize vascularization, × 35. 5, P.60673 in oblique basal view, × 30. 6, P.60673 in oblique basal view, × 30. 7, P.60672 in lateral view, × 35. 9, P.60672 in labial view, note the cusp inclination and longitudinal crest at the top of the crown shoulder, × 30.

Figs. 8, 10. *Anachronistes* sp. from the Lower Permian of Nevada, U.S.A. 8, LACM 11970 in lateral view, × 65. 10, LACM 11970 in labial view, note the development of lateral cusplets, × 60.


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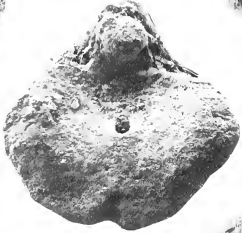
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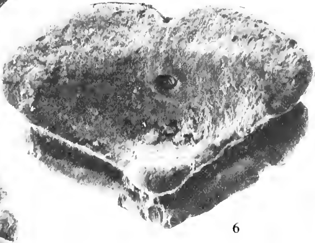
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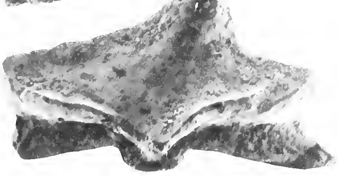
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DUFFIN and WARD, *Anachronistes*

Description. The tooth measures up to 1·1 mm long (mesio-distally). The crown bears a postero-lingually directed central cusp with circular cross-section. The central cusp is flanked by up to two small lateral cusplets on either side (Pl. 14, figs. 8, 10). The occlusal crest is moderate, and runs the length of the crown bisecting the cusp apices. The labial face of the crown possesses a strong basal flange. A longitudinal ridge marks the crest of the labial crown shoulder (Pl. 14, fig. 10). The lingual face of the crown is short and slightly inflated at the base of the central cusp. The crown lacks ornament.

The crown/root junction is deeply incised on the labial side, but smooth on the lingual side. The root projects lingually from the crown undersurface. The labial buttress underlying the basal flange of the crown is well developed (Pl. 14, fig. 8) and gives way lingually to the central pit. The basal face is arched and flat. The root vascularization comprises a median internal canal with a single medio-internal and medio-external entrant foramen.

Remarks. The tooth of *Anachronistes* sp. shows the characteristic basal flange, lateral blade, labial root buttress, and central pit of the genus. The tooth differs from those of *Anachronistes fordi* in the lateral cusplets on the occlusal crest and a longitudinal ridge at the crest of the labial crown shoulder. The tooth certainly belongs to a new species, but is not named here since the currently available material is too sparse to allow adequate definition and diagnosis.

DISCUSSION OF AFFINITIES

The morphology of sharks teeth is very varied and there is no currently accepted analysis of tooth anatomy in phylogenetic terms. For this reason, the individual characters of the tooth anatomy of *Anachronistes* will be considered separately.

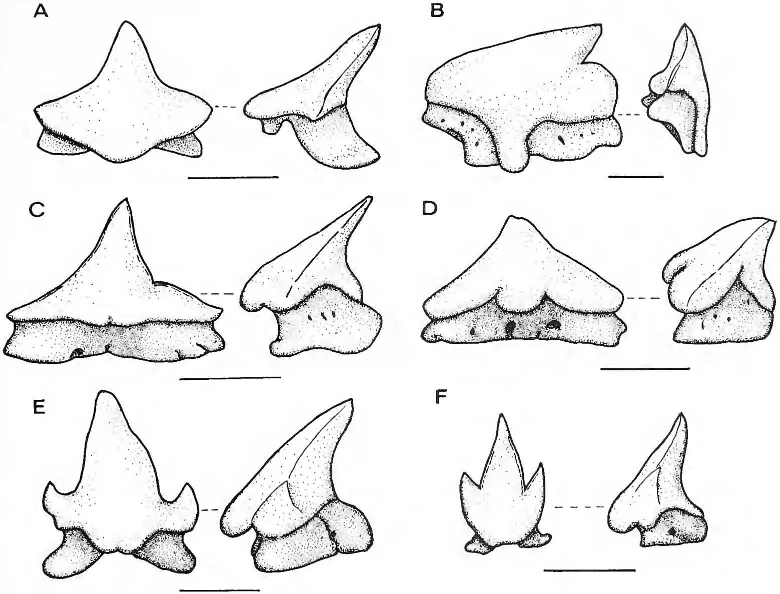
Crown

The teeth of *Anachronistes* possess a crown comprising a conical central cusp flanked by well-developed lateral blades. This is a conservative feature which is variously modified in all four superorders of the Neoselachii to tricuspidate and more complex coronal configurations (Duffin 1980, e.g. Squalomorphii—*Centroscyllium*, *Echinorhinus*; Galeomorphii—*Carcharhinus*, *Odontaspis*, *Brachaelurus*; Squatinomorphii—*Squatina*; Batoidea—*Hypnos*, *Belemnobatis*). Similar morphologies are known in some hybodonts (*Lissodus*, *Hybodus minor*) but are otherwise absent amongst the hybodonts, ctenacanths, xenacanths, and cladoselachians. We believe that the exceptions noted amongst the hybodonts represent convergences with the neoselachian condition since, in other respects, the teeth of these genera are typically hybodont. The conical central cusp flanked by lateral blades is thus probably an apomorphic character of the Neoselachii with respect to the other elasmobranch cohorts, but a plesiomorphic character within the Neoselachii.

There is a labial extension to the base of the crown (basal flange) in the teeth of *Anachronistes* (Pl. 13, figs. 3, 6, 8; Pl. 14, figs. 3, 7, 8; text-fig. 2A). This is a feature found in three of the four superorders of the Neoselachii (Duffin 1980). In the Squalomorphii the labial flange is often plastered on to the labial root face (e.g. *Squalus*, *Oxynotus*, text-fig. 2B), but may be developed as a significant overhang to the crown/root junction, as in *Pristiophorus* and *Pliotrema* (text-fig. 2C, D). In the Galeomorphii, the feature is developed as a labial crown overhang (e.g. *Brachaelurus*, *Stegostoma*, text-fig. 2E, F). In the batoids, the feature is absent, but it is well developed in the Squatinomorphs (*Squatina*). The base of the labial face of the crown is extended in a few hybodonts (*Lissodus*, *Steinbachodus*). In other respects, these genera possess teeth which are typically hybodont; the feature is therefore probably convergent with the neoselachian condition.

Labial root buttress

In the teeth of *Anachronistes* the labial flange development of the crown is supported beneath by a deep labial buttress development of the root (Pl. 13, figs. 1–5, 7, 9; Pl. 14, figs. 1–10). This is flanked medially in basal view by a deep pit which presumably carried blood-vessels to the internal tissues of the crown.



TEXT-FIG. 2. A comparison of the teeth of *Anachronistes* with those of extant neoselachian groups. All teeth are drawn in labial and lateral views. A, *Anachronistes* (BM(NH) P.60670, Lower Carboniferous); B, *Squalus* (Recent); C, *Pristiophorus* (Recent); D, *Pliotrema* (Recent); E, *Brachaelurus* (Recent); F, *Stegostoma* (Recent). Notice that in all cases the crown comprises a conical central cusp flanked by well-developed lateral blades. A prominent basal flange is present in all genera. Bar scale = 1 mm in all diagrams.

The presence of a medial vascular pit and buttressing of the labial flange of the crown is found in only two other genera, to our knowledge: *Squatina* and *Orectolobus* (text-fig. 3). In the teeth of both of these genera the buttressing of the crown is an analogous feature to the condition in *Anachronistes*, since in the former, the root is not directly involved. Instead, the basal flange of the crown is extended basally as a buttress (text-fig. 3A–C). The feature almost certainly arose independently in the Recent and Permo-Carboniferous genera. It may be that the crown modification in the extant genera is more efficient than the condition in *Anachronistes* since it causes less disruption to the vascularization. The function of the labial buttressing of the crown lies presumably in accommodating labially-directed pressure during occlusion, while maintaining a stable tooth row. There is no medial pit in the teeth of Recent *Squatina*. It is present as a possibly variable feature in *Squatina prima* from the English Eocene (text-fig. 3C). In the teeth of this species, multiple vascular foramina are present in the general area occupied by the medial pit in teeth of *Anachronistes* (text-fig. 3D).

In certain species of *Orectolobus* (*O. barbatus*, Recent), the labial buttress is pronounced and the medial pit comprises a single foraminal opening (text-fig. 3B), occasionally carrying several vascular canals.

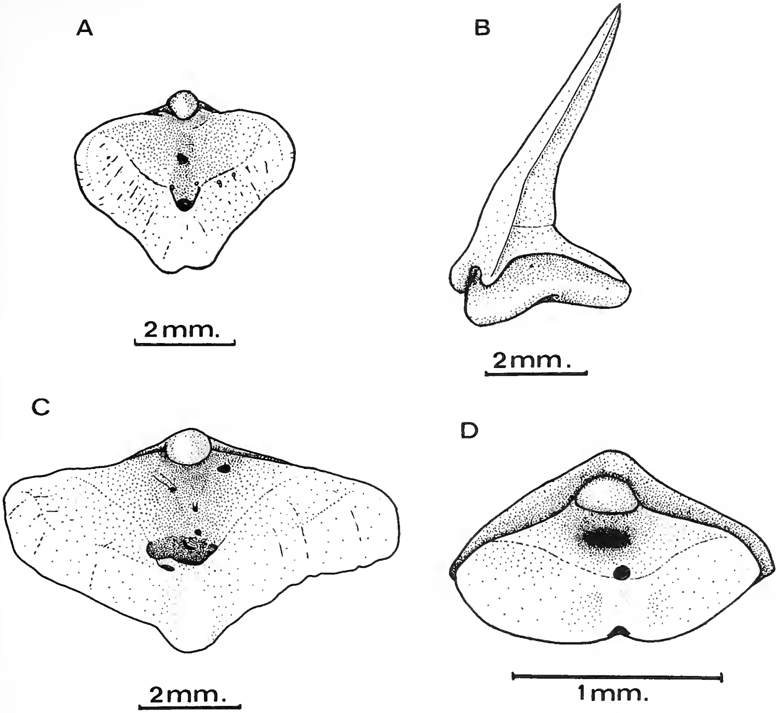
Character Group	Tripartite crown	Labial flange	Labial buttress	Hemiaulacorhize vascularisation	Arcuate root basal face	Central pit	Multiforaminate root	Succession	Heterodonty	Enameloid type
Anachronistes	X	X	X	X	X	X	–	I	?MG	N
Chlamydoselachoids	?	–	–	–	–	–	–	I	MG	T
Hexanchoids	U	–	–	–	–	–	A	A	D,MG	T
Squaliforms	X	X	–	–	X	–	–	A	D,MG	T
Pristiophoriforms	X	X	–	–	X	–	–	Im	MG	?T
Rajiforms	X	–	–	X	X	–	–	I,Im	MG	Ta
Pristiforms	X	–	–	–	X	–	–	Im	MG	?T
Torpediniforms	X	–	–	–	–	–	–	Im	MG	?T
Myliobatiforms	–	–	–	–	–	–	A	Im	MG	?T
Squatiniforms	X	X	X	X	X	X	–	I	MG	T
Heterodontiforms	X	–	–	X	X	–	A	Im	MG	T, S
Orectolobiforms	X	X	X	X	X	X	–	Im	MG	T
Lamniforms	X	–	–	–	X	–	–	I	D, MD	T
Carcharhiniforms	X	–	–	X	X	–	–	I,Im	D,MG,MD	T
Palaeospinax	–	–	–	–	–	–	P	Im	MG	T
Pseudodalatias	X	–	–	–	U	–	P	A	D,MG	S
Hybodonts	–	–	–	–	–	–	P	I, A	D,MG	S
Xenacanths	–	–	–	–	–	–	P	I	MG	?N
Ctenacanths	–	–	–	–	–	–	P	I	?MG	S
Cladodonts	–	–	–	–	–	–	P	I	MG	?S

TABLE 1. The distribution of morphological features in the dentitions of Recent and fossil selachians. X, feature present; —, feature absent; ?, feature may be present; U, feature present in upper dentition only. Multiforaminate root vascularization: A, feature present and considered to be advanced; P, feature present but considered to be primitive. Tooth succession: I, teeth arranged in independent tooth rows; Im, adjacent tooth rows show imbrication; A, adjacent tooth rows alternate. Heterodonty: D, dignathic heterodonty; MG, monognathic gradient heterodonty; MD, monognathic disjunct heterodonty. Enameloid: T, triple-layered; S, single crystallite; N, no enameloid; Ta, tangled fibre enameloid. (Data compiled from Reif 1973, 1974, 1977, 1978; Duffin 1980.)

Vascularization of the root

Casier (1947*a*–*c*) introduced a series of terms for the vascularization patterns found in the roots of extant and fossil sharks teeth (text-fig. 4). He considered that the multiforaminate condition so typical of hybodonts was ancestral to the reduced vascularization of most neoselachians. The multiforaminate teeth he termed 'anaulacorhize' (text-fig. 4A); those teeth possessing a partially covered median root canal he termed 'hemiaulacorhize' (text-fig. 4B), and those with an open median root canal he termed 'holaulacorhize' (text-fig. 4C). The condition with multiple open root canals, as seen in the myliobatiforms, he termed 'polyaulacorhize' (text-fig. 4D). He saw the development of these vascularization types in phylogenetic terms as the sequence anaulacorhize–hemiaulacorhize–holaulacorhize–polyaulacorhize, assuming that the hybodonts were a basal stock.

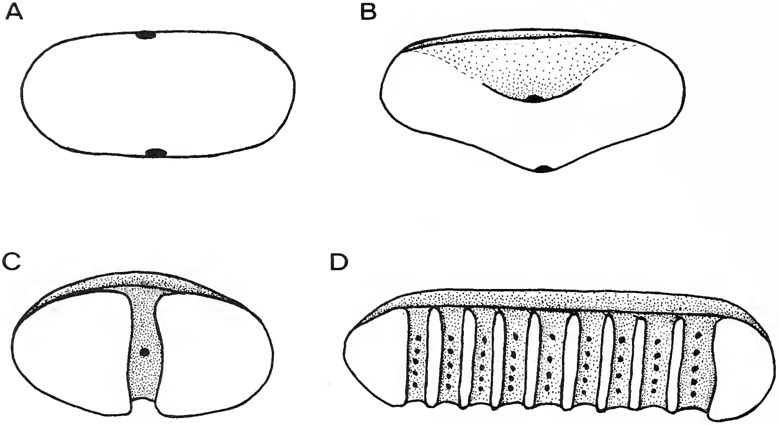
Casier (1947*c*, fig. 1, p. 3) considered that by suppression of entrant vascular foramina, the central cavity within the hybodont root diminished in size, now being fed by a series of labio-lingual internal canals, to become a root of *Synechodus*/*Palaeospinax* appearance. The median, and certain lateral



TEXT-FIG. 3. Labial buttressing and the presence of the medial pit in sharks teeth. A, tooth of *Orectolobus barbatus* (Recent) in basal view. Note the extension of the labial flange to provide a buttress on the labial side of the root, and the presence of a medial pit. B, *O. barbatus* in oblique lateral view. C, tooth of *Squatina prima* (English Eocene) in basal view. Note the labial flange development as a buttress, and the presence of vascular foramina in the area occupied by the medial pit in other genera. D, tooth of *Anachronistes* (BM(NH) P.60673) in basal view. Labial buttressing is provided by a special feature of the root, flanked lingually by a deep medial pit.

internal vascular canals were retained during transformation to a *Squatina* root type, with an enlarged medio-internal foramen at which the median internal canal and central cavity were exposed. There were then two possible evolutionary pathways, according to Casier; elimination of the central cavity together with loss of the roof of the median canal produced roots of *Rhynchobatus* type; enclosing the opening of the central cavity, with its subsequent constriction, within the unroofed median internal canal produced roots of the *Ginglymostoma* and *Scyliorhinus* types.

The hybodont origin of the neoselachians is no longer accepted (Maisey 1975; Herman 1975; Compagno 1973, 1977; Reif 1977, 1978; Duffin 1980). Anaulacorhize vascularization is not restricted to the hybodonts, however, because Recent *Chlamydoselachus*, hexanchoids and squaloids, as well as some Jurassic scyliorhinids and rhinobatids also show this feature. There is no evidence from the fossil record in support of Casiers hypothetical transition from an anaulacorhize, through an hemiaulacorhize to an holaulacorhize vascularization. It is more probable that the vascularization progressed directly from an anaulacorhize to an holaulacorhize condition by loss of the floor of the medio-internal canal (text-fig. 5). The hemiaulacorhize condition is seen in the teeth of *Squatina*, some orectolobids, the anterior teeth of *Heterodontus*, and in *Anachronistes*. The former three groups are mostly specialized benthonic sharks that stabilized in the Middle to Upper Jurassic. It would seem that the hemiaulacorhize condition is a specialization related to bottom feeding habits.



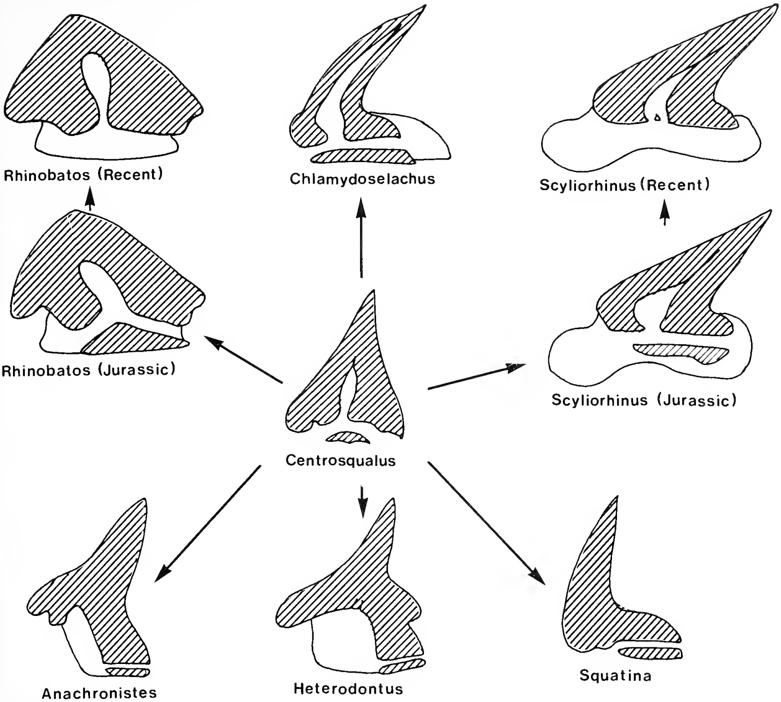
TEXT-FIG. 4. Vascularization patterns in Recent and fossil sharks teeth. All teeth are in basal view (after Casier 1947*c*). A, anaulacorhize vascularization; B, hemiaulacorhize vascularization; C, holaulacorhize vascularization; D, polyaulacorhize vascularization. Casier visualized these vascularization types as a progression, A–D.

Basal face of the root

Duffin (1980) suggested that the arcuate or V-shaped basal root face is typical of neoselachians belonging to the superorders Squalomorphii, Squatinomorphii (text-fig. 4C), and Galeomorphii (text-fig. 4A). It is probably a synapomorphic character of these groups (Table 1). The teeth of *Anachronistes* possess a gently arcuate basal root face in which the apex is directed lingually and the lateral wings are directed labially (see Pl. 14, figs. 2, 4–6; text-fig. 3D).

Tooth succession

The teeth of *Anachronistes* may have been arranged in distinct tooth rows with no overlap of the lateral blades of teeth in adjacent rows (as in *Squatina*, xenacanths, ctenacanths, cladodonts, carcharhiniforms, chlamydoselachoids, and certain rajiforms, hybodonts, and lamnoids—Table 1). Alternatively there may have been some overlap between the lateral blades of teeth in successive tooth rows (imbricate tooth succession, Strasburg 1963) as in pristiophoriforms, pristiforms, torpediniforms, myliobatiforms, heterodontiforms, *Palaeospinax*, orectolobiforms, and certain rajiforms and carcharhiniforms (Table 1). The teeth of one row would not have articulated with those of adjacent tooth rows (as in hexanchoids, squaliforms, *Pseudodalatias*, and certain ?hybodonts—Table 1) since no mesial or distal articular facets are developed on either the root or the crown in *Anachronistes*.



TEXT-FIG. 5. Diagram to show the hemiaulacorhize vascularization in sectioned teeth of various Recent and fossil neoselachians. Morphometric changes from a typical anaulacorhize tooth (*Centrosqualus*) to hemiaulacorhize conditions in various neoselachian lineages. No direct evolutionary relationship is inferred.

Tooth succession does not appear to be a useful taxonomic feature amongst the selachians so far as can be judged at the present time.

Heterodonty

Applegate (1967) identified two types of heterodonty in shark dentitions. The first he termed dignathic heterodonty, involving differences in morphology in those teeth found in corresponding positions in opposite jaws. Monognathic heterodonty involves differences between teeth in different position in the same jaw. There are two types of monognathic heterodonty: gradient monognathic heterodonty involves gradual change in coronal profile of teeth along the length of the jaw; disjunct monognathic heterodonty involves marked dissimilarities between adjacent teeth in the same jaw. Compagno (1970, p. 73) added two further heterodonty types to this list—ontogenetic heterodonty and gynandric (sexual) heterodonty, which are self-explanatory.

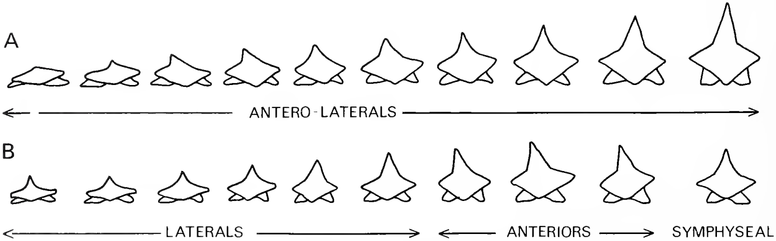
The teeth of *Anachronistes* presently available, show mild gradient monognathic heterodonty. There is no positive evidence for dignathic, gynandric, or ontogenetic heterodonty in the teeth of *Anachronistes*. Monognathic heterodonty is common to all known shark orders (but not to every genus) (Table 1), and so heterodonty is not presently useful as a taxonomic feature, so far as the teeth of *Anachronistes* are concerned.

The usual form of monognathic gradient heterodonty in shark dentitions involves decrease in crown height, increase in mesio-distal width of the crown base, increase in size and number of lateral cusplets or increase in size of lateral blades, and increase in lingual inclination of the central cusp, from teeth in the symphyseal position to those in the commissural position. This basic pattern is found in the Recent genus *Orectolobus*, and is here designated linear gradient monognathic heterodonty. In teeth of Recent *Squatina*, however, there is a general increase in crown height to the fourth distal tooth row, and then a gradual lowering of the crown profile distally. Also, the distal inclination of the central cusp appears to increase symphyseally, and the teeth of the parasymphyseal tooth row possess an almost upright crown. The lateral blade development follows that of linear gradient heterodonty. The pattern of heterodonty shown by the teeth of Recent *Squatina* is here designated non-linear gradient monognathic heterodonty. This type of heterodonty is particularly well developed in the batoids, such as *Rhynchobatus*, *Rhina*, and some species of *Dasyatis*. It is also present in modified form in dentitions of the hybodonts *Acrodus* and *Asteracanthus* (see, for example, Reif 1976, fig. 39), and appears to be an adaptation for durophagous diet.

The samples of teeth of *Anachronistes* presently available are insufficient to judge from the type of gradient monognathic heterodonty it displays. Indeed, the teeth of *Anachronistes* can be equally well arranged to show linear or non-linear gradient monognathic heterodonty (text-fig. 6). The point to be made from the distinction between the two types of heterodonty is that a high-crowned tooth is not necessarily a mesial tooth.

Enameloid ultrastructure

There has been some debate over the tissue covering the crown in sharks teeth. It has been variously identified as true enamel (i.e. ectodermal in origin) and as enameloid (mesodermal in origin) (Applegate 1967; Moss 1977). The tissue will be here referred to as enameloid. Reif (1973, etc.) has found that hybodont and ctenacanth teeth possess a single crystallite enameloid, the individual crystallites of which have no preferred orientation (e.g. Reif 1978, fig. 7*a*, *b*). Neoselachian teeth, on the other hand, possess a triple-layered enameloid comprising a basal enameloid of tangled fibres, a middle enameloid of parallel fibres, and a surface layer of shiny enameloid (Table 1). Reif (1978, p. 53) states that this enameloid type is known in all living sharks and fossil neoselachian sharks. He even uses enameloid ultrastructure to define genera (Reif 1977). There is a discrepancy within the



TEXT-FIG. 6. Possible reconstructions of the dentition of *Anachronistes* showing A, linear gradient monognathic heterodonty, B, non-linear gradient monognathic heterodonty.

enameloid of the teeth of *Heterodontus*. Reif (1977) notes that mesial teeth of *Heterodontus* possess a triple-layered enameloid, but that distal crushing teeth possess a single crystallite enameloid as in the hybodonts, covered by a thick layer of tangled fibre enameloid. Reif (1977, p. 572) interprets the presence of a single crystallite enameloid in lateral teeth of *Heterodontus* as being a convergence with the hybodonts and ctenacanths in order to meet the high pressure stresses set up in the teeth during crushing of food. Bearing the teeth of *Heterodontus* in mind, it might be better to state that triple-layered enameloid indicates neoselachian affinity, but that the converse is not true. The lack of triple-layered enameloid does not necessarily exclude neoselachian affinity, and neither does it therefore positively indicate hybodont or ctenacanth affinity.

One tooth of *Anachronistes fordi* (P.60674) and one tooth of *Anachronistes* sp. was etched in 2N HCl for 3 seconds, dried, covered with a 50 Å thick coating of evaporated gold, and studied using a Cambridge Stereoscan 600 microscope, using an acceleration voltage of 15 kV.

The teeth of *Anachronistes* possess no enameloid layer; the surface of the crown and the occlusal crest appears to comprise compact osteodentine. In our opinion, the lack of enameloid in teeth from Britain and the United States is not due to post-mortem wear. Other teeth in the Steeplehouse Quarry sample possess well-defined enameloid. Neither does the lack of enameloid represent excessive etching since the prepared specimens show sharply defined features (Pl. 14, fig. 10).

Enamel and enameloid have arisen independently in different vertebrate groups. It would not seem unreasonable to suppose that this might be true within the Chondrichthyes. *Anachronistes* could represent a condition pre-dating enameloid acquisition in the neoselachins. Alternatively, *Anachronistes* may have lost enameloid as a secondary feature.

Finally, it should be noted that the tooth form of *Anachronistes* is easily distinguished from that of contemporary petalodonts. The latter possess teeth which are distinct in possessing labio-lingually compressed and scallop-shaped crowns which possess longitudinal ridges basally. The occlusal crest is often serrated or denticulate, and the crown contains 'tubular' dentine.

The tooth shape of *Anachronistes* is probably adapted to bottom feeding. Further evidence in favour of durophagous diet is the nature of the ante-mortem coronal wear. The shark may well have been dorso-ventrally flattened with large pectoral fins as in the Recent Wobbegong (*Orectolobus*) and Angel Shark (*Squatina*). This body form is not without precedent in the Palaeozoic. Lund and Zangerl (1974) describe *Squatinactis caudispinatus* from the Upper Mississippian of Montana. This shark possesses a roughly squatinoid body form together with multicuspid cladodont teeth.

It is also interesting to note here that Zidek (1976) implies the presence of neoselachian sharks in the Carboniferous with the description of an egg capsule named *Palaeoxyris lewisi* from the Pennsylvanian of Oklahoma. Zidek concludes that the Palaeozoic egg capsule shows the closest affinity with egg capsules of *Heterodontus*.

PALAEOECOLOGY

The teeth of *Anachronistes* from Steeplehouse Quarry were found in association with presently undetermined xenacanth, petalodont, palaeoniscid, and *Cladodus* teeth, hybodont teeth and dermal denticles, placoid scales, palaeoniscid scales and vertebrae, and internal casts of textulariid foraminifera (Dr. J. E. Robinson, pers. comm.). The most abundant component of the fauna is the scales of *Petrodus patelliformis* M'Coy (1848) (Ford 1964). The associated invertebrate fauna, as given by Ford (1964, p. 4), comprises the corals *Dibunophyllum bipartitum* M'Coy, *Caninia juddi* (Thomson), *Zaphrentis* spp., *Michelinia tenuisepta* (Phillips), *Emmonsia parasitica* (Phillips), and *Chaetetes septosus* (Fleming); the brachiopods *Echinoconchus punctatus* (J. Sowerby), *Pustula putulosus* (Phillips), *Gigantoproductus giganteus* (J. Sowerby), *Dictyoclostus semireticulatus* (Martin), *Athyris* sp, and *Spirifer bisulcatus* J. de C. Sowerby; numerous bryozoans; and crinoid ossicles.

The associated fauna from Esclusham Mountain is similar to that of Steeplehouse Quarry with regard to the vertebrates, although the quantitative species representation is very different. The vertebrate faunas will be described in detail in a later paper (Duffin, in prep.). Dr. B. Rosen is preparing an account of the coral associations from Esclusham Mountain.

Ford (1964) concludes that the bed yielding *Anachronistes* at Steeplehouse Quarry was deposited in an off-reef area. He concludes that the bed comprises locally derived material which was rapidly deposited, perhaps as a result of an inter-reef scour and subsequent deposition in quieter off-reef waters. Certainly, good biohermal reefs, fore-reef and inter-reef facies, together with lagoonal deposits are known from Steeplehouse Quarry and adjacent quarries in the Coal Hills complex of Wirksworth (Ford 1980; Shirley 1959). The presence of xenacanth shark teeth as part of the faunal association may indicate that certain faunal elements were not indigenous to the broad reef complex, but transported into the area from freshwater areas, possibly lagoons.

CONCLUSIONS

From the above discussion we feel it reasonable to conclude that *Anachronistes* is a neoselachian shark because it possesses a conical central cusp, well-developed lateral blades and a basal flange, a V-shaped basal face to the root, and typical neoselachian root vascularization (hemiaulacorhize).

Anachronistes possesses several characters which are shared by teeth of *Squatina* and *Orectolobus*. These features are the labial buttress on the underside of the labial flange, and the central vascular pit on the root. The complex of characters shown by *Anachronistes* is most closely paralleled in *Squatina* and *Orectolobus*. Both of these genera belong to relatively primitive neoselachian groups, and are coincidentally among the earliest known Jurassic neoselachians. It is unlikely that *Anachronistes* is a stem neoselachian since it is adapted to the specialized habit of a bottom feeder.

The gross morphology of sharks teeth remains a useful taxonomic tool. Two new terms are introduced concerning monognathic heterodonty in shark dentitions. Linear gradient monognathic heterodonty is that in which there is gradual reduction in coronal profile of teeth commissurally (e.g. *Orectolobus*), while non-linear gradient heterodonty involves the presence of high-crowned teeth part way along the jaw, and then subsequent lowering of the coronal profile mesially and distally (e.g. *Squatina*).

The early record of the neoselachians is thus established as extending into the Lower Carboniferous of Britain and the Lower Permian of the U.S.A. It is expected that the Carboniferous record of the neoselachians will prove to be quite diverse, and that the neoselachian lineage is as old as that of the hybodonts, and possibly the ctenacanths and cladoselachians.

Acknowledgements. We are indebted to Miss Alison Longbottom and Dr. Colin Patterson for giving access to material from Esclusham Mountain, and to Dr. Bruce Welton for bringing the Permian material of the United States to our notice, and allowing us to study it. We have benefited greatly from discussions with Dr. Leonard Compagno, and are grateful to Dr. Colin Patterson for critically reading the manuscript.

REFERENCES

AGASSIZ, L. 1843. *Recherches sur les Poissons Fossiles*. 5 vols., 1420 pp., and supplement. Neuchâtel.

APPLEGATE, S. P. 1967. A survey of shark hard parts. *In* GILBERT, P. W., MATHEWSON, R. F. and RALL, D. P. (eds.). *Sharks, skates and rays*, ch. 2, pp. 37–67. Baltimore: Johns Hopkins Press.

BEAUMONT, G. DE. 1960. Observations préliminaires sur trois Sélaciens nouveaux du Calcaire lithographique d'Eichstätt (Baviére). *Eclog. geol. Helv.* **53,** 315–328, 1 pl.

BLOT, J. 1969. Holocéphales et élasmobranches. Systematique. *In* PIVETEAU, J. (ed.). *Traité de Paléontologie*, **4,** 702–776. Masson et Cie: Paris.

CASIER, E. 1947*a*. Constitution et évolution de la racine dentaire des Euselachii. 1. Note préliminaire. *Bull. Mus. r. Hist. nat. Belg.* **23** (13), 1–15.

—— 1947*b*. Constitution et évolution de la racine dentaire des Euselachii. II. Étude comparative des types. Ibid. **23** (14), 1–32, 5 pls.

—— 1947*c*. Constitution et évolution de la racine dentaire des Euselachii. III. Évolution des principaux caractères morphologiques et conclusions. Ibid. **23** (15), 1–45.

COMPAGNO, L. J. V. 1970. Systematics of the genus *Hemitriakis* (Selachii: Carcharhinidae, and related genera). *Proc. Calif. Acad. Sci.*, ser. 4, **38,** 63–98.

—— 1973. Interrelationships of living elasmobranchs. *In* GREENWOOD, P. H., MILES, R. S. and PATTERSON, C. (eds.). *Interrelationships of fishes*, suppl. 1. *J. Linn. Soc. Zool.* **53,** 15–61. London.

—— 1977. Phyletic relationships of living sharks and rays. *Amer. Zool.* **17,** 303–322.

DINKEL, H. 1920. *Untersuchung der Squatinen im Weißen Jura Schwabens.* Unpublished dissertation, University of Tübingen.

DUFFIN, C. J. 1978. The Bath Geological Collections. f. The importance of certain vertebrate fossils collected by Charles Moore: an attempt at scientific perspective. *Geological Curators Group Newsletter*, **2,** 59–67.

—— 1980. A new euselachian shark from the Upper Triassic of Germany. *N. Jb. Geol. Paläont. Mh.* **1980** (1), 1–16.

—— 1981. Comments on the selachian genus *Doratodus* Schmid, 1861, from the Upper Triassic of Germany. Ibid. **1981** (5), 289–302.

FORD, T. D. 1964. A new fish bed in the Carboniferous Limestone of Derbyshire. *Mercian Geol.* **1,** 3–9.

—— 1980. Field Meeting: the economic geology of the Peak District. *Proc. geol. Ass.* **91,** 229–234.

HERMAN, J. 1975. Les Selaciens des terrains neocrétaces & paléocènes de Belgique & des contrées limitrophes. Éléments d'une biostratigraphie intercontinentale. *Mem. serv. Cart. géol. min. Belg.* **15,** 7–450, 21 pls.

LUND, R. and ZANGERL, R. 1974. *Squatinactis caudispinatus*, a new elasmobranch from the Upper Mississippian of Montana. *Ann. Carneg. Mus.* **45,** 43–55.

MAISEY, J. G. 1975. The interrelationships of the phalacanthous selachians. *N. Jb. Geol. Paläont. Mh.* **1975** (9), 553–567.

MOSS, M. L. 1977. Skeletal tissues in sharks. *Amer. Zool.* **17,** 335–342.

REIF, W.-E. 1973. Morphologie und Ultrastrukter des Hai-'Schmelzes'. *Zoologica Scripta*, **2,** 231–250.

—— 1974. *Metopacanthus* sp. (Holocephali) und *Palaeospinax egertoni* S. Woodward (Selachii) aus dem unteren Toarcium von Holzmaden. *Stuttg. Beitr. Naturk.*, ser. B, no. 10, 9 pp.

—— 1976. Morphogenesis, pattern formation and function of the dentition of *Heterodontus* (Selachii). *Zoomorphologie*, **83,** 1–47.

—— 1977. Tooth enameloid as a taxonomic criterion. 1. A new euselachian shark from the Rhaetic-Liassic boundary. *N. Jb. Geol. Paläont. Mh.* **1977** (9), 565–576.

—— 1978. Tooth enameloid as a taxonomic criterion. 2. Is '*Dalatias*' *barnstonensis* Sykes, 1971 (Triassic, England) a squalomorphic shark? Ibid. **1978** (1), 42–58.

—— 1980. Tooth enameloid as a taxonomic criterion. 3. A new primitive shark family from the Lower Keuper. Ibid. **160,** 61–72.

SAINT-SEINE, P. DE. 1949. Les poissons des calcaires lithographiques de Cerin (Ain). *Nouv. Arch. Mus. Hist. nat. Lyon*, **2,** 1–357.

SCHAEFFER, B. 1967. Comments on elasmobranch evolution. *In* GILBERT, P. W., MATHEWSON, R. F. and RALL, D. P. (eds.). *Sharks, skates and rays*, ch. 1, 3–35. Baltimore: Johns Hopkins Press.

SCHWEIZER, R. 1964. Die Elasmobranchier und Holocephalen aus den Nusplinger Plattenkalken. *Palaeontographica*, **A 123,** 58–110.

SHIRLEY, J. 1959. The Carboniferous Limestone of the Monyash–Wirksworth area, Derbyshire. *Q. Jl. geol. Soc. Lond.* **114,** 411–429.

STRASBURG, D. W. 1963. The diet and dentition of *Isistius brasiliensis* with remarks on tooth replacement in other sharks. *Copeia*, **1963** (1), 33–40.

SYKES, J. H. 1971. A new dalatiid fish from the Rhaetic Bone Bed at Barnstone, Nottinghamshire. *Mercian Geol.* **4,** 13–22.

—— 1974. Teeth of *Dalatias barnstonensis* in the British Rhaetic. Ibid. **5,** 39–48.

THIOLLIÉRE, V. J. 1849. Sur un nouveau gisement de poissons fossiles dans le Jura du département de l'Ain. *Annls Soc. Agric. Lyon*, **1,** 43–66.

—— 1854. *Description des poissons fossiles provenant des gisements coralliens du Jura dans le Bugey*, 27 pp., 4 pls. Paris.

TINTORI, A. 1980. Teeth of the selachian genus *Pseudodalatias* (Sykes, 1971) from the Norian (Upper Triassic) of Lombardy. *Riv. ital. Palaeont.* **86,** 19–30.

WAGNER, A. 1857. Charakteristik neuer Arten von Knorpelfischen aus den lithographischen Schiefern der Umgebung von Solnhofen. *Gel. Anz. Akad. Wiss. München*, **44,** 288–293.

WOODWARD, A. S. 1918. On two new elasmobranch fishes (*Crossorhinus jurassicus*, sp. nov., and *Protospinax annectans*, gen. et sp. nov.) from the Upper Jurassic lithographic stone of Bavaria. *Proc. zool. Soc. Lond.*, 1918, 231–235.

ZIDEK, J. 1976. A new shark egg capsule from the Pennsylvanian of Oklahoma, and remarks on the chondrichthyan egg capsules in general. *J. Paleont.* **50,** 907-915.

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A REVIEW OF BRACHIOPOD DOMINATED PALAEOCOMMUNITIES FROM THE TYPE ORDOVICIAN

by MARTIN G. LOCKLEY

ABSTRACT. Recent studies on Ordovician (mainly Llanvirn to Caradoc) faunas from type and classical localities in Wales and the Welsh Borderland have resulted in the publication of a wealth of data representing approximately 200,000 individual identifications from about 2,000 samples (assemblages) collected through some 10 km of strata (average sample interval 5 m). Contributing authors have named at least thirty variously defined assemblages, associations, sets, communities, and palaeocommunities which are reviewed and subjected to cluster analysis. This reveals eight highly correlated ($p > 95\%$) taxonomic subclusters which also closely reflect palaeogeography, stratigraphic relationships, and facies preferences. These are conveniently characterized, using pre-existing guidelines, as the 'mixed' *Dalmanella*, *Hesperorthis*, *Lingulella*, *Onniella*, *Dalmanella*, *Bancroftina-Kjaerina*, *Howellites*, and *Nicolella* palaeocommunities. Other important faunas include inarticulate brachiopod associations dominated by *Monobolina*, *Pseudolingula*, and *Schizocrania*.

Palaeoecological and evolutionary considerations indicate a marked contrast between widespread and diverse, biologically accommodated associations from the middle part of the facies (textural) spectrum and localized, physically limited, low-diversity faunas from extremely coarse (shoreface) facies and more widespread low-diversity faunas from very fine (offshore) facies. This pattern differs from some Silurian models but accords with others. Differences in the Welsh Basin during the two periods suggest that comparisons between supposedly analagous palaeocommunities are tenuous and certainly not viable from a taxonomic viewpoint. Diversity, facies preference, palaeogeography, and taxonomic composition are all shown to be useful guides to palaeocommunity evolution; they indicate that high-diversity, pre-Caradoc, *Dalmanella*-dominated faunas represented the most stable palaeocommunity which evolved in basinal (open-shelf?) rather than basin-margin (shoreface) localities to give rise to associations characterizing the *Nicolella* palaeocommunity of Caradoc times. In contrast, low-diversity shoreface faunas show more rapid and unpredictable change whilst those from argillaceous offshore facies remain unchanged over long periods.

THE aim of this paper is to summarize the results of a long-term, integrated research project on the Ordovician (Llanvirn to Caradoc) shelly facies of the Anglo-Welsh region and to assess the importance of named palaeocommunities and their role in community evolution. The studies on which this review is based were virtually all inspired by Dr. Alwyn Williams, who together with the author and Dr. J. M. Hurst has been largely responsible for the completion of the main quantitative taxonomic and palaeoecological contributions listed in Table 1.

Other important studies by Drs. P. J. Brenchley and R. K. Pickerill, although more localized and involving different methodology, contribute to our knowledge of contemporary ichnofaunas and to the growing pool of interpretative ideas. Indeed, the spate of recent publications (Table 1) has resulted in such an accumulation of data and contrasting ideas on the factors responsible for controlling the distribution of Ordovician faunas that it seems particularly advisable to rationalize and compare contrasting opinions and sometimes ambiguous terminology before proceeding further.

Viewed in the historical context of British Lower Palaeozoic palaeoecological research, the community concept was applied later to Ordovician faunas than to those of the Silurian (e.g. Ziegler 1965) and can consequently be considered more thoroughly in the light of the substantial quantitative research which has been completed in the last decade. To date over fifty distinct faunal associations and communities or palaeocommunities have been named and defined quantitatively. The documented taxonomic composition of these and other representative assemblages (data in

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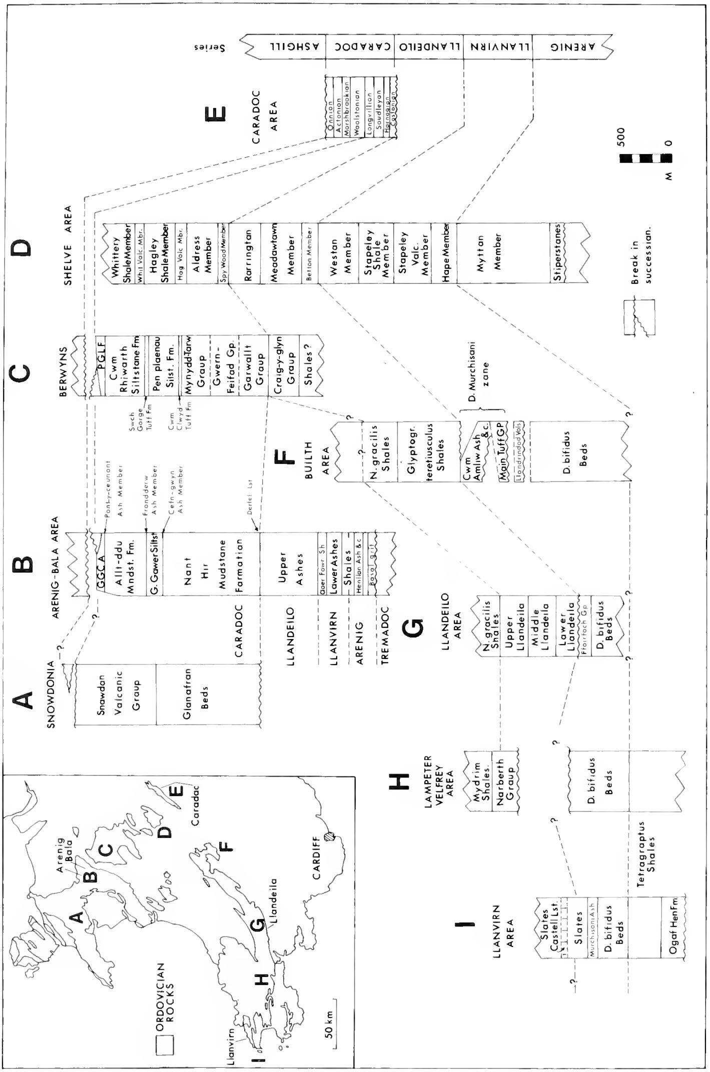


TEXT-FIG. 1. Correlation of type and classical sections in the Ordovician of Wales and the Welsh Borderland.

Table 5) affords the opportunity for a comprehensive cluster analysis which is used as a guideline for delineating major palaeocommunity patterns.

This review deals specifically with Anglo-Welsh faunas, which belong to an entirely different Ordovician province than those of Scoto-Irish or Scoto-American affinity (Williams 1962). Although brief observations on Anglo-Welsh Arenig faunas are relevant to discussion of descendant associations, and those of 'Ashgill' age often resemble ancestral Caradoc faunas, detailed discussion of the faunas of these series is largely outside the scope of this study.

This analysis critically examines known associations, and is broadly divided into two parts. Initial sections attempt to rationalize definitions and ambiguities or inconsistencies in documentation and, like the necessary discussion of local faunas, may be of greater interest to the more specialized reader. The latter part of the paper encompasses more generalized conclusions and outlines the eight major palaeocommunity groupings listed in the abstract (I–VIII of text-fig. 10). These can be shown to have been associated with particular sedimentary deposits located along a facies gradient inferred to represent a generalized shoreface to offshore transect. The model is substantiated by diversity profiles which are analogous to modern and fossil examples for similar transects. Palaeogeographical, palaeoecological, and taxonomic considerations shed light on probable patterns of community evolution.

TABLE 1. Summary of studies relating to Anglo-Welsh, Llanvirn to Caradoc Brachiopoda and palaeoecology (1973–1980); standard sections for key areas shown in text-fig. 1. (*NS* = number of samples; *M* = approximate thickness of strata [metres]; statistics (right) summarized in abstract.)

Area	*Age of faunas*	*Author*	*NS*	kg	*M*
Shropshire	Upper Caradoc	Hurst (1978*a*, *b*; 1979*a*, *b*, *c*) Hurst and Hewitt (1977) Hurst and Watkins (1981) Harper (1978)	260	(2000)	300
	(Lower Caradoc	Hurst and Lockley in prep.)	179	—	300
Shropshire	Arenig–Lower Caradoc	Williams (1974, 1976)	222	—	4500
Bala, Gwynedd, N. Wales	Lower Caradoc	Lockley (1977, 1978, 1980*a*, *b*)	250	1500	1500
Berwyn Hills, Powys Clwyd, N. Wales	Lower Caradoc	Brenchley (1964, 1966, 1969, 1972, 1979) Brenchley and Pickerill (1973, 1980) Pickerill (1973, 1974, 1975, 1976, 1977) Pickerill and Brenchley (1975, 1979)	400+		2000
Llandeilo, Dyfed	Llandeilo	Wilcox (1979) Wilcox and Lockley (1981)	395	1400	1100
Dyfed	Upper Llanvirn–Lower Caradoc	Addison (1974) Lockley (this paper)	80		
Llandeilo and Builth	Upper Llanvirn–Llandeilo	Williams, Lockley and Hurst (1981) Lockley and Antia (1980) Lockley and Williams (1981)	120	800	100+
South-west England	?Llandeilo	Cocks and Lockley (1981) Bassett (1982)			

PALAEOECOLOGICAL DEFINITIONS AND CONCEPTS

Since Williams (1973, p. 242) summarized the implications of his investigations into the Lower Caradoc brachiopod faunas of North Wales (Williams 1963) by suggesting that the *Dinorthis*, *Nicolella*, *Onniella*, and *Howellites* 'associations dominated the brachiopod communities of those times', a considerable volume of mainly quantitative palaeoecological research has been directed towards further investigation of these and related ancestral 'associations'.

It is therefore desirable to provide an unequivocal explanation of the concepts and criteria employed in grouping fossil remains into categories like assemblage, association, or community. Definitions proposed by Pickerill and Brenchley (1975; 1979, p. 237) furnish useful guidelines worth quoting:

(i) An assemblage refers to a single sample.
(ii) An association refers to the recurrent association of taxa in a group of assemblages.
(iii) A community refers to a spatially and temporally recurring group of organisms usually related to specific environmental parameters.

Such a hierarchical arrangement is generally acceptable and at least partially conforms with the terminology applied by other authors. However, ambiguities arise from the finely drawn distinction between the terms 'association' and 'community' and the fact that several authors (e.g. Williams 1976; Hurst 1979*b*; Lockley 1980*a*) have tended to avoid using the latter category because of its inherent biological implications. Indeed Williams (1976) even preferred the 'non-committal' mathematical label 'sets' for groupings defined by cluster analysis, although this term has also been misinterpreted (Raab 1980). Similarly, Williams *et al.* (1981) grouped related 'associations' into 'palaeocommunities', so as to emphasize the residual nature of all fossil faunas.

Although well rationalized, the definitions of Pickerill and Brenchley (1975, 1979) indicate the difficulty of drawing clear distinctions between the terms 'association' and 'community', which are both based on recurrent patterns in constituent taxa. Although they contend that communities are related to environmental parameters, Williams (1973) had already stated that his associations were facies-related. These authors therefore provide examples of the largely synonymous use of the terms 'association' and 'community'; e.g. after considering entire assemblages Pickerill (1974, 1975, 1977) and Pickerill and Brenchley (1979, p. 230) 'adopted' the named associations of Williams (1973) and elevated them to community rank. They also referred to subcommunities 'to distinguish associations within a community which have a different abundance of constituent genera', thereby introducing a new category which barely differs from the other two. Such hazy terminology is undesirable but hard to circumvent; the term 'association' is particularly ambiguous and can apparently be endowed with increasing degrees of 'biological' emphasis until it becomes a 'community' (cf. Pickerill and Brenchley 1979). This may be acceptable where an association of similarly composed recurrent assemblages can be shown to represent an *in situ* residuum of a biological community, but is obviously unacceptable where there is evidence of continued reworking or persistent physical environmental controls.

Where a locally defined association reappears after a temporary displacement it is best referred to as a subsequent 'phase' (*sensu* Hurst 1975, 1979*b*; Lockley 1980*a*; Williams *et al.* 1981); these can be numbered sequentially. The term faunule, used for collective reference to both formally and informally defined associations, phases, and assemblages (Wilcox and Lockley 1981), is too generalized for formal definition and is used only for convenience.

Such rationalizations lead to the following summary of categories for fossil residua:

(1) An 'assemblage' refers to a single sample from a particular horizon. It may be transported, partially 'disturbed' (*sensu* Scott 1974) or an *in situ* residue; it can be analysed conveniently using individual 'census samples' (cf. Williams *et al.* 1981).
(2) An 'association' refers to a group of assemblages all showing similar, recurrent patterns of species composition; its origin, like that of its component assemblages, may vary from one association to the next.

(3) A palaeocommunity (or fossil community) refers to an assemblage, association, or group of associations and/or phases of associations inferred to represent a once distinctive biological entity. The term palaeocommunity helps draw a useful distinction between the small preserved part of a biological community and the more complete entity which may be inferred or represented in exceptional cases. The term is used here only to categorize associations which are closely related in terms of taxonomic composition, palaeogeography, age, and facies preferences. (This definition also accords with that proposed by Kauffman and Scott (1976).)

Having defined an association or paleocommunity, various criteria may be employed in choosing an appropriate name. Fortunately, in the context of British Ordovician research all workers have consistently chosen to name associations and communities after dominant (relatively abundant) constituents. Less dominant species may be chosen and justified on the basis of distributions considered to be ecologically significant when using such parameters as fidelity or exclusiveness (see Krebs 1978 for definitions). However, the naming of communities after rare taxa (e.g. Titus and Cameron 1976) often obscures similarities which might otherwise be immediately apparent (cf. Lockley 1980*a*, pp. 192, 229).

Proportions of residual fossil species within an undisturbed association or community may be considered analogous to proportions found in populations in modern marine communities. Relative abundance % (or persistence of occurrence) and % biomass (b.) have been used to identify '1st, 2nd, and 3rd order characterizing species' and 'associated animals' (respective %:% b. ratios 50:5, 50:5, 70:10, and 25:2%) (Thorson 1957). I have used (Lockley 1980*a*, p. 192) relative abundance (%), but not biomass estimates to identify fossil species analogous to modern 'characteristic and associated' species. Pickerill and Brenchley (1979) followed Johnson (1972) in employing a similar, but less quantitative method for identifying characteristic, intergrading, and ubiquitous species.

THE ROLE OF TAXONOMY IN PALAEOECOLOGY

Since the species is the only biologically meaningful taxonomic category, species level taxonomy must be favoured as a basis for defining associations and hence communities. This is particularly true since most Ordovician species have only been defined after rigorous biometric scrutiny. Nevertheless, generic terminology must also be considered, particularly since it has already been employed in a variety of ways.

Species level taxonomy favours biostratigraphic precision and permits differentiation between associations dominated by different species of the same genera. It is useful in the event of taxonomic revisions (which do not affect the species) and, more commonly, in cases where genera like *Dalmanella* are represented by numerous species whose ages and facies preferences differ (cf. Hurst 1979*b*). Species level terminology is also important in rarer cases where congeneric species occur together and there is a need to distinguish their proportions. A further fundamentally important advantage of species level differentiation is that it permits analysis of 'community evolution' by facilitating our understanding of phylogenies.

However, the use of generic abbreviations is less cumbersome and should be considered acceptably accurate providing the following criteria are met: (1) associations should be named unambiguously after constituent species occurring at specified horizons and localities so that there is no doubt about local faunal composition; (2) where a generic category, e.g. *Dalmanella* community, includes a number of associations containing congeneric species, full details of the specific composition, age, and geographical distribution of the association should be given so that all known parts of that compound palaeocommunity are defined equally and adequately.

Since compound palaeocommunities cannot always be named after a single characteristic species, there is a good case for employing species names for association definitions and generic names for palaeocommunities.

KNOWN ANGLO-WELSH ASSOCIATIONS AND PALAEOCOMMUNITIES

Pre-Llanvirn faunas

Shelly brachiopod faunas of Arenig age are known from Anglesey and Dyfed (Bates 1968; Neuman and Bates 1978; Lockley and Williams 1981) and from the Shelve area of Shropshire (Williams 1974, 1976), but have been subjected to only limited palaeoecological analysis. However, it is evident that by early Ordovician (Arenig) times, coarse-ribbed orthaceans (e.g. *Ffynnonia* and *Orthambonites*) had successfully colonized a variety of mainly shallow-water, peri-insular, arenaceous facies associated with 'a group of islands in the middle of the Proto-Atlantic (or Iapetus) ocean' (Neuman and Bates 1978, p. 578; see also Dean 1976, fig. 5). The former authors reiterated Williams's suggestion (1973, p. 249) that such faunas, particularly those from Anglesey, represented a distinct Celtic 'province' associated with the Irish Sea Horst or Geanticline (see also Dewey 1969 and Neuman 1976). However, as similar contemporaneous facies are not well represented elsewhere in Wales and the Welsh Borderland, evidence for a 'distinct' Celtic province is tenuous. Faunal differences probably relate primarily to facies variations. Indeed, Williams (1974, p. 18; 1976, p. 19) noted small representatives of *Orthambonites proava* (Salter), together with *Monobolina plumbea* (Salter) and *Palaeoglossa attenuata* (Sowerby) characterizing silty, even tuffaceous parts of the Arenig Mytton Member (Whittard 1979) whilst a more diverse *Dalmanella* (*D. elementaria*), *Protoskenidioides*, *Euorthisina* association typified contemporary laminated siltstone and shaly facies. This latter association may be related to brachiopod faunas recently discovered from similar facies in Dyfed (R. A. Fortey and R. M. Owens, pers. comm.), and should be differentiated from the sparser inarticulate-dominated faunas here characterized as the *Monobolina* association, which inhabited argillaceous facies also containing trilobites and graptolites (Fortey and Owens 1977).

According to data presented by Williams (1974, table 1) the two Shelve associations may be differentiated as follows:

	Dominant taxa	$\bar{D}$	*NS*	Typical facies
1. *Monobolina* association	*Monobolina* and *Palaeoglossa*	3	19	mudstone
2. 'Diverse' articulate-dominated association	*Dalmanella* *Protoskenidioides*	6	3	siltstone

$\bar{D}$ = Mean Diversity, *NS* = Number of Samples

Although *Monobolina* is clearly the most dominant and persistent form, Williams (1976) included these faunas in the wide-ranging *Pseudolingula* set based on *P. granulata* (Phillips). However, the term is inappropriate since *Pseudolingula* is virtually absent; the assemblages show little taxonomic similarity (clustering), and should at least be differentiated in the manner proposed herein. Co-occurrence of inarticulate and articulate taxa may simply be due to intergrading (ecotones). This generalized contrast between 'an inarticulate association . . . in the finer clastic sediment and a predominantly articulate one . . . in the coarser . . . siltstones . . . or sandstones' (Williams 1974, p. 23) is indicative of patterns recognizable through much of the Ordovician. Cocks and McKerrow (*in* McKerrow 1978, p. 65) referred to an Arenig '*Orthambonites*-crinoid community' characterizing shallow water facies in Dyfed (see Bates 1969). However, since Neuman and Bates (1978, p. 577) considered these assemblages to be specifically and 'significantly different' from penecontemporaneous faunas such as those from Anglesey, this 'community' is simply a generalized means of characterizing the ubiquity of *Orthambonites*.

Llanvirn to Llandeilo faunas

Similar 'facies-fauna' distributions are noted during the Llanvirn. While volcanism persisted in the Builth-Llandrindod complex, the stout, coarse-ribbed orthacean *Hesperorthis* dominated shallow-water arenaceous facies whilst contrasting, sediment-starved, 'offshore' facies were again characterized by inarticulate, trilobite- and graptolite-dominated faunas. Taxonomic observations by Neuman and Bates (1978) that *Orthambonites* of the *Lenorthis* type may be considered 'a subjective junior synonym' of *Hesperorthis* serve to highlight similarities between Arenig and Llanvirn facies faunas.

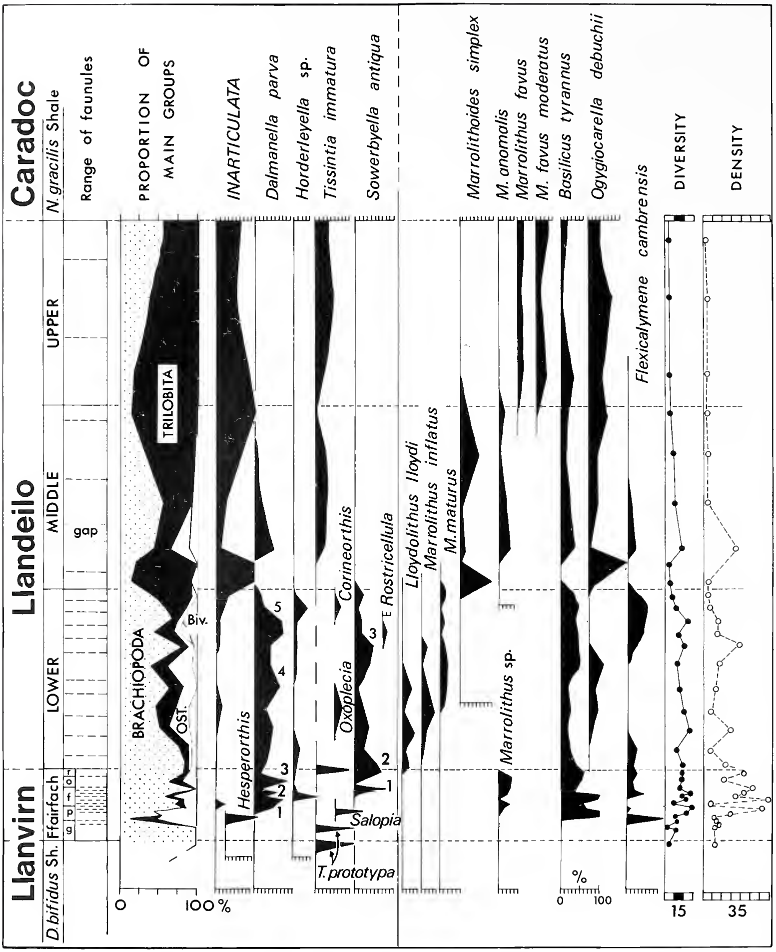
Although Suthren and Furnes (1980) and particularly Furnes (in press) have recently re-evaluated many fossiliferous sedimentary deposits from the Builth area, the conclusions that some coarser *Hesperorthis*-bearing facies represent debris flow or associated fan deposits do not alter the probability of an onshore source. Stratigraphical revisions (Furnes, in press) will alter the nomenclature used in text-fig. 1 and enhance current palaeoenvironmental interpretations.

Contemporaneous finer-grained, silty deposits both here and in the Shelve and Llandeilo areas typically yield *Tissintia* (*T. prototypa* Williams) and *Pseudolingula* (*P. granulata*) forming a distinctive recurrent association (Williams *et al.* 1981; Wilcox and Lockley 1981). Finer, argillaceous, Llanvirn to Lower Caradoc deposits yield, at various horizons, *Obolus*, *Paterula*, *Schizotreta*, *Conotreta*, *Schizocrania*, *Palaeoglossa*, *Lingulella*, *Schmidtites*, *Pseudolingula*, *Tissintia* (*T. immatura* Williams) and *Monobolina* (*M. crassa* Lockley and Williams).

In the Llandeilo area, however, a localized suite of diverse faunal associations is known from sedimentary facies which are texturally intermediate between contrasting orthacean-dominated sandstones and inarticulate-dominated shales. These associations are dominated by articulate brachiopods including *Hesperorthis*, *Salopia*, *Horderleyella*, and in particular *Dalmanella* and *Sowerbyella*. Detailed studies centred on the Llandeilo area (Williams *et al.* 1981; Wilcox and Lockley 1981) indicate that these genera each occupied different habitats circumscribed by highly varied facies distributions. The former three taxa were considered representative of a *Horderleyella* palaeocommunity inhabiting sandy substrates; however, the term *Hesperorthis* palaeocommunity is considered more appropriate because *Horderleyella*-dominated assemblages intergrade with those containing *Dalmanella* and *Sowerbyella* whereas *Hesperorthis* and *Salopia* rarely occur in assemblages containing *Dalmanella* or *Sowerbyella*. Williams *et al.* have shown that both *Dalmanella* (*D. parva* Williams) and *Sowerbyella* (*S. antiqua*), despite co-occurring in some mainly younger assemblages, first appear separately in the succession, show repetitive phases of recurrence, and are more appropriately considered representative of differently structured palaeocommunities. Morphological and taphonomic observations (Williams *et al.* 1981; Wilcox and Lockley 1981) support this contention and tend to conflict with the concept of a generalized *Sowerbyella*–*Dalmanella* community (Cocks and McKerrow: *in* McKerrow 1978).

A summary of the distribution of species in the Ffairfach Group stratotype and succeeding type Llandeilo is given in text-fig. 2, which shows the abrupt faunal changeovers associated with a sequence of rapid Llanvirn facies changes (Williams *et al.* 1981). In contrast, the overlying Llandeilo succession is characterized by a transitional, upward fining facies sequence and corresponding progressive reduction in faunal diversity (Wilcox and Lockley 1981).

Llandeilo faunas from the Shelve area (Williams 1974, tables 6, 7) are dominated initially by *P. granulata*, *P. attenuata*, *Dalmanella salopiensis* Williams, *T. immatura*, and *Rafinesquina delicata* Williams, comprising the trophic nucleus (i.e. 80%; see Neyman 1967) in the silty Meadowtown Member. Subsequently, in the calcareous shales of the Rorrington Member they are dominated by a less diverse inarticulate-dominated fauna characterized primarily by *P. attenuata*, and *D. salopiensis*, with *Schmidtites micula* (M'Coy) and *Lingula displosa* Williams. Clearly this Llandeilo succession is broadly analogous to that recorded in the type area (Wilcox 1979; Wilcox and Lockley 1981) where Lower Llandeilo *Dalmanella parva*-dominated faunules are succeeded by inarticulate-dominated assemblages in the Middle and Upper Llandeilo. It is also interesting to note that Williams (1974, p. 92) considered *D. salopiensis* 'at first sight . . . like the Lower Llandeilo *Dalmanella parva*'. The rare Meadowtown occurrence of *Schizotreta*, *Glyptorthis*, *Kullervo*, and *Murinella* is distinctly reminiscent of similar sporadic occurrences in the *Dalmanella*–*Gelidorthis* association of the Ffairfach Group and the similarities are reflected by a moderate (0·39) coefficient of association (D7/G3 of text-fig. 9 and Table 5). Indeed similarities between Weston, Betton, Meadowtown,



TEXT-FIG. 2. Biostratigraphy of the Ffairfach Group and Llandeilo Series in the type area (faunules based on Williams *et al.* 1981 and Wilcox and Lockley 1981).

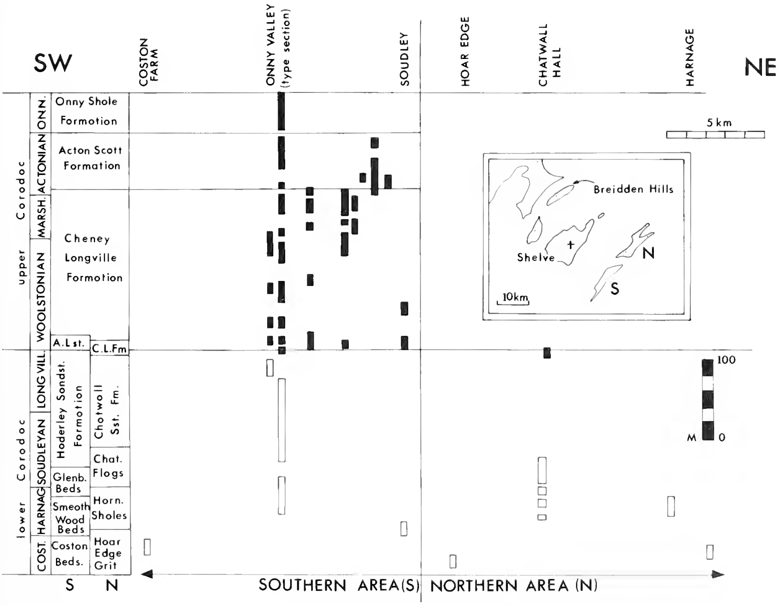
Rorrington, and type Llandeilo faunas are consistently moderate to high (mean coefficient of association $C = 0{\cdot}43$, range 0·23 to 0·64).

McGregor's observation (1961, p. 191) that Upper Llandeilo *Dalmanella* from the Berwyn Hills are conspecific with *D. parva* further substantiates the view that all Llandeilo representatives of this genus are closely related. Amongst the brachiopods and trilobites alone, there are at least twenty species common to both areas (Wilcox 1979, figs. 7, 4–5) and the similarity coefficient ($C = 0{\cdot}58$) is correspondingly high.

Caradoc faunas

Rocks of Caradoc age both in the type area and parts of North Wales are particularly fossiliferous and have therefore been the subject of considerable attention particularly in recent years (Table 1).

(1) *The type area.* Hurst (1979*a*, pp. 185–9) outlined the important contributions made by Bancroft (1929 to 1945) and Dean (1958 to 1964) to our knowledge of the faunal succession in the type area and has himself contributed substantially (Hurst 1978*a*, *b*; 1979*a*, *b*, *c*) to our understanding of this succession. In particular, he formally revised the litho-, bio-, and chronostratigraphy and brachiopod taxonomy for the upper part of the Series (Hurst 1979*a*) and through census sampling of measured sections (text-fig. 3) has identified (1979*b*, *c*) eleven distinctive faunal associations. He



TEXT-FIG. 3. The stratigraphical and geographical distribution of sampled sections in the type Caradoc. Black bars represent sections studied by Hurst (1979*a*, *b*, *c*); white bars represent sections collected by Hurst and currently only partially analysed.

also identified two other ‘events’ characterized as an ‘interregnum’ and an ‘invasion’ (Table 2) and discussed the palaeoecological and evolutionary implications of his conclusions.

TABLE 2. Faunal associations defined by Hurst (1979*b*, *c*) from the upper part of the type Caradoc, listed according to age. N.B. Since Hurst (1979*a*, p. 252) suppressed *B. robusta* as a junior synonym of *B. typa*, his association* should be named after this taxon. *D. lepta* is considered a junior synonym of *D. indica* so again this latter taxon should give its name to the association† (see Cocks 1978)

11	*Onniella broeggeri–Sericoidea homolensis* association	ONNIAN
10	*O. depressa* association	
7b	*O. reuschi–Soerbyella sericea* association (Phase 2)	ACTONIAN
6c	*Dalmanella unguis* association (Phase 3)	
9	*Leptestiina oepiki* association	
8	*O. reuschi–Chonetoidea radiatula* association	
7a	*O. reuschi–S. sericea* association (Phase 1)	MARSHBROOKIAN
6a, b	*D. unguis* association (Phases 1 and 2) (*D. wattsi* invasion)	
5	*D. multiplicata–S. sericea* association	
4	*Kjaerina typa* association	WOOLSTONIAN
3b	*B. typa* association (Phase 2)* (*Heterorthis alternata* interregnum)	
3a	*B. typa* association (Phase 1)*	LONGVILLIAN
2	*D. indica* association†	
1	*Howellites antiquor* association	

Although reminiscent of the older zonal categories of Bancroft (1933, 1945), these associations were defined using rigorous quantitative biostratigraphical procedures and, as such, are directly comparable to other similarly defined associations (Lockley 1980*a*; Williams *et al.* 1981).

However, despite acquiring substantial Lower Caradoc collections from relatively widely separated sections (text-fig. 3), Hurst was unable to complete their analysis and reported (1979*a*, p. 185) that I had inherited the material. This is now housed mainly in the British Museum (Natural History) and the new forms which have been discovered are presently being studied for future description.

Since current studies of the type Lower Caradoc are incomplete, we must rely on Dean (1958), Williams (1973), and Pickerill and Brenchley (1979) for up-to-date, albeit brief, interpretations of the faunal succession. Table 3 shows the biostratigraphical subdivisions proposed by Dean, Williams, Brenchley, and Pickerill in the most recent relevant publications. Note that Dean's classification reflects Bancroft's Correlation tables (1933) and that zones 8b and 8c are now reflected by Hurst's associations.

Since Hurst (1979*a*, *b*, *c*) completed his studies of the type Caradoc, the Onny Valley road (A489) has been widened creating continuous exposures of the Cheney Longville Formation. This has provided Drs. P. J. Brenchley and G. Newall with an opportunity to reassess both the facies and fauna. They report (pers. comm. and MS) that the sedimentary succession is not a simple fining upwards sequence (cf. Hurst 1979*b*) but rather exhibits alternating sandstones and mudstones of a shallow subtidal environment influenced by the periodic development of wave-affected sand lobes. They also confirm that the mudstones contain a low-density, *Kjaerina*-dominated background fauna which contrasts with the more variable, transported faunas of the sandstone units. They consider, therefore, that the faunal associations differentiated by Hurst (1979*b*) show considerable intergradation and even contain hitherto unrecorded elements like *Nicolella*.

Cocks and McKerrow (*in* McKerrow 1978) outlined two communities based partly on type Caradoc faunas. The first, the *Sowerbyella–Dalmanella* community, is more generalized and apparently encompasses pre-Caradoc faunas in which these genera dominate. The second, the

TABLE 3. Biostratigraphical subdivisions of the type Lower Caradoc

Biostratigraphical Subdividions			
Stage	Modified after Dean (1958, text-fig. 3)	After Williams (1973, text-fig. 1)	After Pickerill (1979) and Brenchley and Pickerill (1980)
LONGVILLIAN	8c *Bancroftina typa* 8b *Dalmanella indica* 8a *D. horderleyensis*		
SOUDLEYAN	7 *Reuschella horderleyensis* and *Broeggerolithus soudleyensis* 6 *Onniella avelinei* and *Broeggerolithus broeggeri*	*Dinorthis* association	*Dinorthis* community
HARNAGIAN	5 *Salterolithus* (*Ulricholithus*) *ulrichi* 4 *S. caractaci* 3 *Smeathenella harnagensis*, *Salopia salteri*, *Reuscholithus reuschi*, and *Salterolithus smeathenensis*	*Onniella* association	
COSTONIAN	2 *Horderleyella plicata* and *Costonia ultima* 1 *Harknessella vespertilio* and *Dinorthis flabellulum*	*Dinorthis* association	*Dinorthis* subcommunity

Dinorthis flabellulum community, refers more specifically to existing classifications (cf. Table 3). Although both were described briefly for the benefit of the non-specialist student, and as such contain only selected detail, recent studies (Table 1) add new and significant information.

As stated above, *Sowerbyella* and *Dalmanella* are often mutually exclusive in older (Llanvirn) associations and, in the Llandeilo (Wilcox and Lockley 1981), had their distributions at least partially controlled by transportational processes. In the type Caradoc (Table 2) their co-occurrence locally warrants the naming of a *Dalmanella–Sowerbyella* association (Hurst 1979*b*) although elsewhere *Sowerbyella* occurs more abundantly with the other dalmanellids *Bancroftina*, *Howellites*, and *Onniella*. The differentiation noted in the Llanvirn never entirely breaks down, and in the Llandeilo and Caradoc (Williams 1974; Lockley 1980*a*) *Sowerbyella* frequently occurs independently in characteristic 'Bursts' first noted by Bancroft (1945). Cocks and McKerrow (*in* McKerrow 1978, p. 80) also included *Kjaerina* and *Oxoplecia* as distinctive representatives of their community. Whilst this may be true of *Kjaerina*, which now gives its name to Hurst's association (No. 4 of Table 2), *Oxoplecia* is unknown in the Caradoc; its closest relative (Williams 1974) is *Bicuspina*, which was rare in late Caradoc times in the type area (Hurst 1979*b*) and is in need of paleoecological documentation for the type area in early Caradoc times. It is surprising that Cocks and McKerrow did not refer to the original associations of Williams (1973) on his work on *Dalmanella* and *Sowerbyella* phylogenies (1976). Recently Hurst has further explored the phylogeny of *Dalmanella* and other dalmanellids.

The Caradoc *Dinorthis flabellulum* community outlined by Cocks and McKerrow (*in* McKerrow 1978, p. 78) as a fauna in which 'only . . . *Dinorthis* and *Harknessella* were at all common', was first characterized by Williams (1973, p. 242) as an association 'with *Biscuspina*, *Dalmanella*, *Heterorthis*, and *Leptaena*'. Such brief and vague descriptions are unsatisfactory and reflect poor definition of the *Dinorthis* community; this poor delineation is reaffirmed by the cluster analysis (text-fig. 10), which reveals only a low correlation ($C = 0{\cdot}29$) between *Dinorthis* faunas from Shropshire (C_4) and North Wales (C_2). Pickerill and Brenchley (1979) have shown that *Heterorthis* may comprise 25–53% of the community whilst other forms occur locally in significant proportions. There is also no documentation to support the assertion (Cocks and McKerrow: *in* McKerrow 1978, p. 78) that 'the inarticulate brachiopods were represented by the lingulid *Palaeoglossa*'; this genus is almost invariably associated with facies in which the *Dinorthis* community is largely or totally unrepresented.

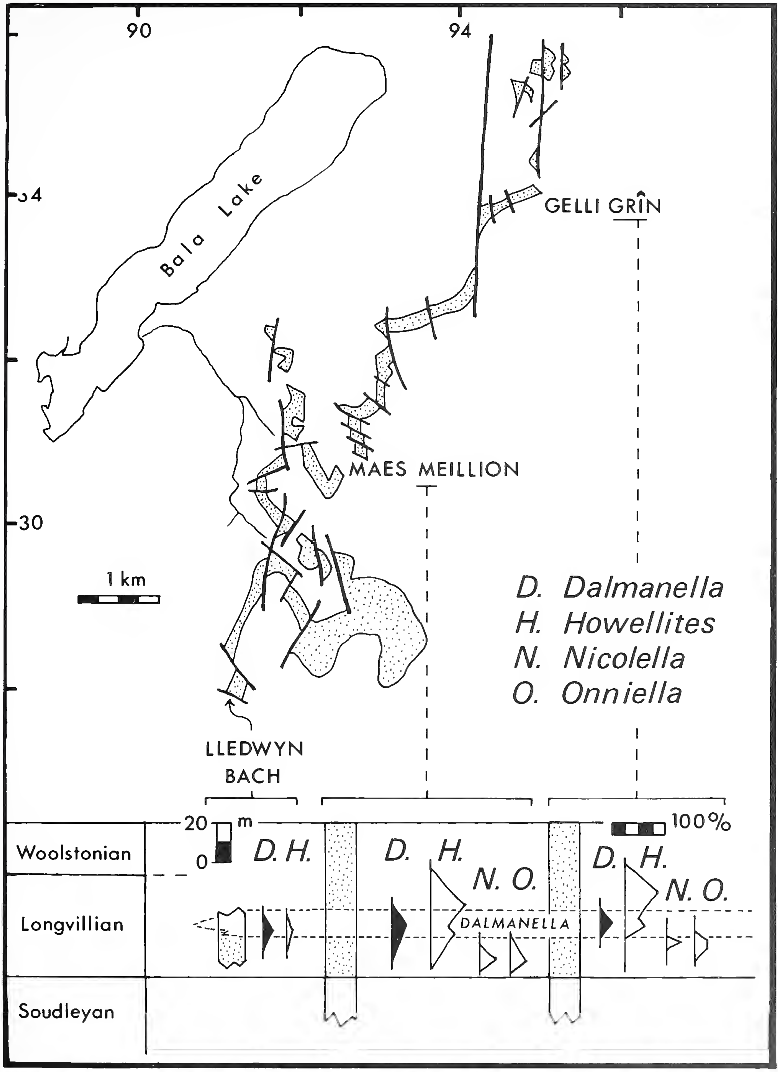
(2) *Caradoc faunas of North Wales.* Since Williams (1963, 1973), Bassett, Whittington and Williams (1966), and Whittington (1962–1968) completed a major phase of research on the Lower Bala Group (Costonian to Longvillian), further studies in the Bala and adjacent Berwyns area (see Table 1) have largely focused on analysis of the faunal associations outlined by Williams (1973). Pickerill and Brenchley (1979, p. 230) 'adopted' the associations of Williams (1973), which they recognized in the Berwyns area and 'elevated to community rank'. Apart from giving a quantitative outline of the relative abundance (%) and persistence of occurrence (presence %) of genera at studied localities and subdividing their *Dinorthis* community into a *Dinorthis* and a *Macrocoelia* subcommunity, perhaps their most novel contributions were the recognition of a *Dalmanella* community in North Wales, and the presentation of palaeoenvironmental interpretations.

Although I have commented (Lockley 1980*a*, p. 228) on the similarity ($\bar{C} = 0{\cdot}73$, range 0·63 to 0·84) between the *Dalmanella*, *Howellites*, and *Dinorthis* communities in the Berwyn areas, the restricted stratigraphical occurrence of the *Dalmanella* community (Pickerill and Brenchley 1979, text-figs. 5, 6, 8) enhances potential for precise correlations. The 'local association containing *Dalmanella Leptestiina* and *Howellites*' in the Gelli-grîn Formation south of Bala (Lockley 1980*a*, p. 184) is evidently indicative of the temporary development of a *Dalmanella*-dominated association (text-fig. 4) representing a transitional stage between the *Nicolella–Onniella* and *Howellites–Kloucekia* associations (*sensu* Lockley 1980*a*). The younger Longvillian *Dalmanella* (*D. indica*)-dominated faunas of the Berwyns region (Pickerill and Brenchley 1979, text-fig. 6) are probably contemporaneous with this Bala association characterized by *D. modica*, a species considered 'superficially like *D. indica*' (Williams 1963, p. 385). Such an interpretation accords with Pickerill and Brenchley's observations (1979, text-figs. 5, 6) on the diachronism of Longvillian facies and implies that older Longvillian *D. horderleyensis* zone faunas from the Berwyns region are probably coeval with the oldest Gelli-grîn faunas from Bala, characterized as the *Nicolella–Onniella* association (Lockley 1980*a*). Similarly, such correlations would emphasize the affinities between upper Longvillian (Woolstonian of Hurst 1979*a*) faunas from the Pen y Garnedd Limestone Formation and the 'Bala' Cymerig Limestone Member. It is worth noting the statistically significant taxonomic similarities ($C = 0{\cdot}24$–$0{\cdot}39$) between the *Leptestiina oepiki* association of Shropshire (E_{12} of text-fig. 9), the Gelli-grîn faunas (B_5), the *Nicolella* community of the Berwyns (C_6), and the *Bicuspina* set of the Whittery shales (D_{15}). Since such diverse *Nicolella* palaeocommunity faunas are considered to have arisen from pre-Caradoc *Dalmanella*-dominated faunas it is not surprising that species of *Dalmanella* locally dominate by a 2:1 ratio (Williams 1974, table 8; Lockley 1980*a*, fig. 12). However, the term *Dalmanella* palaeocommunity is best reserved for type Marshbrookian associations where the genus consistently dominates in greater proportions (Hurst 1979*b*).

Shelve faunas

Material collected by Whittard and studied by Williams (1974, 1976) could not be subjected to the same biostratigraphically and quantitatively precise analysis afforded material from most other areas. Consequently Williams (1976) employed the 'non-committal' term 'set' when grouping the useful quantitative data presented in his monograph (1974).

It has already been shown that the term '*Pseudolingula* set' should either be abandoned or, where appropriate, supplanted by the term '*Tissintia–Pseudolingula* association'. The term '*Bicuspina* set' is also of limited value and essentially a junior synonym of the term *Nicolella* association (Williams 1974, pp. 22, 23; Pickerill and Brenchley 1980). This similarity may be substantiated quantitatively



TEXT-FIG. 4. The stratigraphical and geographical distribution of *Dalmanella* (*D. modica* Williams) in the Gelli-grîn Formation (stippled) of the Bala area; data modified after Lockley (1980*a*, *b*).

(text-fig. 9); respective mean *C* values of 0·37 (range 0·26–0·50) and 0·29 (0·22–0·36) indicate a moderate association between Shelve faunas and those from Bala and the Berwyns. *Bicuspina* is only recorded abundantly at two Shelve horizons (Williams 1974, tables 8 and 11) and in the Gelli-grîn Formation (Lockley 1980*a*), and in both areas *Bicuspina*, *Reuschella*, and *Onniella* rank amongst the five most abundant and ubiquitous genera.

It is not surprising that the Hagley Shale faunas are reminiscent of the *Onniella–Sericoidea* association (cf. Hurst 1979*b*; Lockley 1980*a*) since such faunas are commonly associated with those containing *Nicolella*.

Finally, the *Lingulella* set appears to be a useful concept. Not only does this genus and/or *Palaeoglossa* (its close relative and possible junior synonym; Williams 1974) characterize a number of known faunas from fine-grained facies, but they fall into a recognizable taxonomic cluster (text-fig. 10).

Representative shelly faunas from Dyfed

Addison's studies (1974) on the Llandeilo to Caradoc faunas of Dyfed indicate the presence of a suite of little-known, yet diverse assemblages in strata assigned to the 'Narbeth Group' (see Bassett, Ingham and Wright 1974, fig. 7). Consequently, following the publication of Addison's more important regional stratigraphical conclusions (*in* Williams *et al.* 1972, and *in* Bassett *et al.* 1974), a detailed census sample study of this group was undertaken, based on the Lampeter Velfrey section (see Addison 1974, text-figs. 28, 30; Bassett *et al.* 1974, fig. 7). Preliminary results are summarized here in text-fig. 5, which shows the distribution of brachiopod taxa (species) in the most arenaceous part of the section, the 'Bryn Sion Sandstone Member'. These results are important since the section has since been partially covered and because they highlight the facies 'preference' of *Heterorthis*, which elsewhere is also commonly associated with arenaceous facies. Other heterorthids (e.g. *Tissintia* and *Heterothina*) also represent important or virtually monospecific constituents of the fauna elsewhere in this succession (Addison 1974) and particularly in South Wales appear to have enjoyed a degree of early to mid Ordovician proliferation rivalled only by the contemporary and subsequent success of the closely related dalmanellids.

Ordovician faunas from south-west England

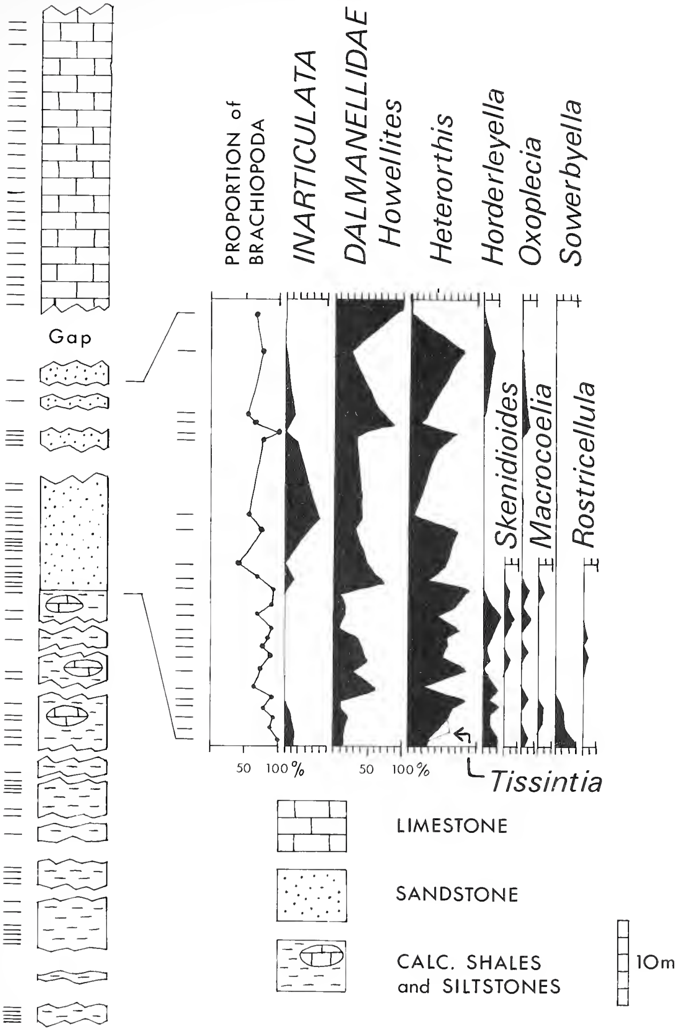
A reasssessment of the brachiopod faunas from the Budleigh Salterton pebble bed (Cocks and Lockley 1981) has shown that the dominant species, the small orthide commonly known by the specific name *budleighensis* Davidson is in fact a heterorthid recognized by Havlíček (1970) as a representative of the genus *Tafilaltia*. This largely monospecific occurrence in association with an arenaceous facies, also locally containing *Corineorthis*, *Salopia*, and ?*Hesperorthis* is noteworthy because it is also reminiscent of contemporary Welsh associations.

SYNTHESIS

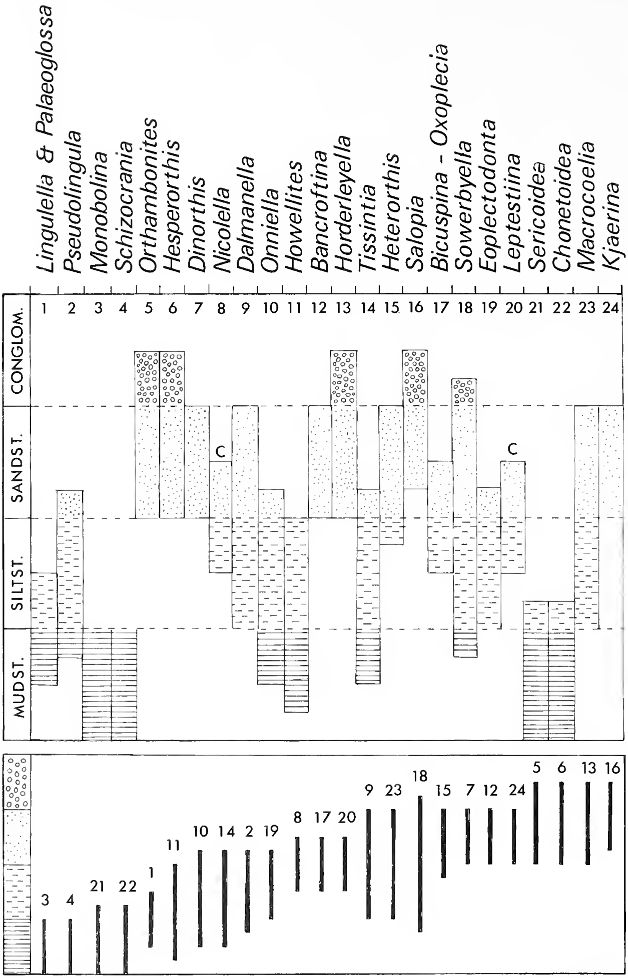
General models

Evaluating the significance of the associations and communities outlined above, which, excluding obvious synonyms, number about thirty, can be approached with the type of 'matrix' presentation shown in text-fig. 6. Although there are some shortcomings, such as the inevitably generalized textural classification of sediments which results from synthesizing the observations of palaeontologists, certain clear patterns do emerge. At the coarser end of the textural spectrum, facies are dominated by coarse-ribbed orthaceans (e.g. *Hesperorthis* and *Dinorthis*) together with forms like *Heterorthis*, *Tafilaltia*, *Salopia*, and the dalmanellid *Bancroftina*, whilst in finer-grained argillaceous facies inarticulate brachiopods are dominant and articulates represented only by plectambonitacean aegiromenids such as *Sericoidea* and *Chonetoidea*.

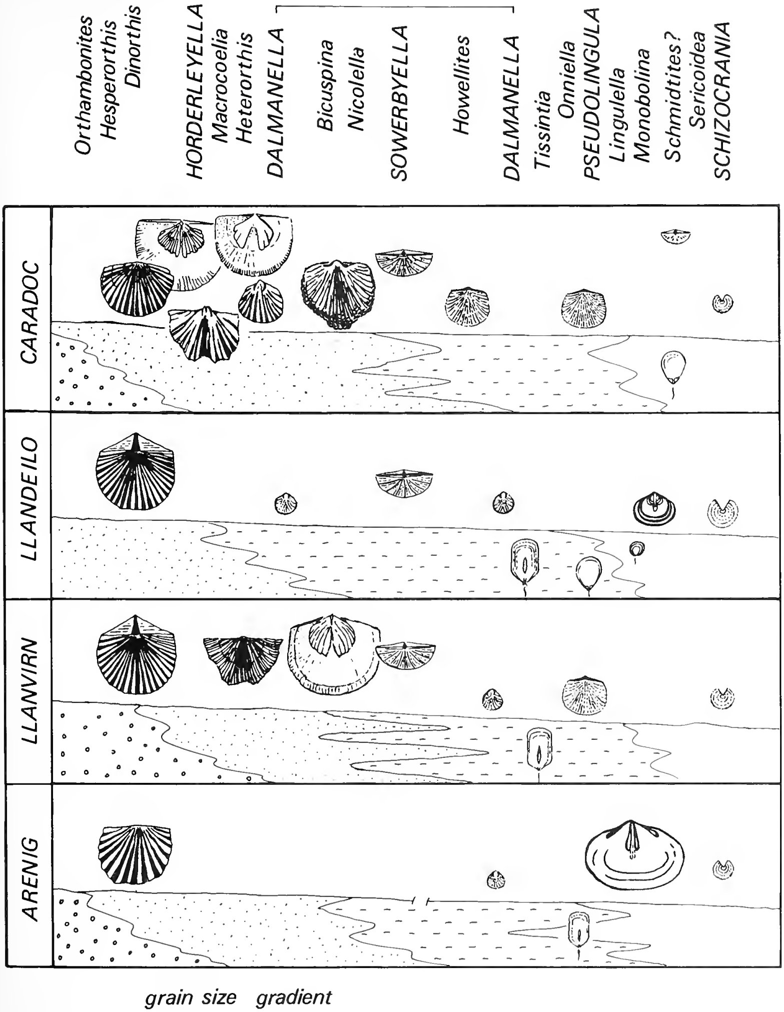
The silty middle part of the facies spectrum is dominated largely by dalmanellids, related heterorthids (e.g. *Tissintia*), and the larger plectambonitaceans (e.g. *Sowerbyella*), all of which appear to be eurytopic in their relatively wide facies ranges (text-fig. 7).



TEXT-FIG. 5. The distribution of dominant Brachiopoda in the arenaceous Bryn Sion member of the Narberth Group at Lampeter Velfry.



TEXT-FIG. 6. Apparent facies ranges of brachiopod genera representing named associations (and/or palaeocommunities) discussed in text. Facies ranges cannot be defined precisely in terms of grain size (Ø scale) so arbitrary quartiles are used to suggest range of taxa into fine, medium, or coarser textural spectra. The taxonomic classification (1-24) is rearranged in lower box to show distribution of taxa in relation to facies gradient.



TEXT-FIG. 7. Facies relationships of key brachiopods throughout the Ordovician showing consistent 'preferences' of some taxa.

This simple, threefold division serves as a useful preliminary model for further scrutiny and refinement. The obvious facies-fauna relationships highlighted by this summary (text-figs. 6, 7) indicate the urgent need for greater understanding of the entombing sedimentary facies. Despite attempts by Hurst (1979*b*, *c*), Pickerill and Brenchley (1979), and Wilcox and Lockley (1981) to broaden our understanding of Ordovician facies by using generalized sedimentological observations to present environmental reconstructions, no thorough sedimentological studies have been undertaken on the facies under discussion. None has even been defined in terms of standard textural (Ø scale) or mineralogical classifications and as such may be wrongly categorized. For example, the apparently equable distribution of sandstones, siltstones, and mudstones shown in text-fig. 6 hardly conforms with normal distributions seen in nature (Shea 1974) and probably implies that the extent of sandy, particularly medium 1-2 Ø sandstone facies has been underestimated. Furthermore, varying degrees of textural inhomogeneity are also inevitably masked by simplistic classifications. Although such subtle sedimentological variation may elude the palaeontologist it is undoubtedly of considerable significance to benthic organisms and as such should warrant more detailed study.

Despite these shortcomings, a growing volume of data on relationships between facies and fauna continues to enhance our understanding of Ordovician palaeoenvironments and suggest the need for appropriate interpretations. Pickerill and Brenchley (1979, p. 260) suggested comparisons between certain Silurian communities and inferred, facies-related Ordovician analogues from North Wales. They proposed (p. 229) that the apparently relatively shallow depth ranges (0-30 m) for these Ordovician communities might suggest . . . 'that benthic faunas progressively migrated into deeper waters throughout the Lower Palaeozoic', a popular idea which appears to reiterate the suggestion of Cocks and McKerrow (*in* McKerrow, 1978, p. 62) that there was a 'gradual colonization of deeper environments by the brachiopods'.

These suggestions presuppose that Ordovician communities are accepted as analogues of Silurian counterparts, when in fact little detailed taxonomic or ecological comparison has been attempted. Comparison of the two pairs of proposed analogues (see Table 4) indicates minimal taxonomic similarity; only a few of the dominant constituents even belong to the same order and none are well-recognized homoeomorphs. Hurst and Watkins (1981) independently noted that 'taxonomically' other potentially comparable Ordovician and Silurian communities were 'vastly different'.

Pickerill and Brenchley used Boucot's (1975) Benthic Assemblage concept to equate these communities on the primary assumption that they inhabit similar hatitats. Although detailed evidence for such assumptions is tenuous, comparisons of inferred habitats of palaeocommunities (as in text-fig. 7) obviously has potential, *providing* that palaeoenvironments are correctly inferred from sedimentary facies. It should be remembered that such comparisons ignore the possibility that the considerable differences reflect differential preservation of various shoreface and open-shelf deposits in the type successions. Since many of the Ordovician faunas discussed herein derive from deposits associated with insular volcanic centres (text-figs. 1, 8) it seems prudent to be cautious of a model which implies any great similarity between Ordovician and Silurian Welsh Basin environments. Direct comparisons seem most feasible only in the vicinity of the south-east margin of the basin, where similar Ordovician and Silurian shelf deposits occur (Hurst and Watkins 1981).

Quantitative summary

The most rational approach to a quantitative synthesis of described faunal associations (and palaeocommunities) is to compare the proportion of taxa in common throughout the whole spectrum of described faunas. This is done by cluster analysis using the data presented in Table 5 and text-fig. 9.

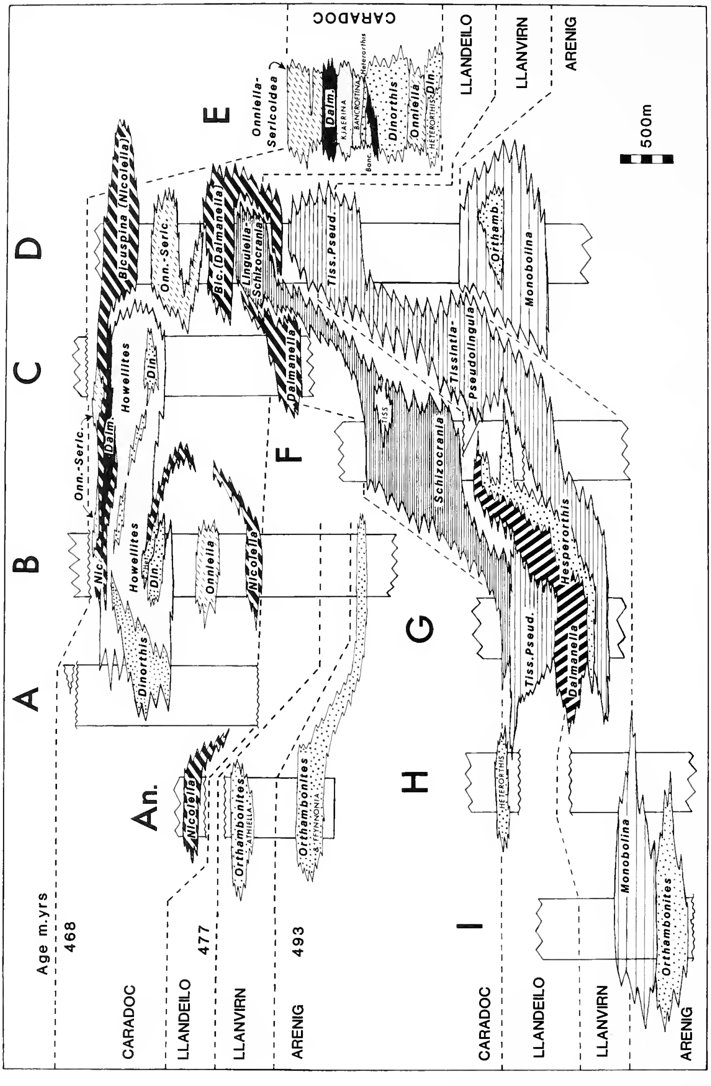
The first step involves identifying all recorded taxa and the associations in which they occur; Table 5 shows that species representative of some 124 genera occur in the fifty-eight representative Welsh associations listed A_1-H_1. Cross comparison of the composition of all these faunas using Dice's formula $2C/(N_1+N_2)$ (see Whittington and Hughes 1974, p. 204), where C represents

TABLE 4. Dominant genera in supposedly analogous Ordovician (*left*) and Silurian (*right*) communities from Wales and the Welsh Borderland (data from Pickerill and Brenchley 1979, tables 4, 7; and Ziegler, Cocks and Bambach 1968, figs. 3, 7). Dominant forms comprising 80% of these communities (i.e. the Trophic Nucleus *sensu* Neyman 1967) rarely belong to the same groups; e.g. in the *Dinorthis-Eocoelia* comparison only 11% are common to the same family, the ubiquitous Dalmanellidae, whilst in the *Nicolella-Costricklandia* comparison none even belong to the same order.

ORDOVICIAN		SILURIAN	
Dinorthis community		*Eocoelia* community	
	%		%
Heterorthis	53	*Eocoelia*	47
Howellites	11	'*Camarotoechia*'	18
Reuschella	4	*Dalejina*	12
Dinorthis	8	*Strophochonetes*	9
Sowerbyella	13		
	—		—
	89 = Trophic nucleus		86
Nicolella community		*Costricklandia* community	
	%		%
Nicolella	34	*Costricklandia*	49
Dolerorthis	21	*Pholidostrophia*	14
Platystrophia	16	*Eocoelia*	11
Skenidioides	9	*Eospirifer*	7
	—		—
	80		81

conspecific (1·0) or congeneric (0·5) taxa in common and N_1 and N_2 the number of species in compared assemblages, yielded 1653 coefficient of association values (text-fig. 9). The sample size represented by so many permutations is sufficiently large to generate a histogram and curve exhibiting a classic negative exponential pattern. The principles of probability theory can be used to assess the significance of these values; if 25% is chosen as the minimum confidence level then only *C* values of 0·19 or more can be considered to depart significantly from zero; values equal to or greater than 0·33, 0·45, and 0·68 respectively would correspond to the 10%, 5%, and 1% confidence limits. These constraints allow the *C* values to be ranked as insignificant, low, moderate, high, or very high (text-fig. 9).

A dendrogram constructed from the matrix data (text-fig. 10) clearly highlights the similarity between many related associations and provides quantitative substantiation of many authors' more qualitative observations and predictions. Indeed the taxonomically related subclusters also reflect age, close geographical relationships, and facies preferences and are therefore of great value in defining the major palaeocommunity groupings (I–VIII) outlined below. For example, the Soudleyan *Howellites* community of the Berwyn Hills area (Pickerill and Brenchley 1979), although similar to the contemporaneous *Howellites-Paracraniops* association, is hard to differentiate from the Berwyns *Dinorthis* community. The North Wales (Berwyns) *Dinorthis* community bears little relationship to the *Dinorthis* community in Shropshire. Such observations suggest that the term



TEXT-FIG. 8. Stratigraphical and geographical distribution of named associations (and/or palaeocommunities) in the Ordovician of Wales. Areas A–I as in text-fig. 1; An = Anglesey; biostratigraphical subdivisions in areas E and G have been further refined. Scale of section E doubled.

'*Dinorthis* community' is problematical and should provisionally be restricted to description of the Shropshire faunas, while the North Wales expression of this fauna should be regarded as limited, intergrading into the dominant *Howellites* community.

The Longvillian faunas of the Bala area cluster together and are closely related to contemporaneous faunas from the Berwyns and Shelve areas, all of which show high *C* values and bear some relationship to the *Nicolella* association. This predominantly North Wales cluster is most closely related to type Caradoc faunas from Shropshire which, with the exception of the distinctive Onnian faunas, all form a discrete cluster exhibiting high *C* values. These Caradoc faunas fall into age-differentiated subclusters dominated successively by the dalmanellids *Bancroftina*, *Dalmanella*, and *Onniella*. Remaining Caradoc faunas (C_4, A_2, B_1, E_{13}, and E_{14}; text-fig. 10) exhibit low to moderate *C* values.

Pre-Caradoc faunas all fall into an entirely separate cluster which is less clearly subdivided. However, three distinct subcluster groupings are evident; the first approximates closely to the *Lingulella* set of Williams (1976) and includes one of only two 'anachronistic' (i.e. post-Caradoc) faunas in the entire cluster; the second subcluster is dominated by *Hesperorthis*, whilst the third includes *Dalmanella*-, *Horderlyella*-, and *Sowerbyella*-dominated associations from the Ffairfach Group. It is worth emphasizing the distinction between these latter two groupings since it largely justifies the suggested re-evaluation of groupings proposed by Williams *et al.* (1981).

Most remaining faunas in the pre-Caradoc subcluster bear some relationship to the Shelve inarticulate faunas or the mid-Wales *Tissintia–Pseudolingula* faunas described by Williams *et al.* (1981) and Wilcox and Lockley (1981). High *C* values indicate that the latter faunas are more closely associated with the main clusters than the Shelve Group, which exhibit mainly moderate to low *C* values. Such observations substantiate the view that the term '*Pseudolingula* set' should be abandoned.

Cluster analysis provides a valuable method of comparing the taxonomic composition of faunas throughout the whole spectrum of described associations, palaeocommunities, and other representative groupings. It furnishes us with an unequivocal picture of the taxonomic interrelationship between faunas and strongly corroborates previous subjective observations by providing precise quantitative comparisons (*C* values). Used in conjunction with probability theory these values are more than sufficient in number to permit the development of a confidence-limited scale objectively defining insignificant, low, moderate, high, and very high degrees of association (*C*).

Despite the obvious advantages derived from thorough quantitative comparisons there are two obvious limitations. First, cluster analysis does not take into account the relative abundance of taxa in compared samples. As stated in the introduction to this review, many associations or palaeocommunities are named after their dominant constituents, which may make up a large proportion of the trophic nucleus. Unfortunately, cluster analysis weights rare elements equally so that two faunas showing a low *C* value at the trophic nucleus level (i.e. comparison of dominant 80%) might, having rarer elements in common, show a high *C* value when fully compared. Despite this drawback, full analysis can be very useful since it will help to identify intergrading between associations from the same geographical area. The *Howellites* and *Dinorthis* communities of the Berwyn Hills in North Wales provide a good example of faunas which are differentiated on the basis of relative proportions but have overall taxonomic similarities attributed to intergrading (Pickerill and Brenchley 1979). As shown, the same is true for some of the Ffairfach Group associations. (Allied to this problem of species proportions is the whole issue of non-brachiopod faunas. However, this is of no direct concern here since virtually all recorded type Ordovician associations are named after brachiopods and are accompanied by full lists of proportions of non-brachiopod elements.) Secondly, cluster analysis cannot take account of facies variation, which most authors agree has a very important bearing on the distribution of faunas. Again, the Ffairfach Group provides examples of associations like those dominated by *Horderleyella* and *Dalmanella*, which although similar in taxonomic composition not only show pronounced variation in species proportions but also exhibit quite distinct facies preferences. Nevertheless, as stated above, the taxonomic clusters often reflect similar facies preferences amongst related assemblages.

Bearing these three important criteria of taxonomic compositions (*C* values), species proportions, and facies relationships in mind, a final assessment of palaeocommunities is possible.

Perspective on palaeocommunities

Known pre-Upper Llanvirn faunas from Anglesey and Shelve show no significant taxonomic relationship discernible with present data. Even within the Shelve area *C* values are generally only moderate and the all-embracing term '*Pseudolingula* set' is abandoned in favour of the categories proposed here (text-fig. 8) and elsewhere (Williams *et al.* 1981; Wilcox and Lockley 1981).

The development of the Llanvirn *Tissintia–Pseudolingula* association closely coincides with the establishment of other consistently recognizable faunas, in particular those dominated by *Dalmanella.* These fall into a number of categories (Williams *et al.* 1981) whose relationships are only partially understood. Even where the best quantitative biostratigraphical data are available, problems hinge primarily on deciding which of the three fundamental criteria are most important. For example, is the *Horderleyella* association related to the *Salopia* and *Hesperorthis* associations from similar facies? Or on the basis of taxonomic composition, does it bear a closer resemblance to *Dalmanella* associations (text-fig. 10)? Although Williams *et al.* (1981) named a *Horderleyella* palaeocommunity, the latter hypothesis is favoured here. Indeed, as the *Horderleyella* association becomes less distinctive with time so the *Dalmanella* and *Sowerbyella* palaeocommunities (Williams *et al.* 1981) intergraded more in the less differentiated facies of the type Llandeilo. Elsewhere,

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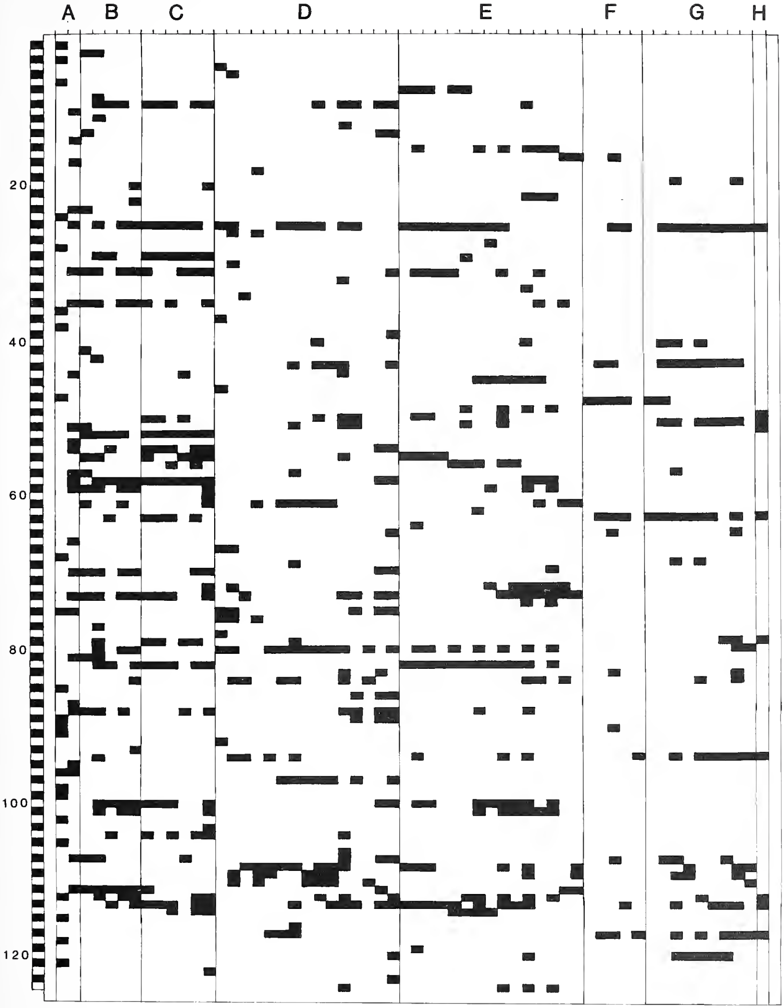
TABLE 5. Distribution of taxa (genera 1–124) in representative faunas from Wales and the Welsh Borderland.

Genera are as follows: 1, *Ahtiella*, *Anisopleurella*, *Antigonambonites*, *Apsotreta*, *Astraborthis*, *Atelelasma*, *Bancroftina*, *Bellimurina*, *Bicuspina*. 10, *Bilobia*, *Binuria*, *Bystromena*, *Caeroplecia*, *Camerella*, *Chonetoidea*, *Christiania*, *Clitambonites*, *Conotreta*, *Corineorthis*. 20, *Cremnorthis*, *Cryptothyris*, *Cyclospira*, *Cyrtonella*, *Dactylogonia*, *Dalmanella*, *Desmorthis*, *Destombesium*, *Diaphelasma*, *Dinorthis*. 30, *Diparelasma*, *Dolerorthis*, *Drabovia*, *Elliptoglossa*, *Eocramatia*, *Eoplectodonta*, *Estlandia*, *Euorthisina*, *Ffynnonia*, *Furcitella*. 40, *Gelidorthis*, *Glossorthis*, *Glyptomena*, *Glyptorthis*, *Harknessella*, *Hedstroemina*, *Hespernomia*, *Hespernomiella*, *Hesperorthis*, *Heterorthina*. 50, *Heterorthis*, *Horderleyella*, *Howellites*, *Ilmarinia*, *Kïaromena*, *Kjaerina*, *Kjerulfina*, *Kullervo*, *Leptaena*, *Leptestiina*. 60, *Lingulasma*, *Lingulella*, *Lingulops*, *Macrocoelia*, *Marionites*, *Mcewanella*, *Metacamerella*, *Monobolina*, *Monorthis*, *Murinella*. 70, *Nicolella*, *Nocturniella*, *Obolus*, *Onniella*, *Orbiculoidea*, *Orthambonites*, *Orthis*, *Orthisocrania*, *Oslogonites*, *Oxoplecia*. 80, *Palaeoglossa*, *Palaeostrophomena*, *Paracraniops*, *Parastrophinella*, *Paterula*, *Paurorthis*, *Petrocrania*, *Plaesiomys*, *Platystrophia*, *Plectorthis*. 90, *Porambonites*, *Productorthis*, *Protoskenidioides*, *Protozyga*, *Pseudolingula*, *Ptychoglyptus*, *Ptychopleurella*, *Rafinesquina*, *Rectotrophia*, *Reinversella*. 100, *Reuschella*, *Rhactorthis*, *Rhynchorthis*, *Rhynchotrema*, *Rostricellula*, *Rugostrophia*, *Salacorthis*, *Salopia*, *Schizocrania*, *Schizotreta*. 110, *Schmidtites?*, *Sericoidea*, *Skenidioides*, *Sowerbyella*, *Strophomena*, *Taffia*, *Tazzarinia*, *Tissintia*, *Treioria*, *Trematis*. 120, *Triplesia*, *Tritoechia*, *Vellamo*, *Whittardia*, *Zygospira*.

Faunal assemblages, associations, and other groupings used in cluster analysis: (text-figs. 9, 10) A_{1-2} respectively pre-Costonian and Costonian Anglesey faunas after Bates 1968 (revised by Neuman and Bates 1978), B_{1-5} Caradoc faunas from the Bala area respectively characterized as the *Nicolella–Onniella* association (Phases 1 and 2), the *Howellites–Paracraniops* association, the *Howellites–Kloucekia* association, and the *Onniella–Sercoidea* association after Lockley (1980*a*; supplementary data from Whittington and Williams 1955 and Williams 1963); C_{1-6} Caradoc faunas from the South Berwyn Hills respectively characterized as the *Howellites* community, the *Dinorthis* and *Macrocoelia* subcommunities, the *Dinorthis* community (Shropshire), the *Dalmanella* and *Nicolella* communities; D_{1-15} Faunal assemblages from the Shelve area after Williams (1964) with subdivisions proposed by Williams (1976); $E_{1,\,1a,\,2-14}$ Upper Caradoc associations from the type area, Shropshire, after Hurst (1979*a*, *b*, *c*). (E_1 and $_{2-14}$ after Hurst 1979*b*, table II with supplementary data from Hurst 1979*a*; E_{1a} after Hurst 1979*c*); F_{1-5} Llanvirn faunas from the Builth area, respectively collections BW 10, BW 11, BW 13, NMW.68.376G. 150–161 after Williams *et al.* (1981 tables 3, 4), and *Tissintia–Pseudolingula* fauna from Camnant Brook (Lockley and Williams 1981, p. 46); G_{1-7} respectively Llanvirn faunas from the Llandeilo area characterized as the *Hesperorthis*, *Salopia*, *Dalmanella–Gelidorthis*, *Schizocrania*, *Dalmanella* (3 phases), *Horderleyella*, and *Sowerbyella* (2 phases) associations of Williams *et al.* (1981); G_8 and G_9 respectively Lower to early Middle and Middle to Upper Llandeilo faunas (Wilcox 1979; Wilcox and Lockley 1981); H_1 Bryn Sion faunas of the Narberth group (text-fig. 5 herein).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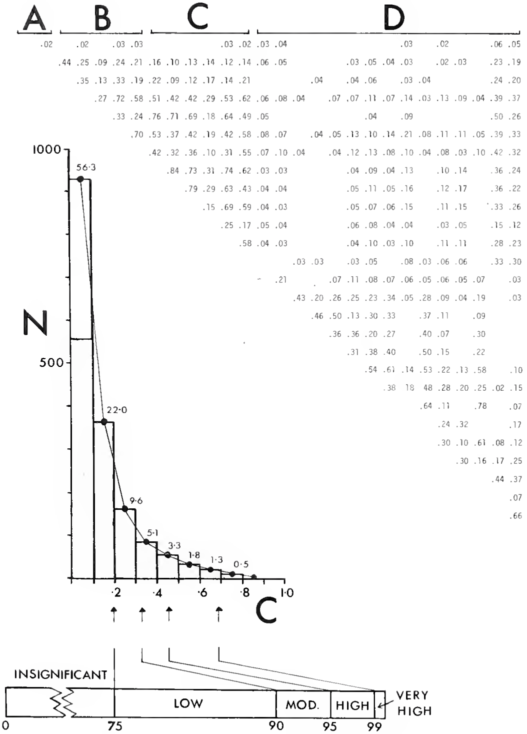

TEXT-FIG. 9. Cluster analysis matrix, resultant histogram, and scale of *C* values derived from comparison of fifty-eight representative faunas listed in Table 6; blank parts of histogram and matrix represent zero values. (See text for further details.)

	E															F				G									H
A						.03	.03		.02		.02		.03				.03							.03			.03		.03
	.03	.05	.06	.03		.06	.05	.06	.09	.03	.06	.08	.10	.09	.06		.06	.03			.09	.10	.03	.05	.06	.09	.05	.03	.06
B	.08	.06	.07	.13	.03	.04	.03	.04	.08	.03	.07	.10	.09	.16	.13		.04				.08	.09		.03	.04	.07			.07
	.10	.19	.18	.11	.13	.16	.22	.16	.24	.13	.29	.18	.34	.13	.07		.06	.04	.04		.07	.08	.03	.09	.10	.12	.10	.10	.15
	.18	.16	.14	.25	.15	.10	.17	.10	.14	.21	.19	.05	.08	.05	.06	.07	.05	.13		.08	.06	.08	.06	.09	.16	.10	.11		.18
	.04	.13	.15	.05	.13	.12	.24	.17	.23	.13	.27	.26	.39	.22	.14		.04	.05			.04	.03	.05	.07	.04	.04	.06	.09	.11
	.17	.22	.25	.22	.23	.15	.29	.19	.30	.23	.35	.24	.39	.20	.08		.04	.09			.04	.06	.04	.10	.08	.07	.14	.08	.10
C	.21	.22	.29	.26	.19	.11	.16	.11	.22	.19	.16	.10	.12	.16	.08	.05	.07	.14		.05	.08	.09	.08	.10	.15	.14	.15	.04	.24
	.21	.22	.26	.22	.19	.14	.19	.14	.23	.24	.21	.08	.14	.05	.05	.06	.09	.18		.07	.10	.11	.11	.08	.14	.13	.14	.05	.25
	.19	.17	.20	.20	.22	.17	.25	.17	.21	.26	.20	.15	.13	.14	.05	.05	.08	.16		.06	.09	.10	.10	.11	.17	.12	.13	.05	.19
	.12	.16	.19	.19	.11	.10	.08	.05	.10		.06	.04	.04				.10	.07			.11	.08	.06	.04	.05	.14	.07	.06	.18
	.22	.19	.22	.27	.28	.23	.23	.12	.23	.16	.17	.03	.19			.05	.07	.14		.05	.08	.10	.09	.14	.12	.15	.15	.04	.25
	.17	.16	.18	.21	.16	.12	.27	.19	.21	.22	.33	.17	.31	.16	.07			.04				.03		.06	.09	.06	.08		.11
D	.06	.04	.05	.07	.11	.05	.04	.06	.07		.03		.04				.05	.07			.06	.04	.06	.05	.06	.05	.11	.19	.05
	.05	.11	.09	.06	.10	.04	.04	.05	.10		.08	.04	.04	.05	.05		.04	.06	.07		.05	.15	.16	.20	.14	.13	.31	.37	.08
	.09	.05	.07					.08	.13	.08	.13	.12		.17	.09				.14			.10	.18	.23	.15	.13	.29	.36	.06
	.08	.05	.06						.08		.09	.06		.07	.23							.10	.31				.17	.31	
	.09	.11	.13		.08		.05		.17		.17		.05		.18	.22	.13		.42			.26	.36	.12	.15	.20	.43	.64	.13
	.15	.10	.18	.08	.13	.06	.10	.07	.16	·	.13	.17	.04	.14	.15	.18	.18	.09	.22		.07	.10	.23	.16	.07	.12	.35	.46	.11
	.15	.14	.17	.11	.14	.13	.11	.05	.25	.05	.15	.08	.03	.09	.10	.17	.17	.17	.13		.19	.39	.25	.35	.36	.46	.60	.45	.24
	.08	.05	.13	.09	.14	.07	.10	.07	.08		.10	.06	.05	.08	.17		.06	.10			.08	.10	.25	.06	.07	.06	.23	.42	.06
	.11	.15	.18	.06	.10	.14	.16	.05	.23		.22	.04	.11	.05	.17	.13	.14	.06			.21	.19	.39	.21	.15	.14	.32	.39	.13
	.14	.14	.17	.08	.12		.09		.15	.06	.15	.05	.04	.07	.21	.17	.11	.08			.13	.23	.50	.10	.19	.17	.38	.43	.05
	.18	.20	.22	.15	.14	.17	.21	.03	.31	.10	.26	.06	.14	.07	.07	.08	.16	.08			.18	.14	.18	.24	.17	.23	.35	.19	.19
	.18	.16	.14	.19	.16	.15	.17	.05	.24	.16	.14	104	.04	.05	.06		.05	.13			.11	.08	.06	.09	.16	.14	.11	.06	.18
		.06	.08		.09		.06		.05		.11	.07	.06	.10									.22	.13			.21	.44	
	.10	.10	.12	.10	.09		.17	.04	.19	.17	.18	.08	.20	.09	.05		.04	.05			.04	.07	.10		.04	.08	.06		.04
	.07	.14	.15	.11	.13	.06	.11	.03	.19	.13	.23	.06	.24	.03	.10	.07	.18	.04			.10	.11	.07	.09	.13	.15	.18	.07	.06
E		.50	.63	.73	.43	.27	.26	.21	.29	.29	.19		.10		.08		.06	.20			.08	.10	.25	.06	.14	.13	.18	.25	.12
			.83	.31	.41	.17	.33	.23	.47	.27	.23	.04	.21		.05		.04	.11	.06		.05	.11	.15	.08	.14	.13	.20	.25	.16
				.67	.50	.21	.48	.28	.46	.33	.26		.20				.05	.14			.06	.08	.19	.05	.11	.10	.19	.25	.14
					.62	.21	.28	.23	.22	.31	.13		.10				.07	.22			.08	.11	.09	.06	.15	.13	.10	.09	.13
						.53	.52	.24	.31	.38	.15		.17				.06	.17			.07	.14	.07	.05	.13	.11	.13	.14	.11
							.45	.29	.33	.35	.15		.17				.05	.08			.13	.04	.07	.14	.12	.05	.08	.07	.15
								.48	.58	.46	.34	.13	.43				.04	.06			.05	.07	.05	.08	.10	.09	.10	.11	.13
									.31	.44	.24	.11	.26	.07			.06	.08			.07	.05	.07	.05	.06	.06	.04	.07	.05
										.54	.39	.14	.48	.04	.08		.04	.09	.05		.08	.12	.08	.13	.16	.04	.21	.21	.32
											.39	.21	.26	.20	.04			.08				.05	.14		.06	.06	.08	.07	.05
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																	.06										.14	.17	
F																.40	.18	.40		.67	.25						.12	.14	.08
																	.57	.38	.17	.67	.55	.28	.40	.25	.50	.28	.25		.13
																		.43	.08	.33	.59	.38	.44	.27	.33	.40	.42	.13	.10
																				.67	.54	.33	.40	.25	.50	.42	.30	.20	.27
																						.19		.21	.20	.25	.17	.38	.08
G																					.44	.13	.25	.14	.20		.11		.08
																						.57	.46	.42	.53	.58	.35	.15	.17
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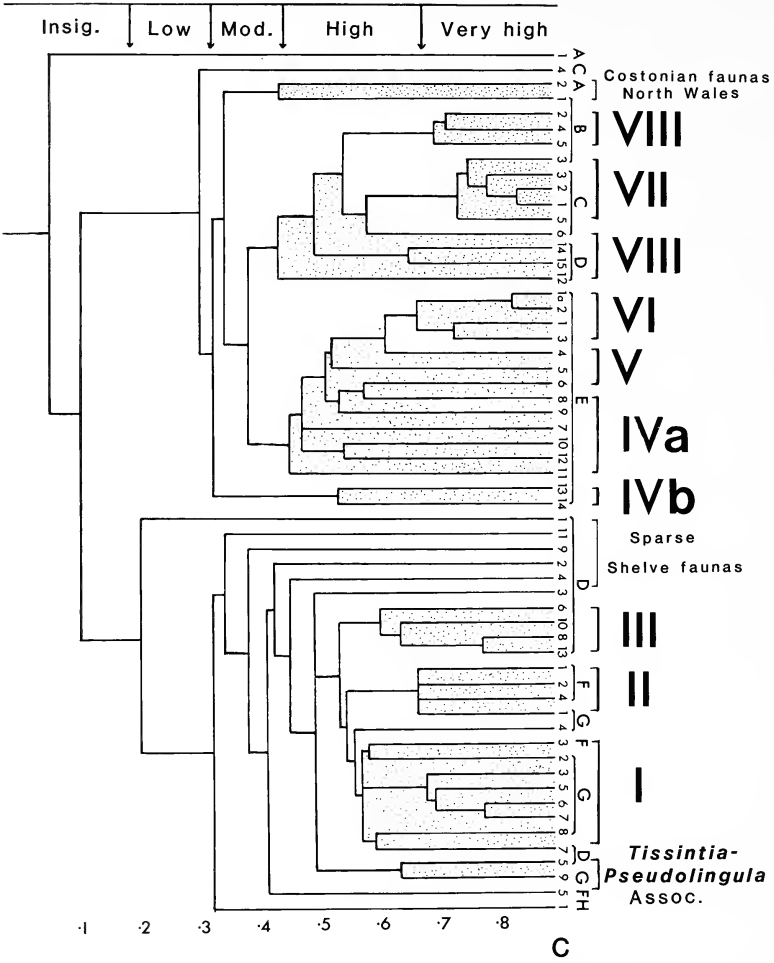


TEXT-FIG. 10. Dendrogram derived from cluster matrix (text-fig. 9). Subclusters I–VIII represent major Palaeocommunity groupings referred to in the text.

however, differentiation remains evident; for example, *Sowerbyella* occurs in only three of the fifty-nine Shelve samples listed by Williams (1974, tables 6 and 7) whereas *Dalmanella* occurs in twenty-six. In the face of this dilemma the *Dalmanella* and *Sowerbyella* palaeocommunities (*sensu* Williams *et al.* 1981) have been included in a single category (palaeocommunity I; text-fig. 10); however, this procedure is not meant to obscure the clear differences which have been described. In particular, the sporadic stratigraphical occurrence of *Sowerbyella* has been considered to be a possible result of adaptations allowing mobility in response to currents (Williams *et al.* 1981).

It is particularly instructive to note that the closest association (C) between pre-Caradoc and Caradoc faunas are the 'anachronistic' examples, where type Lower Llandeilo faunas show a moderate degree of association with those from the Shelve Spywood Grit; the succeeding Upper Llandeilo faunas show even greater association ($C = 0{\cdot}44$) with Aldress Shale faunas. These faunas (D_{11} and D_{13} of Table 5) are closely related to *Nicolella*- and *Onniella*-dominated faunas from North Wales (Lockley 1980*a*; and Pickerill and Brenchley 1979) and confirm the observation of Wilcox and Lockley (1981) that Lower Llandeilo faunas represent 'an early expression of the type of association referred to as the *Bicuspina* set' (now the *Nicolella* palaeocommunity).

Relationships between diverse pre-Caradoc and Caradoc faunas are of obvious interest from an evolutionary viewpoint; Lockley and Williams (1981, p. 3) have already observed that there is an 'intriguing' relationship between diverse Llanvirn and Caradoc faunas and 'intercalated restricted faunas of the Llandeilo series'. Present data (text-fig. 8) suggest that over a period of about thirty million years (Ross *et al.* 1978) an equal number of associations (excluding obvious synonyms) were established, replaced, and re-established in the Welsh Basin area. Although this implies an average duration of about 1 m.y. for associations, in most cases they represent longer-lived palaeocommunities.

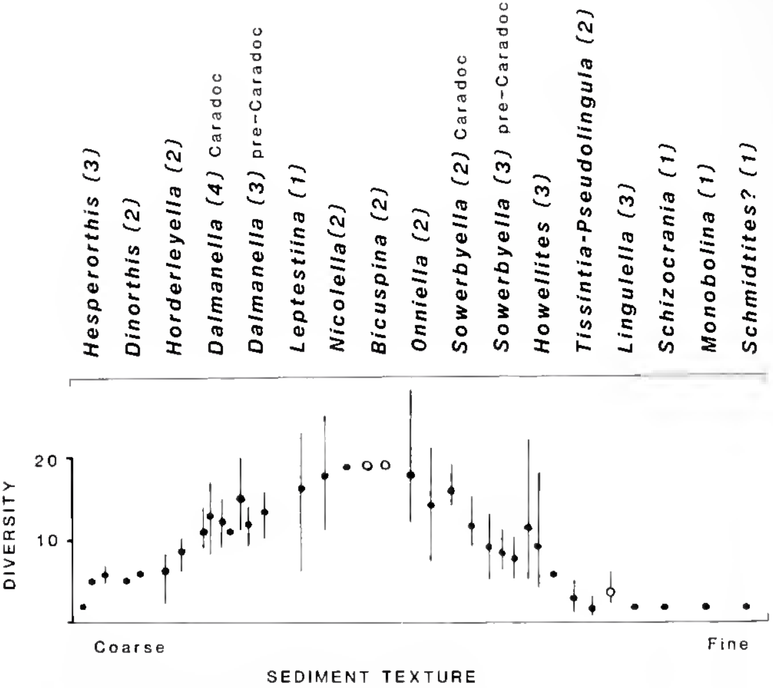
Clearly, Lower and Upper Llandeilo faunas do show significant relationships to descendant associations from Shelve. The 'mixed *Dalmanella*' palaeocommunity (I) was widespread and successful in mid-Wales in pre-Caradoc time. Despite being replaced locally during the latter part of the Llandeilo by *Tissintia–Pseudolingula*-dominated faunas (Wilcox and Lockley 1981, fig. 7), it survived successfully into Upper Llandeilo times in the Berwyn Hills area, where the fauna, described by MacGregor (1961), shows a high degree of similarity ($C = 0{\cdot}58$) to type Lower Llandeilo antecedents. Such faunas gave rise to equally diverse Caradoc associations (text-figs. 11, 12).

Palaeoecological perspectives

Although faunas from arenaceous Llanvirn and Caradoc facies exhibit some general taxonomic similarities (text-fig. 7) these are not as great as those exhibited by faunas associated with medium- to fine-grained facies. This suggests that such facies represented optimum environments for sustaining successful, long-lived stocks.

The physical stresses encountered in shoreface environments apparently restricted diversity, as in the *Hesperorthis* association, whereas in more open shelf regions there was more scope for the development of diverse, biologically accommodated faunas (cf. Sanders 1968, 1969). Finer-grained facies also exhibit reduced diversity, apparently due to other limiting physical stresses. Representative data from sources listed here (Table 1) allow a diversity plot complementary to text-figs. 6 and 7; this shows a clear trend towards maximum values in the middle part of the facies spectrum (text-fig. 11). The apparent relationships between the older 'mixed *Dalmanella*' palaeocommunity (I), and the *Nicolella* palaeocommunity (VIII) are emphasized by these observations, which show a theme of maximum diversity in related associations at different times.

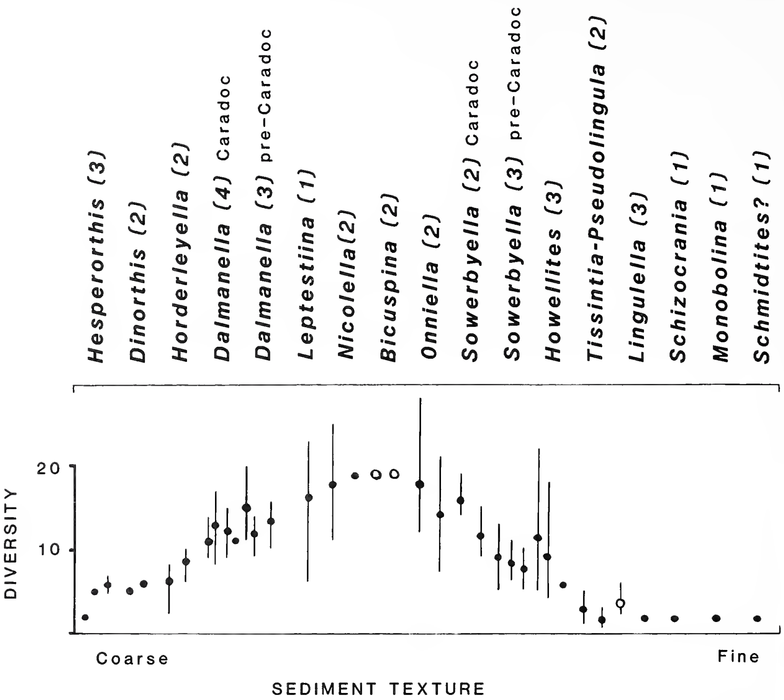
Since diverse *Dalmanella*-dominated faunas are locally associated with the *Nicolella* palaeocommunity in North Wales (see above) there is clearly some Llanvirn-to-Caradoc continuity, particularly in Welsh basin localities. The fact that the *Nicolella* palaeocommunity in the type Caradoc is poorly represented or found only in more offshore facies, *and* that type Caradoc *Dalmanella*-dominated faunas show no significant relationships with ancestral associations, serves to emphasize the importance of Welsh basin rather than basin-margin localities as the more stable sites for the



TEXT-FIG. 11. Plot of average diversity values from named associations and palaeocommunities arranged along a textural facies gradient; ranges given by vertical bars where known. Open circles refer to brachiopod diversities only and are therefore relative underestimates.

evolution of diverse, well-established palaeocommunities. Such observations do not support claims by Bretsky and Lorenz (1970, p. 2449) that 'diversity is negatively correlated with biotic stability'; their model is also disputed elsewhere. In contrast, described faunas from shoreface environments in Shropshire differ more radically. The more persistent physical environmental influences apparently led to more localized, rapid, and unpredictable changes in forms like *Dalmanella* and in the faunal composition generally.

Assuming that such a stability-stress model is valid it *may* be reasonable to consider the diverse, biologically accommodated communities as somewhat analogous to climax communities (Williams 1976). Hurst (1979*b*) has alluded to various problems associated with the 'climax community' model, suggesting that for any palaeocommunity successional stages must be clearly identified before conclusions are drawn. He also suggests that where perturbating influences interfere with stability it will be hard to identify such stages. These conclusions seem valid, support my observations as outlined above, and imply that a test of the climax model would be best undertaken



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Such palaeoecological considerations take into account the widespread Caradoc radiation of dalmanellids, which is a complex phenomenon best understood through the type of thorough analysis attempted by Williams (1963) and Hurst (1978*a*, *b*). They also indicate that well-established *Dalmanella*-dominated faunas are generally confined to more arenaceous near-shore facies and are replaced in finer-grained facies by *Howellites*, and *Onniella*-dominated associations (Hurst 1978*a*, fig. 5; Pickerill and Brenchley 1979, fig. 7). These latter associations are often more diverse than those containing *Dalmanella* (Hurst 1979*b*) although *Howellites* may occur in low diversity, sandy facies with *Heterorthis* and *Dinorthis*.

This radiation altered the established pre-Caradoc pattern. In many areas *Howellites* and *Onniella*, both fairly generalized forms, replaced *Dalmanella*, which developed some quite distinctive specializations such as the 'very coarse plicae' (Hurst 1979*a*, p. 246) of *D. unguis*. Paedomorphosis may have played an important role in such radical evolutionary developments (cf. McNamara, in press). Similarly allopatric speciation may have operated in restricted shoreface environments where environmental controls predictably reduced diversity more than in open-shelf environments, where stabilizing selection operated more effectively.

Although such trends had a limited effect on *Dalmanella*-dominated faunas they are more clearly seen (text-fig. 11) in older *Hesperorthis* and *Horderlyella* associations (text-fig. 11) and the Caradoc *Dinorthis* community (*sensu* Pickerill and Brenchley 1979).

CONCLUSIONS

In the final analysis few of the associations, communities, palaeocommunities, or sets named by the authors listed herein (Table 1) are so ill-conceived as to be considered invalid. There are a number of obvious partial synonyms such as the *Howellites* community (Pickerill and Brenchley 1979) and the *Howellites–Paracraniops* association (Lockley 1980*a*), or the *Onniella–Sericoidea* associations of Hurst (1979*b*) and Lockley (1980*a*); however, although some of these show very highly significant correlations ($C > 0{\cdot}68$) and can be grouped together in the fashion proposed above (text-fig. 10), others, as in the latter example, at best exhibit barely significant ($C = 0{\cdot}20$) coefficients of association and must therefore be considered separately.

In other cases, e.g. the *Pseudolingula* and *Bicuspina* sets and the *Dinorthis* community, constituent assemblages are so varied that they defy convenient classification.

Although faunas have already been assigned to various named associations (or communities, sets, etc.), eight (I–VIII) major groupings are identifiable (text-fig. 10). These are all represented by subclusters showing high or very high *C* values and reflect geographical proximity, age, and distinct facies preferences. Using the introductory rationalizations presented above they are best referred to as palaeocommunities and are in approximate order of age (oldest–youngest) as follows:

I. The 'mixed' *Dalmanella* palaeocommunity; age, Llanvirn to Llandeilo; distribution, the Llandeilo, Builth, Shelve, and Berwyn Hills areas; facies, typically fine, often calcareous clastics, mainly siltstones; includes the separately defined *Dalmanella* and *Sowerbyella* palaeocommunities and a part of the *Horderleyella* palaeocommunity (*sensu* Williams *et al.* 1981); ($\bar{C} = 0{\cdot}65$, range 0·58–0·78).

II. The *Hesperorthis* palaeocommunity; age, Upper Llanvirn; distribution, Builth and Llandeilo areas; facies, typically coarse and granule–pebble sandstones; comment, this low-diversity palaeocommunity is distinct from the *Horderleyella* palaeocommunity (*sensu* Williams *et al.* 1981) although some intergrading occurs ($\bar{C} = 0{\cdot}67$).

III. The *Lingulella* palaeocommunity; age, late Upper Llanvirn to early Caradoc (Harnagian); distribution, Shelve area; facies, typically dark shales and mudstones (*sensu* Whittard 1979) and siltstones (Williams 1976); comment, includes four of the five assemblages used to define the *Lingulella* set (Williams 1976); the fifth (D_7) is more closely related to contemporary *Dalmanella*-dominated faunas from mid-Wales ($\bar{C} = 0{\cdot}68$, range 0·61–0·78).

IV. The *Onniella* palaeocommunity; age Caradoc (latest Marshbrookian to Onnian); distribution, Shropshire type area; facies, typically bioturbated, often calcareous silts and muds, *sensu* Hurst (1979*b*); comment, consists of a pre-Onnian and an Onnian phase (respectively IVa and IVb of text-fig. 10); the former phase intergrades with the *Dalmanella* palaeocommunity; pooled C values for associations E_4–E_{12} average 0·52, range 0·46–0·58.

V. The *Dalmanella* palaeocommunity; age Caradoc (Marshbrookian); distribution, Shropshire type area; facies, typically sands and silts *sensu* Hurst (1979*b*), includes *Dalmanella*-dominated associations defined by Hurst (1979*b*); comment, intergrades, particularly through *D. unguis* association (Phase 3), with *Onniella* palaeocommunity (C values given above).

VI. The *Bancroftina–Kjaerina* palaeocommunity; age Caradoc (Longvillian–Woolstonian); distribution Shropshire (type area); facies, typically sands and silts *sensu* Hurst (1979*b*); includes associations defined by Hurst (1979*b*, *c*), see Table 4 ($\bar{C} = 0{\cdot}74$, range 0·67–0·83); comment, most highly correlated subcluster in type Caradoc.

VII. The *Howellites* palaeocommunity; age Lower Caradoc; distribution, Bala, Berwyn Hills, Breidden Hills, and Snowdonia; facies, typically mixed clastics mainly in the silt–fine-sand spectrum; includes Soudleyan faunas from all four areas which are in many cases dominated by *Heterorthis*, *Macrocoelia* (*Dinorthis* community of Pickerill and Brenchley 1979); also includes Lower Longvillian *Dalmanella* from Berwyns, which intergrades with palaeocommunity VIII ($\bar{C} = 0{\cdot}78$, range 0·74–0·84); comment, most highly correlated cluster.

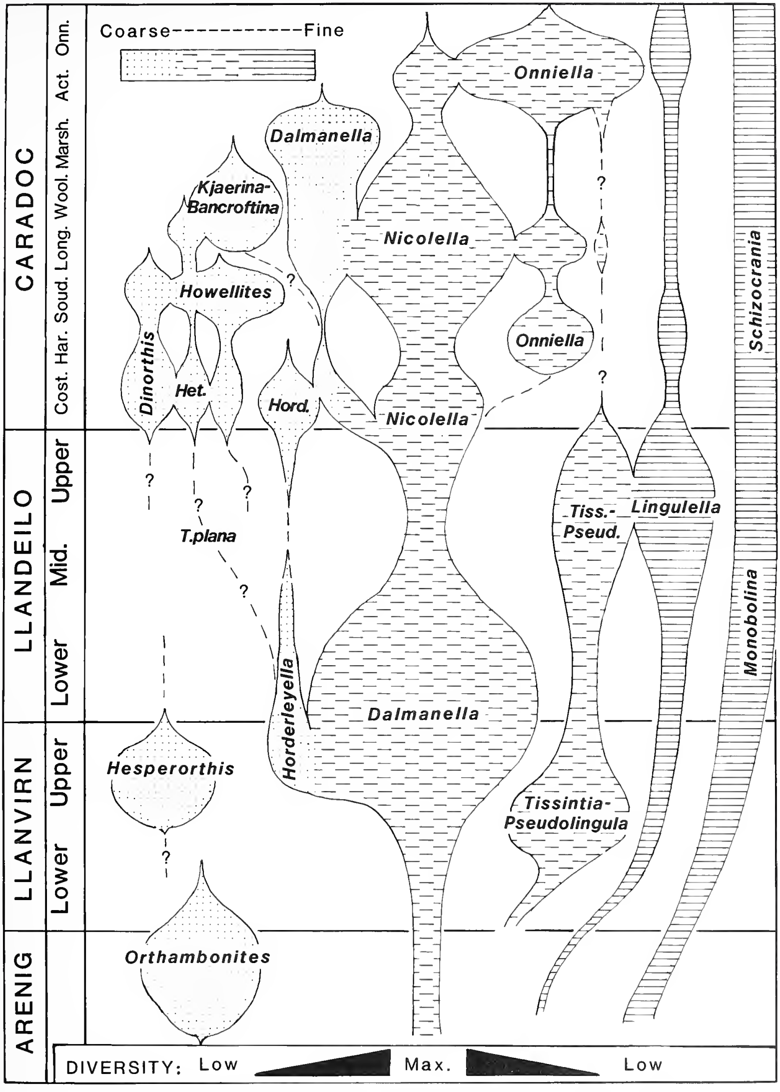
VIII. The *Nicolella* palaeocommunity; age Lower Caradoc; distribution, Bala, Berwyn Hills, and Shelve areas; facies, typically fine calcareous clastics and limestones; includes the Longvillian faunas of the former two areas and most of the Shelve *Bicuspina* set; ($\bar{C}$ value 0·59, range 0·44–0·72); comment, includes *Dalmanella*-dominated assemblages in the Bala and Shelve areas.

All identified palaeocommunities exhibit high to very high mean C values and largely reflect previous ideas on grouping of assemblages into higher categories. Sparse faunas such as those from Shelve and assemblages representative of the *Tissintia–Pseudolingula* association do not show high correlations. The same is true for a few other faunas which, in addition to being taxonomically distinct, are geographically isolated. The inferred evolutionary relationships between the main palaeocommunities and other associations outlined above are presented in text-fig. 12, which also incorporates generalized facies and diversity gradients. It is particularly important to note that the diverse, ancestral 'mixed *Dalmanella*' palaeocommunity gave rise to the *Nicolella* palaeocommunity and that descendant *Dalmanella*-dominated faunas, epitomized by the Shropshire palaeocommunity (V), show significantly changed taxonomic composition and facies preference. The relationship of the *Nicolella* and *Onniella* palaeocommunities is first evident in the early Caradoc and is noted again in mid and later Caradoc times.

Faunas dominated by *Heterorthis* and *Dinorthis* appear in the early Caradoc of Shropshire where the term *Dinorthis* community (*sensu* Pickerill and Brenchley 1979) is locally appropriate. Contemporary faunas from Dyfed (text-fig. 5) are dominated by *Heterorthis* and *Howellites*, both of which, as depicted in text-fig. 12, remain dominant in the *Howellites* palaeocommunity, whilst *Dinorthis* plays a subordinate, intergrading role. *Heterorthis* probably arose from ancestral *Tissintia* (Havlíček 1970), which is represented in Wales by three distinct species (Lockley and Williams 1981). The most likely ancestor is *T. plana*, a large species associated with sandy facies in Dyfed. It is more specialized than *T. immatura*, which persists in more argillaceous type Llandeilo facies (Wilcox and Lockley 1981) and may be the ancestor of some closely related Caradoc dalmanellids.

Considerations of evolutionary relationships between low diversity, inarticulate-dominated faunas of the argillaceous facies indicates limited change through time; only *Monobolina* exhibits apparent species level evolution (Lockley and Williams 1981). *Schizocrania* occurs with *Monobolina* in many assemblages but can quite reasonably be considered representative of a different palaeocommunity (*sensu* Williams *et al.* 1981) because of its very different life habits (Lockley and Antia 1980). Locally both forms are associated with the *Lingulella* palaeocommunity.

Finally, the diversity-stress model presented here is evidently supported by analogous examples



TEXT-FIG. 12. Inferred evolutionary relationships between named associations and palaeocommunities from the Ordovician of Wales and the Welsh Borderland. (See text for details.)

elsewhere. Silurian models in particular have been the subject of much debate, not least because of speculations about absolute depth (Hancock, Hurst and Fursich 1974; Johnson and Potter 1976; Shabica and Boucot 1976). Although this aspect of the debate need not concern us here, it is evident that some models are broadly analogous, showing that 'diversity . . . increases with depth', and eventual decreases in the deepest facies (Hancock *et al.* 1974). More recently, Hurst and Watkins (1981) have emphasized such analogous patterns by noting that 'Caradoc and Ludlow species diversity increases into more distal shelf environments' but then, in certain cases 'decreases in offshore environments'. Such near-to-offshore diversity trends have also been recorded for modern brachiopod faunas (Foster 1974).

Since recurrent diversity profile patterns would hardly . . . 'develop in stratigraphically separated sequences if' they 'did not reflect original patterns' (Hurst and Watkins 1981) the model receives further support. However, it should be stressed that the model is only tentative and assumes that the facies gradients can be equated with an onshore-offshore palaeoenvironmental transect. More convincing interpretation of a greater variety of sedimentary facies is needed to infer palaeocommunity habitats confidently. When this is achieved the potential for inter-community comparisons will be realized more fully.

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REFERENCES

ADDISON, R. 1974. The biostratigraphy of the Llandeilo facies of South Wales. Ph.D. thesis (unpubl.), Queens University, Belfast.

BANCROFT, B. B. 1929. Some new genera and species of Strophonemacea from the Upper Ordovician of Shropshire. *Mem. Proc. Manchr. lit. phil. Soc.* **73,** 33-65, pls. 1, 2.

—— 1933. *Correlation tables of the Stages Costonian to Onnian in England and Wales.* Blakeney, Glos. [Privately printed.] 4 pp., 3 tables.

—— 1945. The brachiopod zonal indices of the Stages Costonian to Onnian in Britain. *J. Paleont.* **19,** 181-252, pls. 22-38.

BASSETT, D. A., INGHAM, J. K. and WRIGHT, A. D. (eds.), 1974. *Ordovician System Symposium. Field excursion guide to type and classical sections in Britain.* Palaeontological Association. 66 pp.

—— WHITTINGTON, H. B. and WILLIAMS, A. 1966. The stratigraphy of the Bala district, Merionethshire. *Q. Jl geol. Soc. Lond.* **122,** 219-271.

BASSETT, M. G. 1982. The Ordovician brachiopods of Cornwall. *Geol. Mag.* **118,** 647-664.

BATES, D. E. B. 1968. The Lower Palaeozoic brachiopod and trilobite faunas of Anglesey. *Bull. Br. Mus. nat. Hist.* (Geol.), **16,** 127-199, pls. 1-14.

—— 1969. Some early Arenig brachiopods and trilobites from Wales. Ibid. (Geol.), **18,** 1-28, pls. 1-9.

BOUCOT, A. J. 1975. *Evolution and extinction rate controls.* Elsevier, Amsterdam. 427 pp.

BRENCHLEY, P. J. 1964. Ordovician ignimbrites in the Berwyn Hills, North Wales. *Geol. J.* **4,** 43-54.

—— 1966. The Caradoc rocks of the north and west Berwyns, North Wales. Ph.D. thesis (unpubl.), University of Liverpool.

—— 1969. The relationship between Carodocian volcanicity and sedimentation in North Wales. *In* WOOD, A. (ed.). *The Pre-Cambrian and Lower Palaeozoic rocks of Wales*, 181-202. University of Wales Press, Cardiff, 461 pp.

—— 1972. The Cwm Clwyd Tuff, North Wales: a palaeogeographic interpretation of some Ordovician ash shower deposits. *Proc. Yorks. geol. Soc.* **39,** 199-224.

—— 1978. The Caradoc rocks of the north and west Berwyn Hills, North Wales. *Geol. J.* **13,** 137-164.

—— and NEWALL, G. (in press). Wave affected shallow subtidal sand lobes in the Caradoc of Shropshire. *J. sedim. Petrol.*

—— *and* PICKERILL, R. K. 1973. Recognition of Caradoc Communities. *Pal. Assoc. Symp.* Abstr. 1.

—— —— 1980. Shallow subtidal sediments of Soudleyan (Caradoc) age in the Berwyn Hills, North Wales, and their palaeogeographic context. *Proc. Geol. Ass.* **91** (3), 177-194.

BRETSKY, P. W. and LORENZ, D. M. 1970. An essay on adaptive strategies and mass extinction. *Bull. geol. Soc. Am.* **81,** 2449-2456.

COCKS, L. R. M. 1978. A review of British Lower Palaeozoic brachiopods. *Palaeontogr. Soc.* [*Monogr.*], 1-256.

—— and LOCKLEY, M. G. 1981. Reassessment of the Ordovician brachiopods from the Budleigh Salterton Pebble Bed, Devon. *Bull. Br. Mus. nat. Hist.* (Geol.), **35,** 111-124.

DEAN, W. T. 1958. The faunas succession of the Caradoc Series of south Shropshire. Ibid. **9,** 257-296.

—— 1976. Some aspects of Ordovician correlation and trilobite distribution in the Canadian Appalachians. *In* BASSETT, M. G. (ed.). *The Ordovician System: proceedings of a Palaeontological Association symposium, Birmingham, September 1974*, 227-250. University of Wales Press and National Museum of Wales, Cardiff. 696 pp.

DEWEY, J. G. 1969. Evolution of the Appalachian/Caledonian Orogen. *Nature*, **222,** 124-129.

FORTEY, R. A. and OWENS, R. M. 1978. Early Ordovician (Arenig) stratigraphy and faunas of the Carmarthen district, south-west Wales. *Bull. Br. Mus. nat. Hist.* (Geol.), **30,** 225-294.

FOSTER, M. W. 1974. Recent Antarctic and Subantarctic brachiopods. *Am. Geophys. Union.* Antarctic Res. Ser. 21. 189 pp.

FURNES, H. (in press). Geology of the Builth Inlier, Wales. *Geol. J.*

HANCOCK, N. J., HURST, J. M. and FURSICH, F. T. 1974. The depths inhabited by Silurian brachiopod communities. *Q. Jl geol. Soc. Lond.* **130,** 151-156.

HARPER, D. A. T. 1978. The occurrence of the Ordovician brachiopod *Heterorthis alternata* (J. de C. Sowerby) in the topmost Onnian of the type Caradoc area. *Geol. Mag.* **115,** 301-304.

HAVLÍČEK, V. 1970. Heterorthidae (Brachiopoda) in the Mediterranean province. *Sb. geol. Věd Praha.* **12,** 7-39.

HURST, J. M. 1975. Wenlock carbonate, level bottom, brachiopod dominated communities from Wales and the Welsh Borderland. *Palaeogeogr. Palaeoclimat. Palaeoecol.* **17,** 227-255.

—— 1978*a*. A phenetic strategy model for dalmanellid brachiopods. *Palaeontology*, **21,** 535-554.

—— 1978*b*. Morphological variation in some Lower Palaeozoic dalmanellid brachiopods. *Paläont. Z.* **52,** 246-256.

—— 1979*a*. The stratigraphy and brachiopods of the upper part of the type Caradoc of South Salop. *Bull. Br. Mus. nat. Hist.* (Geol.), **32,** 183-304.

—— 1979*b*. Evolution, succession and replacement in the type Upper Caradoc (Ordovician) benthic faunas of England. *Palaeogeogr. Palaeoclimat. Palaeoecol.* **27,** 189-246.

—— 1979*c*. The environment of deposition of the Caradoc Alternata Limestone contiguous deposits of Salop. *Geol. J.* **14,** 15-40.

—— and HEWITT, R. A. 1977. On tubular Problematica from the type Caradoc (Ordovician) of England. *Neues Jb. Geol. Paläont. Abh.* **153,** 147-169.

—— and WATKINS, R. 1981. Lower Paleozoic clastic, level-bottom community organization and evolution based on Caradoc and Ludlow comparisons. *In* GRAY, J., BOUCOT, A. J. and BERRY, W. B. N. *Communities of the past*, 69-100. Dowden, Ross and Hutchinson.

JOHNSON, J. G. and POTTER, E. C. 1976. The depths inhabited by Silurian brachiopod communities, comment and reply. *Geology*, **4,** 189-191.

JOHNSON, R. G. 1972. Conceptual models of benthic marine communities. *In* SCHOPF, T. J. M. (ed.). *Models in Paleobiology*, 148-159. Freeman-Cooper.

KAUFFMAN, E. G. and SCOTT, R. W. 1976. Basic concepts of community ecology and paleoecology. *In* SCOTT, R. W. and WEST, R. R. (eds.). *Structure and classification of paleocommunities*, 1-28. Dowden, Ross and Hutchinson.

KREBS, C. J. 1978. *Ecology: the experimental analysis of distribution and abundance.* Harper and Row. 678 pp.

LOCKLEY, M. G. 1977. The geology of the Llanuwchllyn to Llanymawddwy area, with special reference to the Caradoc faunal associations of the area between Bala and Llanymawddwy. Ph.D. thesis (unpubl.), University of Birmingham.

—— 1978. The application of ecological theory to palaeoecological studies, with special reference to equilibrium theory and the Ordovician System. *Lethaia*, **11,** 281-291.

—— 1980*a*. Caradoc faunas associations of the area between Bala and Dinas Mawddwy, North Wales. *Bull. Br. Mus. nat. Hist.* (Geol.), **33,** 165-235.

—— 1980*b*. The geology of the Llanuwchllyn to Llanymawddwy area, south Gwynedd, North Wales. *Geol. J.* **15,** 21-41.

—— and ANTIA, D. D. J. 1980. Anomalous occurrence of the Lower Palaeozoic brachiopod *Schizocrania. Palaeontology*, **23,** 707-713.

LOCKLEY, M. G. and WILLIAMS, A. 1981. Ordovician Brachiopoda from mid and south Wales. *Bull. Br. Mus. nat. Hist.* (Geol.), **35,** 1-78.

MCGREGOR, A. R. 1961. Upper Llandeilo brachiopods from the Berwyn Hills, North Wales. *Palaeontology*, **4,** 177-209, pls. 19-23.

MCKERROW, W. S. 1978. *The ecology of fossils.* Duckworth Press. 384 pp.

MCNAMARA, K. J. (in press). The earliest *Tegulorhynchia* (Brachiopoda: Rhynchonellida) and its evolutionary significance. *J. Paleont.*

NEUMAN, R. B. 1976. Ordovician of the eastern United States. *In* BASSETT, M. G. (ed.). *The Ordovician System: proceedings of a Palaeontological Association symposium, Birmingham, September 1974*, 195-207. University of Wales Press and National Museum of Wales, Cardiff. 696 pp.

—— and BATES, D. E. B. 1978. Reassessment of Arenig and Llanvirn age (early Ordovician) brachiopods from Anglesey, north-west Wales. *Palaeontology*, **21,** 571-613, pls. 63-68.

NEYMAN, A. A. 1967. Limits to the application of the trophic group concept in benthic studies. *Oceanology*, **1,** 149-155. [Translated from Russian.]

PICKERILL, R. K. 1973. *Lingulasma tenuigranulata*—palaeoecology of a large Ordovician linguloid that lived within a strophomenid-trilobite community. *Palaeogeogr. Palaeoclimat. Palaeoecol.* **13,** 143-156.

—— 1974. Geology of the south Berwyn Hills, North Wales, with particular reference to Upper Ordovician marine benthic communities. Ph.D. thesis (unpubl.), University of Liverpool.

—— 1975. Application of ichnology to the study of ancient marine benthic community paleoecology. A discussion and case example. *Marit. Sediments*, **11,** 49-52.

—— 1976. Vermiforichnus borings from the Ordovician of central Wales. *Geol. Mag.* **113,** 159-164.

—— 1977. Trace fossils from the Upper Ordovician (Caradoc) of the Berwyn Hills, Central Wales. *Geol. J.* **12,** 1-16.

—— and BRENCHLEY, P. J. 1975. The application of the community concept in Paleontology. *Marit. Sediments*, **11,** 5-8.

—— —— 1979. Caradoc marine benthic communities of the south Berwyn Hills, North Wales. *Palaeontology*, **22,** 229-264.

RAAB, P. V. 1980. Equilibrium theory and paleoecology. *Lethaia*, **13,** 175-181.

ROSS, R. J. Jr. *et al.* (13 authors), 1978. Fission-track dating of Lower Paleozoic volcanic ashes in British stratotypes. *Open File Rep. U.S. geol. Surv.* **78-701,** 363-365.

SANDERS, H. L. 1968. Marine benthic diversity, a comparative study. *Am. Nat.* **102,** 243-282.

—— 1969. Marine benthic diversity and the Stability-Time hypothesis. *In* WOODWELL, G. M. and SMITH, H. H. (eds.). *Brookhaven Symp. Biol.* **22,** 71-81.

SCOTT, R. W. 1974. Bay and shoreface benthic communities in the Lower Cretaceous. *Lethaia*, **7,** 315-330.

SHABICA, S. V. and BOUCOT, A. J. 1976. The depths inhabited by Silurian brachiopod communities. Comment and reply. *Geology*, **4,** 132, 187-189; 710-712.

SHEA, J. H. 1974. Deficiencies of clastic particles of certain sizes. *J. sedim. Petrol.* **44,** 985-1003.

SUTHREN, B. J. and FURNES, H. 1980. Origin of some bedded welded tuffs. *Bull. volcan.* **43,** 61-71.

THORSON, G. 1957. Bottom communities (sublittoral or shallow shelf). *In* HEDGPETH, J. W. (ed.). Treatise on marine ecology and paleoecology, 1. *Mem. geol. Soc. Am.* **67** (1), 461-534.

—— 1966. Some factors influencing the recruitment and establishment of marine benthic communities. *Neth. J. Sea Res.* **3,** 267-293.

TITUS, R. and CAMERON, B. 1976. Fossil communities in the Lower Trenton Group (Middle Ordovician) of central and northwestern New York State. *J. Paleont.* **50,** 1209-1225.

WHITTARD, W. F. 1979. An account of the Ordovician rocks of the Shelve Inlier in west Salop and part of north Powys. [Compiled by W. T. Dean.] *Bull. Br. Mus. nat. Hist.* (Geol.), **33,** 1-69.

WHITTINGTON, H. B. 1962-1968. The Ordovician trilobites of the Bala area, Merioneth, Pt. I. *Palaeontogr. Soc.* [*Monogr.*], **116** (1962), 1-32, pls. 1-8; Pt. II, **118** (1965), 33-62, pls. 9-18; Pt. III, **120** (1966), 63-92, pls. 19-28; Pt. IV, **122** (1968), 93-138, pls. 29-32.

WILCOX, C. J. 1979. A palaeoenvironmental study of the Llandeilo Series in the type area. Ph.D. thesis (unpubl.), Glasgow University.

—— and LOCKLEY, M. G. 1981. A reassessment of facies and fauna in the type Llandeilo (Ordovician) Wales. *Palaeogeogr. Palaeoclimat. Palaeoecol.* **34,** 285-314.

WILLIAMS, A. 1953. The geology of the Llandeilo area Carmarthenshire. *Q. Jl geol. Soc. Lond.* **108,** 177-207.

—— 1962. The Barr and Lower Ardmillan Series (Caradoc) of the Girvan district, south-west Ayrshire, with descriptions of the Brachiopoda. *Mem. geol. Soc. Lond.* **3,** 1-267, pls. 1-25.

WILLIAMS, A. 1963. The Caradocian brachiopod faunas of the Bala district, Merionethshire. *Bull. Br. Mus. Nat. Hist.* (Geol.), **8,** 327-471, pls. 1-16.

—— 1973. Distribution of brachiopod assemblages in relation to Ordovician palaeogeography. *In* HUGHES, N. G. (ed.). Organisms and continents through time. *Spec. Pap. Palaeont.* **12,** 241-269.

—— 1974. Ordovician Brachiopoda from the Shelve district, Shropshire. *Bull. Br. Mus. nat. Hist.* (Geol.), Supp. **11,** 1-163, pls. 1-28.

—— 1976. Plate tectonics and biofacies evolution as factors in Ordovician correlation. *In* BASSETT, M. G. (ed.). *The Ordovician System; proceedings of a Palaeontological Association symposium, Birmingham, September 1974,* 29-66. University of Wales Press and National Museum of Wales, Cardiff. 696 pp.

—— STRACHAN, I., BASSETT, D. A., DEAN, W. T., INGHAM, J. K., WRIGHT, A. D. and WHITTINGTON, H. B. 1972. A correlation of Ordovician rocks in the British Isles. *Spec. Rep. geol. Soc. Lond.* **3,** 1-74.

—— LOCKLEY, M. G. and HURST, J. M. 1981. Benthic palaeocommunities represented in the Ffairfach Group and coeval Ordovician successions of Wales. *Palaeontology,* **24,** 661-694.

ZIEGLER, A. M. 1965. Silurian marine communities and their environmental significance. *Nature,* **207,** 270-272.

—— COCKS, L. R. M. and BAMBACH, R. K. 1968. The composition and structure of Lower Silurian marine communitites. *Lethaia,* **1,** 1-27.

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CORALLINE ALGAE FROM THE MIOCENE OF MALTA

by DANIEL W. J. BOSENCE

ABSTRACT. The morphology and systematics of ten coralline algae are described from the Miocene of Malta. The corallines occur in great abundance and are the principal constructors of rhodoliths and frameworks of the Coralline Algal Biostrome. The corallines are well preserved and many show previously undescribed reproductive structures. The eleven species comprise two species of *Archaeolithothamnium*, two of *Lithothamnium*, two of *Mesophyllum*, four of *Lithophyllum*, and one species of *Lithoporella*. Two new species of *Lithophyllum* (*L. bahrijense* and *L. mgarrense*) are described.

The morphology of the framework-building *Mesophyllum commune* is described in detail. The success of this species as a limestone constructor is attributed to its foliaceous growth habit combined with various methods of crust division, fusion, and branch growth.

This coralline flora is most similar to that of the Miocene of North Africa.

THE algae described in this paper are the dominant rock builders of the Miocene Coralline Algal Biostrome of the Maltese Islands (Pedley 1978, Bosence and Pedley 1982). The biostrome (20 × 5 km × 16 m thick) outcrops along the western coast and plateaus of Malta and the eastern coast of Gozo (text-fig. 1). It is cut by a number of NNE/WSW growth faults. Bosence and Pedley (1982) have described the sedimentology and palaeoecology of the biostrome and we have divided it into six facies. Three of the facies contain limestones constructed by more or less *in situ* coralline algae, the remaining three being derived and transported equivalents of these facies. Each facies is characterized by particular types of rhodolith.

In situ coralline algal sediments	Transported coralline algal sediments
Crustose Algal Marl facies	Algal Debris Wackestone facies
Rhodolith Pavement facies	Algal Branch Packstone facies
Crustose Pavement facies	Algal Crust Packstone facies

Beneath and to the west of the biostrome *Heterostegina*, rich biomicrites of the Ghajn Znuber and Zebbug Beds occur. To the east are micritic sediments of the Mtarfa member (text-fig. 1).

The biostrome develops on a series of relic sand ridges of the Ghajn Znuber Beds (text-fig. 1). Sheltered areas between ridges accumulate 1–2 m thick sequences of Crustose Algal Marl and Algal Debris Wackestone facies. The Crustose Algal Marl facies contains a high algal, bryozoan, brachiopod, and crustacean biota preserved largely *in situ*. Leafy rhodoliths of *Mesophyllum commune* (Lemoine) grow from turned crusts originally growing over the marl surface. Open branched rhodoliths of *M. commune*, *Lithophyllum albanense* (Lemoine) and *L. mgarrense* (n.sp.) also occur. The Algal Debris Wackestone facies occurs interbedded and laterally adjacent to the Crustose Algal Marls. Fossils are fragmented and aligned along bedding planes. Rhodoliths are mainly discoidal (being derived from planar crusts); they are larger and more densely branched than those from the preceding facies. These wackestones are considered to be transported from pre-existing sediment of the Crustose Algal Marl facies. The Rhodolith Pavement facies is the most abundant facies and dominates the centre of the biostrome with units up to 14 m thick and 10 km wide. The sediments are plane or trough cross-bedded and are composed of alternating

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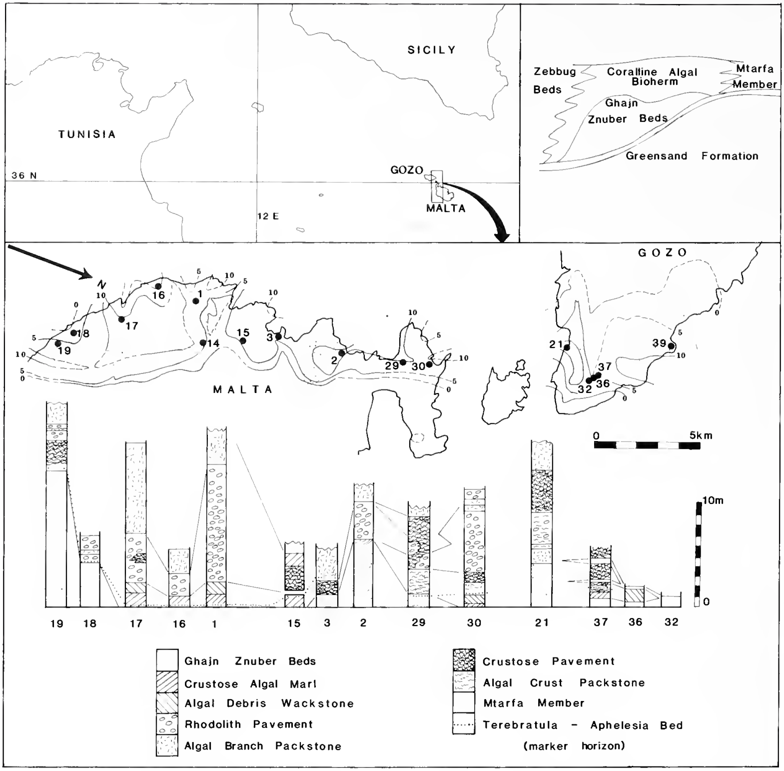


TEXT-FIG. 1. Location, stratigraphic setting, isopachytes (at 5 m intervals), and sections through Coralline Algal Biostrome, Malta and Gozo.

rhodoliths and biomicrites. Within fault-bound biostrome units rhodoliths have similar long axis orientations which are normal to palaeocurrents obtained from cross-beds and channels. The mainly ellipsoidal rhodoliths originate from laminar cores of *M. commune* and *Lithoporella melobesioides* (Foslie), to columns of *M. commune*, *Lithophyllum albanense*, *L. mgarrense*, *L. bahrijense* (n.sp.) and *Archaeolithothamnium affine* (Howe). Growth sequences occur from branched, through branches with flattened apices and lateral branches, to laminar concentric growths: they record periods of turbulence during rhodolith growth. The biomicrites are thought to have been deposited in quieter periods. Closely associated with this facies is the Algal Branch Packstone facies which is rich in coralline debris and smaller, spheroidal abraded rhodoliths of the same taxa as those of the preceding facies. This facies frequently terminates the biostrome and represents higher energy conditions of deposition.

The Crustose Pavement facies represents the only *in situ* framework within the bioherm. This framework is constructed of leafy growths of *M. commune* with *Lithoporella melobesioides*. The construction of this framework is described in detail in this paper. The framework had little original relief and provided a suitable hard substrate for bryozoans, serpulids, foraminifers, and brachiopods. Discoidal rhodoliths, derived from eroded crusts, are preserved along erosion surfaces in the Crustose Pavement facies. The rhodoliths from this facies contain many species of corallines. Laminar concentric cores of *M. commune*, *L. melobesioides*, *Lithophyllum bahrijense*, and *Lithothamnium praefructiculosum* (Maslov) are succeeded by outer branches and columns of *M. commune*, *Lithophyllum albanense*, *L. bahrijense*, *Lithothamnium magnum*, and *L. praefructiculosum*. Interbedded with the Crustose Pavement facies occurs the Algal Crust Packstone facies. This facies is composed of eroded and transported coralline crusts with discoidal rhodoliths of *M. commune*, *Lithophyllum albanense*, and *Lithothamnium magnum* and represents a transported Crustose Pavement facies.

The biostrome had little original relief and the facies would have occurred as a mosaic on the sea bed at any one time (text-fig. 1). The closest modern analogue known is the 'Coralligène de Plateau' of the Mediterranean (Laborel 1961; Pérès 1967). This occurs in depths of 50–150 m and contains leafy *in situ* coralline frameworks, rhodoliths, and coralline and shell gravels. These water depths are also indicated in the Miocene material by the present-day depth ranges of the coralline genera.

In this paper I describe the morphology and taxonomy of these limestone building coralline algae, and is the first description of Maltese coralline algae apart from the early, inadequately described, and unillustrated work of Samsonoff (1917*a*, *b*). A more thorough statistical approach to the description of fossil corallines is presented and two new species of *Lithophyllum* are described. The constructional abilities of the polymorphic *M. commune* are described. Details of the reproductive structures of many of these corallines are described and illustrated for the first time.

METHODS AND PROBLEMS IN CLASSIFICATION

About forty well-exposed localities (text-fig. 1) were visited in August/September 1978. The sections were logged and the majority of the corallines were collected as rhodoliths. Others were from coralline frameworks and some occurred as fragmented grains in sediment samples. Samples were impregnated in green stained Araldite 800 prior to sectioning and staining. For the study of the corallines, sections were taken only when carefully oriented normal to the crusts. All measurements of tissue and cell sizes were carried out with calibrated micrographs.

There are many problems concerning the taxonomy of fossil corallines at both the generic and specific levels. At the generic level there are recent taxa where diagnostic morphological features have not been recognized in fossil material. For example, the differentiation of *Lithothamnium*, *Leptophytum*, and *Phymatolithon* is to a large extent based on epithallial and staining characteristics (Adey 1970). The coralline epithallus has not to my knowledge been recognized in fossil material and therefore these genera are still grouped under *Lithothamnium* until fossilizable characteristics can be differentiated. Recent keys for generic identification of corallines (Adey and MacIntyre 1973) contain epithallial characteristics and pit connections, which again have not been found in fossil corallines. However, these do not alter the traditional generic groupings. Poignant (1979) gives a key for identification of fossil coralline genera.

At the specific level the major problems concern the small number of taxonomic criteria, their variability, and the lack of detail in previous descriptions. The main taxonomic criteria at species level are cell and conceptacle sizes. These vary with the orientation of the section, with zoned thalli and with interruptions to growth. Some species are more variable than others. Unfortunately previous workers have only given size ranges with no indication of the number of measurements made, thus making comparisons sometimes impossible. In this paper I record means, standard deviations, and ranges (e.g. mean (standard deviation), range is recorded as 10 μm (1·6), 5–16 μm). It is hoped in the future to use numerical taxonomy to differentiate fossil species.

The following data are taken from 10 to 40 measurements of up to eight parameters on sixty-six oriented specimens. Cells are measured from their middle cell walls and conceptacles at their widest and highest measurements in vertical section. Unipored conceptacles are measured from the lowest point of the floor to the base of the pore.

SYSTEMATIC PALAEONTOLOGY

Holotypes or representative material of each species are housed at the British Museum (Natural History), BM(NH), under numbers V.60922–V.60931.

Class RHODOPHYTA Wettstein, 1901
Order CRYPTONEMIALES Schmidtz, in Eugler 1892
Family CORALLINACEAE (Lamouroux) Harvey 1849
Subfamily MELOBESIODEAE Lemoine 1939
Genus ARCHAEOLITHOTHAMNIUM Rothpletz 1891
Archaeolithothamnium affine Howe 1919

Plate 15, figs. 1–2; text-fig. 2

1919 *Archaeolithothamnium affine* Howe, pp. 11–12, pl. 4, fig. 1; pl. 5.
1939 *Archaeolithothamnium affine* Howe; Lemoine, p. 60, pl. 11, fig. 8; text-fig. 25.

Description. Laminar crusts giving rise to columnar perithallial tissue. Columns 1·8–3·7 mm in diameter and up to 3 mm high. A poorly developed hypothallium is seen in one specimen only. The hypothallium is 90–150 μm thick with cells measuring 25 μm (s.d. 6·7), 18–35 μm long × 12 μm (s.d. 2·2), 10–15 μm wide. Perithallium multistromatic with cells either arranged in rows or in filaments. Cells are square and measure 10 μm (s.d. 1·6), 5–16 × 9 μm (s.d. 1·1), 7–13 μm (Pl. 15, figs. 1–2). Sporangia are ellipsoidal and measure 75 μm (s.d. 1·5), 55–85 μm high and 43 μm (s.d. 3·3), 28–55 μm wide.

Remarks. These specimens are close to Howe's (1919) material except for the perithallial cell length which he records as 8–28 μm. Howe's (1919) figure may be on the high side as his illustrated sections appear slightly oblique. Howe does not record a mean value.

Occurrence. *A. affine* occurs occasionally in rhodoliths from the Rhodolith Pavement and Crustose Pavement facies. It either forms monospecific rhodoliths or is intergrown with *M. commune* and *Lithothamnium praefructiculosum*, Maslov.

Archaeolithothamnium intermedium Raineri 1924

Plate 15, figs. 3–5; text-fig. 2

1924 *Archaeolithothamnium intermedium* Raineri, p. 29, fig. 1.

Description. Columnar growths 2·5 mm in diameter and up to 2 mm high. The hypothallus 50 μm thick, non-coaxial but too poorly preserved to measure cell dimensions. Perithallium multistromatic with rectangular cells arranged in filaments (Pl. 15, figs. 4–5) and measure 17 μm (s.d. 3·9), 11–26 μm long × 12 μm (s.d. 1·9), 10–17 μm wide. Sporangia occur in rows usually arched over the apical region of columns. They are elliptical and measure 61 μm (s.d. 7·2), 50–75 μm wide and 101 μm (s.d. 14·4), 75–120 μm high.

Occurrence. A multispecific rhodolith composed dominantly of *A. intermedium* with outer laminae of *M. commune* was found in the Algal Bank Packstone facies. A broken fragment was also found in the Algal Debris Wackestone facies.

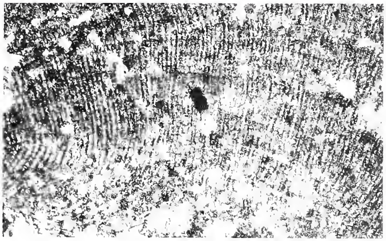
EXPLANATION OF PLATE 15

Figs. 1, 2. *Archaeolithothamnium affine*. 1, basal non-coaxial hypothallium and perithallium with filament walls dominating. Loc. 20, × 80. 2, zoned columnar perithallium with ellipsoidal sporangia borne in rows. Loc. 15, × 80. BM(NH) V.60921.

Figs. 3, 4. *Archaeolithothamnium intermedium*. 3, overgrowing fertile branch of *Mesophyllum commune* and overgrown by large oblique celled *Lithoporella melobesioides* and foraminifera. Loc. 21, × 30. BM(NH) V.60922. 4, detail of perithallium with thick filament walls and sporangia. Loc. 21, × 80. BM(NH) V.60922.

Figs. 5–7. *Lithothamnium magnum*. 5, zoned medullary tissue from branch. Loc. 30, × 120. BM(NH) V.60924. 6, perithallium in crust with filament walls dominating structure. Loc. 16, × 80. 7, fertile branch with large hemispherical multipored conceptacles. Loc. 16, × 20. BM(NH) V.60924.

PLATE 15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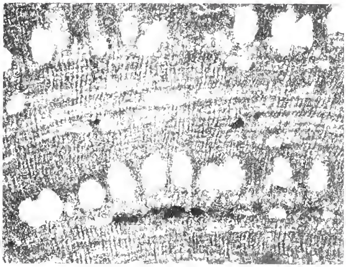
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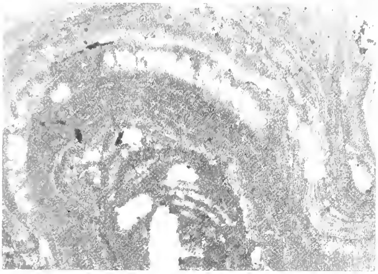
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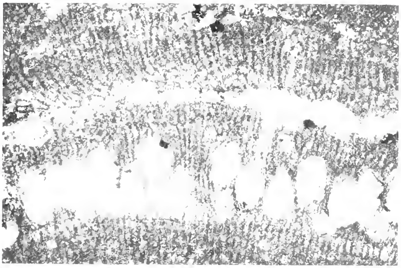
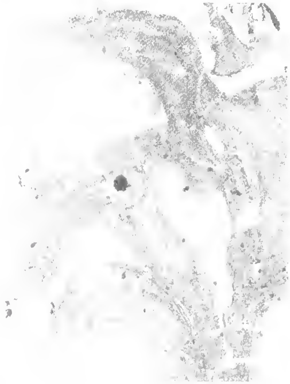
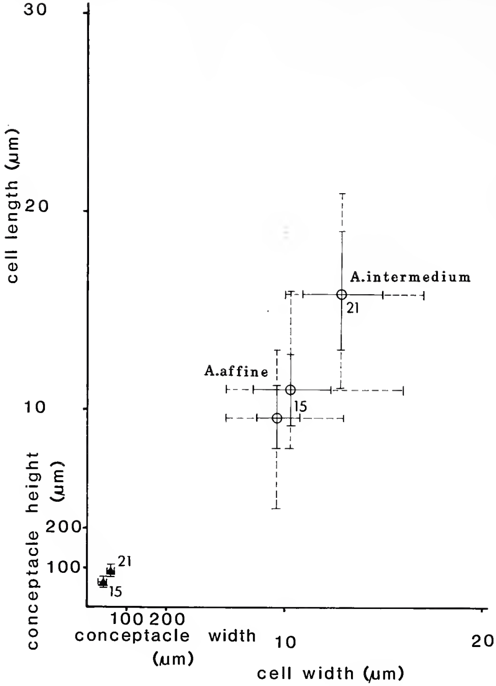

4


5


6


7

BOSENCE, *Miocene coralline algae*



TEXT-FIG. 2. *Archaeolithothamnium intermedium* and *A. affine*: Perithallial cell length and width (mean ○, standard deviation —⊣ , and range — —⊣) and conceptacle height and width (mean ▲ and range — —⊣) from localities 15 and 21 (see text-fig. 1).

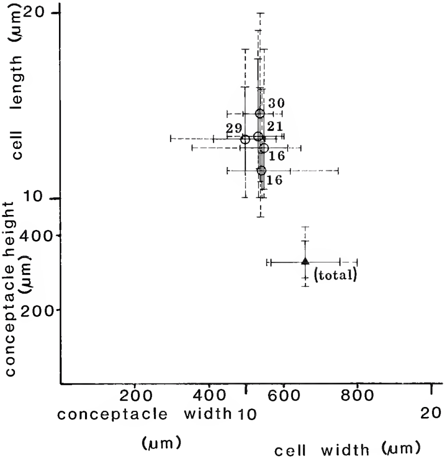
Genus LITHOTHAMNIUM Philippi 1835

Lithothamnium magnum Capeder 1900

Plate 15, figs. 6–7; text-fig. 3

1900	*Lithothamnium magnum* Capeder, p. 179, pl. vi, fig. 10.
1926	*Lithothamnium magnum* Capeder; Lemoine, pp. 248–249, text-figs. 7, 8.
1939	*Lithothamnium magnum* Capeder; Lemoine, p. 73, text-figs. 34, 35.

Description. Branching thalli with very large distinctive semicircular superficial conceptacles. Branches measure 2 mm (s.d. 0·5) in diameter and up to 5·6 mm long. Also occurs as 0·4–0·6 mm thick crusts with multistromatic perithallus. No hypothallium has been seen. Branches are constructed of distinctively and regularly zoned (107 µm (s.d. 3·5) thick) perithallium with a central medullary tissue (Pl. 15, figs. 6–7) arranged in filaments with rectangular cells measuring 13·3 µm (s.d. 3·6), 9–20 µm long and 10 µm (s.d. 1·9), 7–13 µm wide. Conceptacles are



TEXT-FIG. 3. *Lithothamnium magnum*: Perithallial and conceptacle measurements. (Symbols as for text-fig. 2.)

superficial and commonly apical in position on branches. The multipored conceptacles are covered by a roof 5–10 cell thick. Conceptacles have a flat base and a distinctive semicircular vertical cross-section (Pl. 15, fig. 7). Conceptacle dimensions are 652 μm (s.d. 92), 557–800 μm at their widest point and 342 μm (s.d. 60), 287–430 μm at their highest.

Remarks. Perithallial cells are larger (but overlap) with those of Lemoine (4–9 μm long: 1926, 1939). Although her drawings (fig. 34) suggest common cell-lengths of around 10 μm. The distinctive conceptacles suggest that this is the same species showing some variability in cell size.

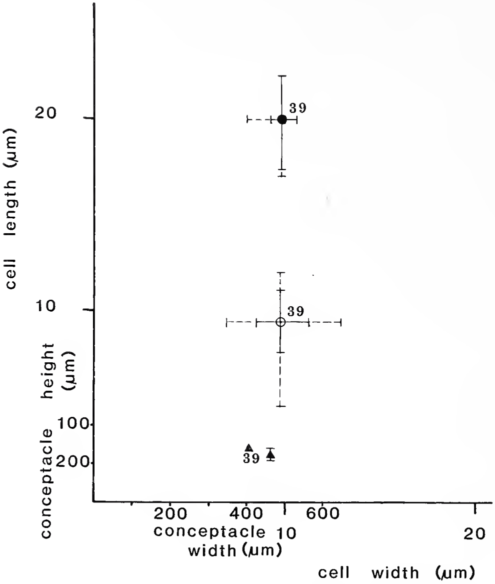
Occurrence. *L. magnum* is found occasionally in the Crustose Pavement facies. Here it occurs on the outer layers of multispecific rhodoliths coating *M. commune*. Similar examples are also found in rhodoliths of the transported sediments of the Algal Crust Packstone facies. One branching rhodolith was found in the Rhodolith Pavement facies.

Lithothamnium praefructiculosum Maslov 1956

Plate 16, figs. 1–2; text-fig. 4

1956 *Lithothamnium praefructiculosum* Maslov, p. 149, pl. lii, figs. 1–3.

Description. Occasional fertile crusts 0·5–0·7 m thick in rhodoliths. Hypothallium weakly developed, non-coaxial (60 μm thick) with rectangular cells measuring 20 μm (s.d. 2·3), 17–22 μm long and 9·7 μm (s.d. 1·7), 8–10 μm wide. Perithallial tissue is multistromatic, weakly zoned with cells arranged in sinuously curved filaments. Cells measure 9 μm (s.d. 1·6), 5–12 μm long and 10 μm (s.d. 1·4), 7–13 μm wide. The multipored conceptacles have vertical walls and flat tops giving distinctive rectangular vertical sections (Pl. 16, fig. 1). Conceptacles measure 437 μm, 407–467 μm wide, and 129 μm (s.d. 17·9), 112–145 μm high.



TEXT-FIG. 4. *Lithothamnium praefructiculosum*: Perithallial, hypothallial (mean ●, standard deviation —⊣, and range — —⊣) cell and conceptacle measurements. (Symbols as for text-fig. 2.)

EXPLANATION OF PLATE 16

Figs. 1, 2. *Lithothamnium praefructiculosum*. 1, fertile crust with multipored sporangial conceptacles. Loc. 39, × 20. BM(NH) V.60925. 2, detail of fig. 1 illustrating poorly preserved hypothallium and weakly zoned perithallus with conceptacle. Loc. 39, × 80. BM(NH) V.60925.

Figs. 3–7. *Mesophyllum commune*. 3, typical crust with variable (coaxial to non-coaxial) hypothallium and perithallium. Loc. 39, × 80. 4, zoned, columnar perithallial tissue. Loc. 39, × 30. 5, fertile column with multipored asexual conceptacles. Loc. 39, × 20. BM(NH) V.60926. 6, asexual conceptacle with preserved spores. Loc. 3, × 40. 7, unipored sexual conceptacle. Loc. 1, × 40.

Figs. 8–10. *Mesophyllum koritzae*. 8, fragment of crust with hypothallium, perithallium, and ripe conceptacles. Loc. 36, × 20. BM(NH) V.60927. 9, detail of fig. 8 showing coaxial hypothallium and grid-like perithallium. Loc. 36, × 80. BM(NH) V.60927. 10, detail of fig. 8 showing multipored asexual conceptacle with preserved spores. Loc. 36, × 80. BM(NH) V.60927.

PLATE 16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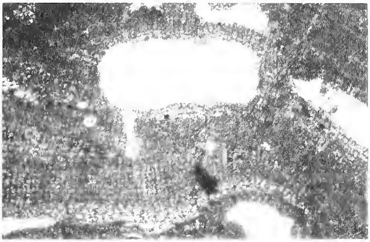
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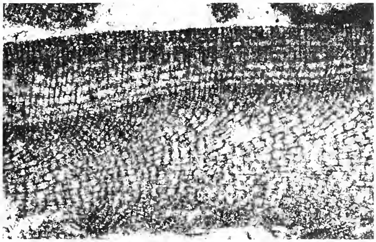
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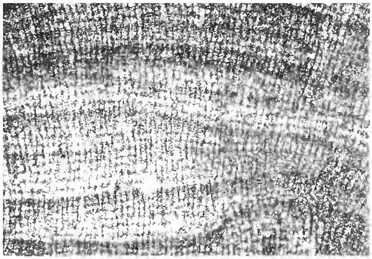
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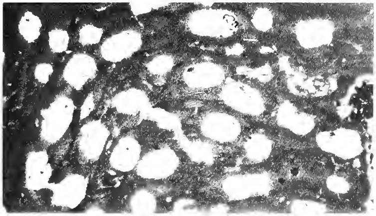
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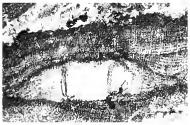
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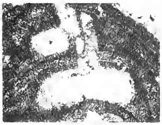
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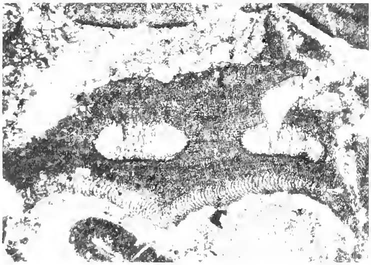
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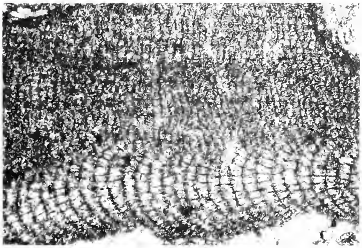
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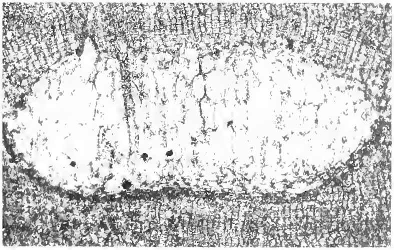
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BOSENCE, Miocene coralline algae

Remarks. This species has not to my knowledge been found by any workers since Maslov's original description. The hypothallium is first described here.

Genus MESOPHYLLUM Lemoine 1923
Mesophyllum commune Lemoine 1939

Plate 16, figs. 3–7; Plates 17, 18, figs. 3–6, text-figs. 5, 12

1939 *Mesophyllum commune* Lemoine, p. 86, text-figs. 54, 56, 57.
1972 *Mesophyllum commune* Lemoine; Orszag-Sperber and Poignant, p. 120.

Description. This polymorphic genus (Orszag-Sperber and Poignant 1972) is the major limestone building alga from the Upper Coralline Limestone Formation of Malta. It occurs as both *in situ* frameworks and rhodoliths as described below (see *Occurrence*, p. 167). Thalli occur as crusts, bifurcating crusts, branches, and columns. Crusts with hypothallium and perithallium are commonly about 350 μm thick but the perithallium may continue growing to produce a thick, multistromatic crust 500–600 μm thick. These thick crusts commonly develop into columns. Columns ('Mammelons' of Lemoine 1939) are distinct from branches by their size and shape 6·6 mm (s.d. 1·7) high and 6·3 mm (s.d. 1·2) wide and a variable internal structure. Columns may be formed by zoned arched layers of perithallial tissue or successive crust layers with both hypothallium and perithallium present. Branches arising from crustose perithallial tissue have diameters of 3·1 mm (s.d. 0·4) and are up to 20 mm high. They have a coaxially zoned central medulla and layered outer cortex. Branches may bifurcate dichotomously or laterally.

The hypothallium is of variable thickness (143 μm (s.d. 45), 70–210 μm) and construction. Filaments may be arranged to form coaxial, partially coaxial, or non-coaxial hypothalli (Pl. 16, fig. 3). Hypothallial cells are rectangular and measure 22 μm (s.d. 3·5), 17–34 μm long and 12 μm (s.d. 1·8), 10–18 μm wide. Perithallial tissue is most commonly arranged in rows or a grid but may also have filament walls dominating. The perithallium is commonly zoned; particularly in columns and branches where the zones measure 80 μm (s.d. 22) thick in the apical region. Perithallial cells in crusts are square and measure 11 μm (s.d. 1·7), 7–16 μm long and 10 μm (s.d. 1·4), 6–13 μm wide. Those in the medullary tissue of columns and branches are longer and measure 13·5 μm (s.d. 3·3), 8–20 μm long and 11 μm (s.d. 1·7), 8–18 μm wide. Asexual conceptacles are multipored, mainly elliptical in vertical section (Pl. 16, figs. 5–6) and measure 397 μm (s.d. 114), 275–630 μm wide and 171 μm (s.d. 41), 120–300 μm high. A possible sexual conceptacle was found measuring 440 μm × 176 μm. The distinctive raised floor of the conceptacle and the single large pore can be seen in Pl. 16, fig. 7.

Remarks. The wide variability in the morphology of this species previously led to its assignment to the genus *Lithothamnium* by Bosence and Pedley (1979). Subsequent study of the variable hypothallium has shown it to be a species of *Mesophyllum* which rarely develops a truly coaxial hypothallium.

For the occurrence and details of framework construction see below: *M. commune*—Occurrence, framework construction, and functional morphology (p. 167).

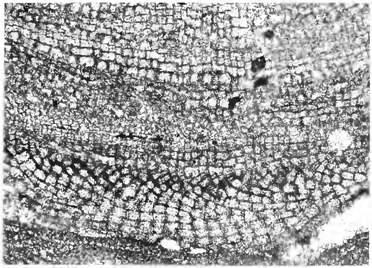
EXPLANATION OF PLATE 17

Figs. 1–4. *Lithophyllum albanense.* 1, crust with coaxial hypothallium and typical irregular grid-like perithallium. Loc. 2, ×80. BM(NH) V.60928. 2, zoned columnar perithallial tissue. Loc. 2, ×80. BM(NH) V.60928. 3, asexual conceptacle illustrating characteristic wide, flared pore with conical infilling by later tissue. Loc. 2, ×80. BM(NH) V.60928. 4, sexual conceptacle with preserved cystocarps? Loc. 14, ×80.

Figs. 5, 6. *Lithophyllum mgarrense.* 5, detail of fig. 6 showing perithallial tissue dominated by filament walls and asexual conceptacle with characteristic elongate roof cells. Loc. 15, ×60. BM(NH) V.60930. 6, fertile crust illustrating perithallial tissue and asexual conceptacles. Loc. 15, ×25. BM(NH) V.60930.

Figs. 7–9. *Lithophyllum bahrijense.* 7, crust illustrating partly coaxial hypothallium and perithallium. Loc. 19, ×60. BM(NH) V.60929. 8, asexual conceptacle. Loc. 19, ×60. BM(NH) V.60929. 9, sexual (cystocarpic) conceptacles. Loc. 1, ×60. BM(NH) V.60929.

Fig. 10. Epilithic crusts of Recent *Lithophyllum* sp. showing growth ridges arising where adjacent crusts meet and attempt to overtop neighbours. Loc. Kimmeridge Bay, Dorset, ×2.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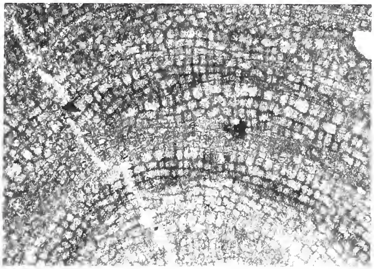
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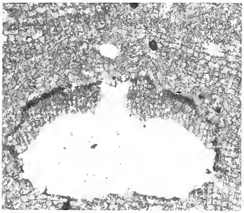
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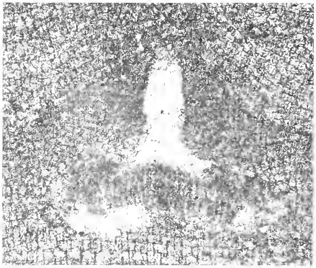
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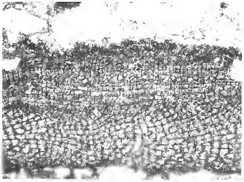
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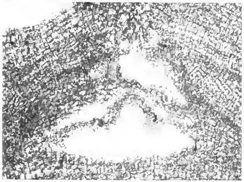
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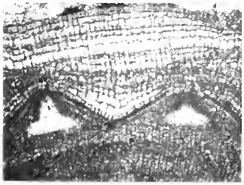
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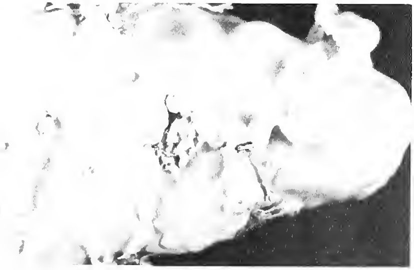
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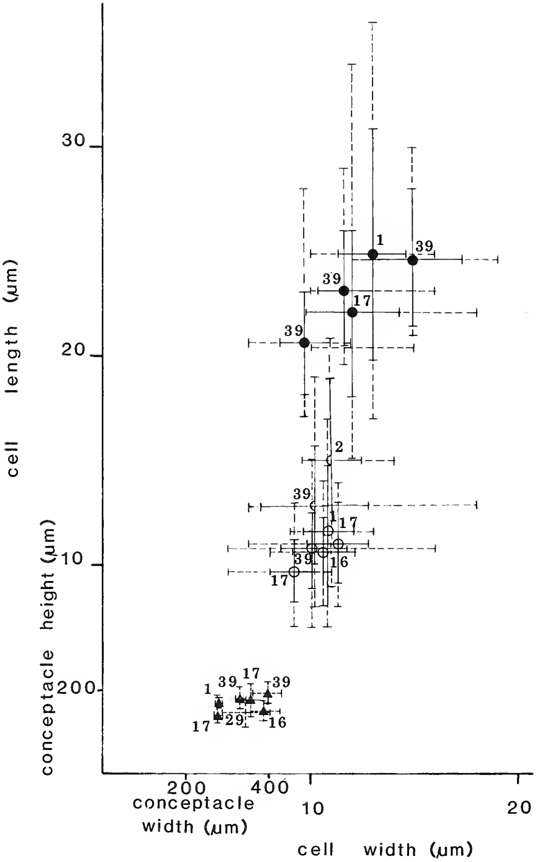
BOSENCE, Miocene coralline algae

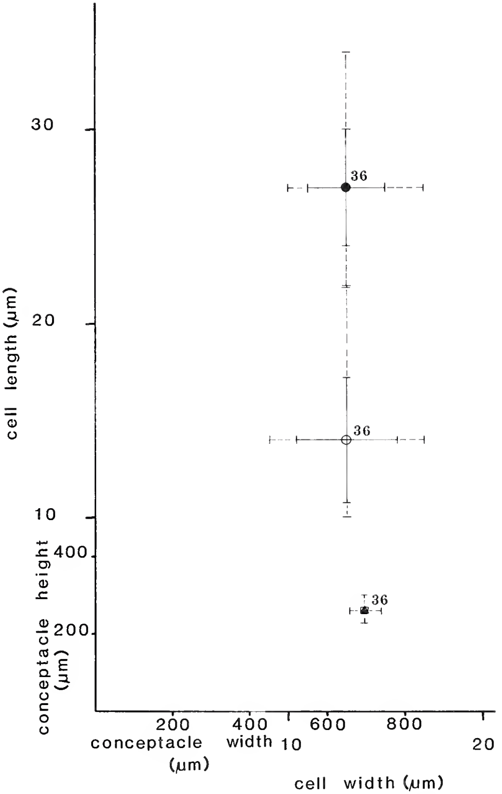


TEXT-FIG. 5. *Mesophyllum commune*: Perithallial (columnar perithallium mean-C), hypothallial and asexual conceptacle measurements. (Symbols as for text-figs. 2–4.)

Mesophyllum koritzae Lemoine 1939

Plate 16, figs. 8–10; text-fig. 6

1939 *Mesophyllum koritzae* Lemoine, p. 84, text-figs. 49, 50, 51.
1972 *Mesophyllum koritzae* Lemoine; Orszag-Sperber and Poignant, p. 120, pls. 2, 5.



TEXT-FIG. 6. *Mesophyllum koritzae*: Hypothallial, perithallial and conceptacle measurements. (Symbols as for text-figs. 2–4.)

Description. M. koritzae occurs rarely as concentric laminar cores to rhodoliths and as fragments of crust. Hypothallium is distinctly coaxial and measures 125 µm (s.d. 32), 80–175 µm thick. Cells are rectangular measuring 27 µm (s.d. 3), 22–33 µm long and 13 µm (s.d. 2), 10–17 µm wide. Perithallium is unevenly zoned with square cells arranged in rows. Cells measure 12 µm (s.d. 2), 7–22 µm long by 11 µm (s.d. 1·8), 8–17 µm wide. Multipored conceptacles are elliptical and measure 324 µm (s.d. 60), 209–390 µm wide and 149 µm (s.d. 24), 110–180 µm high. Pl. 16, fig. 10 illustrates mature conceptacles with preserved spores.

Occurrence. M. koritzae occurs in discoidal rhodoliths from the Algal Crust Packstone facies and as fragments from the Algal Debris Wackestone facies.

Genus LITHOPHYLLUM Philippi 1837
Lithophyllum albanense Lemoine

Plate 17, figs. 1-4; text-fig. 7

1924 *Lithophyllum? albanense* Lemoine, p. 281, text-figs. 8, 9.
1956 *Lithophyllum albanense* Lemoine; Maslov, p. 155, pls. 40-41, text-figs. 78-79.

Description. 1-2 mm crusts giving rise to thick (5·3 mm (s.d. 1·6), 315-7·5 mm) branches up to 25 mm long. Hypothallium coaxial and of variable thickness (183 μm (s.d. 73), 80-380 μm). Hypothallial cells rectangular and measuring 25 μm (s.d. 4·7), 15-39 μm long and 15 μm (s.d. 3·5), 9-23 μm wide. Perithallial cells typically form a zoned grid of irregularly sized and shaped cells (Pl. 17, figs. 1-3). Cells in crusts measure 15 μm (s.d. 4·8), 9-23 μm long and 14 μm (s.d. 4·3), 8-24 μm wide. Cells in branches arranged in zones (73 μm (s.d. 11·6) in apical thickness) and are larger than crust cells (15 μm (s.d. 4·8), 10-25 μm long and 16 μm (s.d. 3·9), 10-25 μm wide).

Both asexual and sexual conceptacles are present (Pl. 16, figs. 3-4). Asexual conceptacles have short/wide pores in which overgrowing tissue infills with a distinctive conical plug (Pl. 17, fig. 3). Conceptacles measure 430 μm (s.d. 108), 316-567 μm wide and 179 μm (s.d. 72), 120-275 μm high. Sexual conceptacles are flatter with longer necks measuring 455 μm (s.d. 9), 450-467 μm wide and 130 μm (s.d. 9), 120-136 μm high. One example (Pl. 17, fig. 4) shows presumed cystocarps.

Remarks. The distinctive aspects of this species are the irregular arrangement of the cells and the variable conceptacle size and shape. The high variability in cell sizes is reflected in the large standard deviations and the conceptacle size ranges are similar to those of Lemoine (350-575 μm wide: Lemoine 1924, 1939).

Occurrence. L. albanense is common and occurs in all of the biostrome facies. Its most frequent habit is to overgrow small rhodoliths of *M. commune* with firstly a crust and then branches to form large branching rhodoliths. Occasionally it forms a laminar core to rhodoliths intergrown with *M. commune.*

Lithophyllum bahrijense n.sp.

Plate 17, figs. 7-9; text-fig. 8

1982 *Lithophyllum* sps. 'b', Bosence and Pedley.

Holotype. BM V.60929 from branching rhodoliths in Rhodolith Pavement facies, locality 1 (Bosence and Pedley 1982). *Times of Malta* map grid. ref. 402 726.

Derivation. Named after village of Bahrija, Malta; adjacent to locality.

Description. Distinctive, finely branched (2·2 mm (s.d. 0·48), 1·4-3·4 mm wide and up to 15 mm long) spheroidal rhodoliths. Partly coaxial hypothallium (Pl. 17, fig. 7) 175 μm (s.d. 43·8), 120-230 μm thick with elongate

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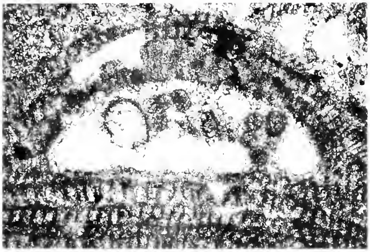
EXPLANATION OF PLATE 18

Fig. 1. *Lithoporella melobesioides.* Fertile crust with monostromatic thallus and large ripe conceptacle with preserved spores. Loc. 14, × 80. BM(NH) V.60931.

Fig. 2. Cf. *Lithophyllum prelichenoides.* Fragment of crust illustrating thick, coaxial hypothallium and thinner, poorly preserved perithallium. Loc. 14, × 80.

Figs. 3-6. *Mesophyllum commune.* 3, crustose Pavement facies of coralline Algal Biostrome with leafy, *in situ* framework of *M. commune.* Loc. 14, coin 25 mm. 4, framework with branches arising from subhorizontal leafy crusts. Loc. 14, × ⅙. 5, framework in thin section showing fusion of overgrowing crusts to basal crust. A short vertical branch arises between the two overgrowing crusts. For sketch of filaments and growth zones see text-fig. 12C. Loc. 14, × 20. 6, framework illustrating leafy crusts, crust divisions branches, and encrusting byozoans. Loc. 3, × 1½.

Figs. 7, 8. *Mesophyllum lichenoides* (Recent). 7, side view of framework illustrating crust divisions and fusions, overgrowth of old crusts and articulated corallines. Note epiphytes and debris on older lower crusts. Loc. Kimmeridge Bay, Dorset, × 5. 8, upper surface of leafy framework. Note overgrowth of lower crusts and articulating corallines. Loc. Kimmeridge Bay, Dorset, × 2.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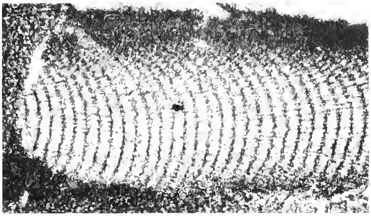
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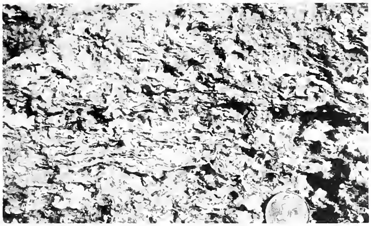
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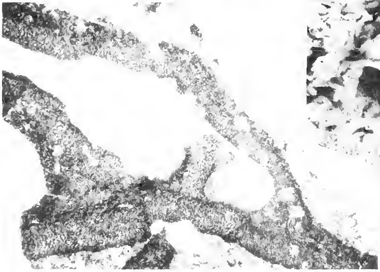
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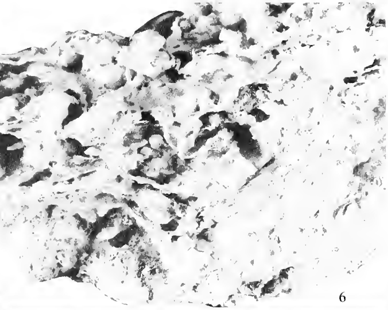
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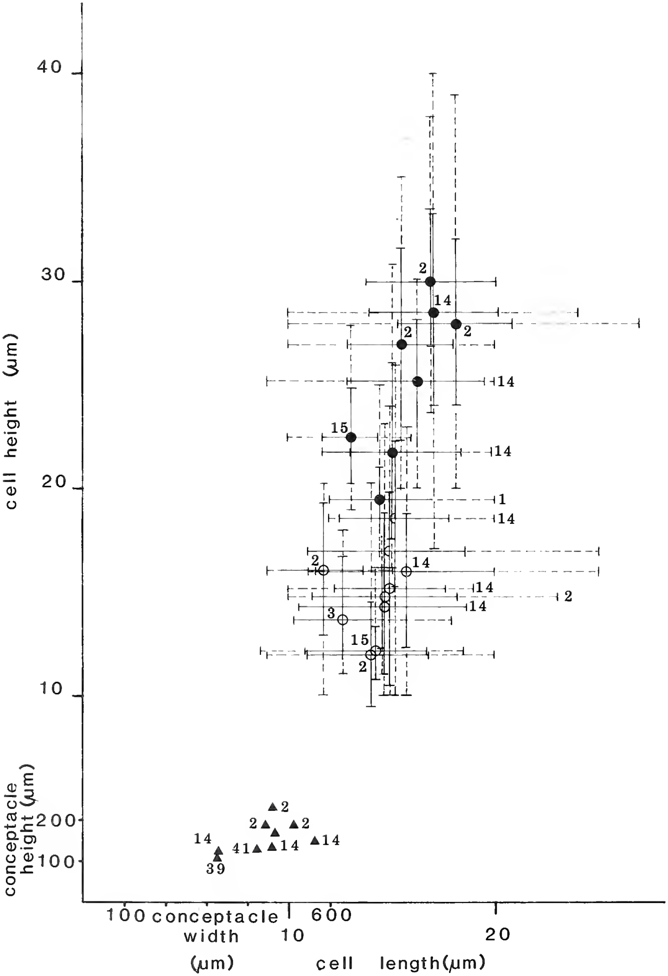
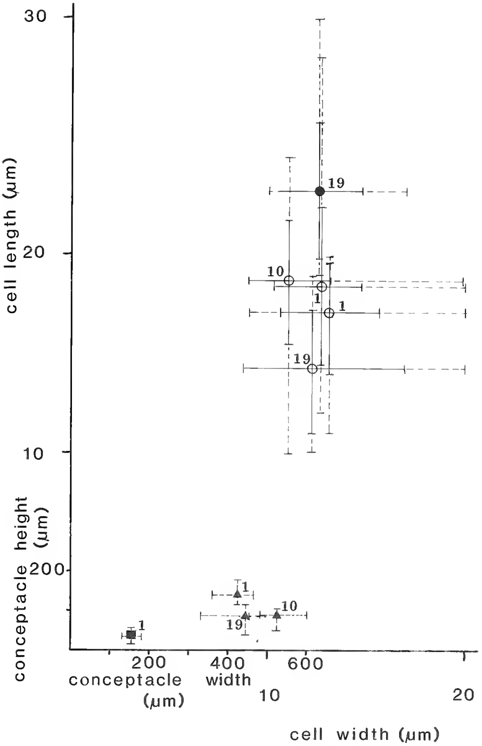
BOSENCE, Miocene coralline algae



TEXT-FIG. 7. *Lithophyllum albanense*: Hypothallial, perithallial, columnar perithallial (C), asexual (▲), and sexual (■) conceptacle measurements. (Symbols as for text-figs. 2–4.)



TEXT-FIG. 8. *Lithophyllum bahrijense*: Hypothallial, perithallial, asexual (▲), and sexual (■) conceptacle measurements. (Symbols as for text-figs. 2–4.)

rectangular cells measuring 23 μm (s.d. 3·7), 20–30 μm long and 13 μm (s.d. 2·3), 10–17 μm wide. Perithallium irregularly zoned with cells arranged in rows or a grid. Cells vary in shape from elongate, to square, to depressed, to polygonal (Pl. 17, figs. 7–9). Perithallial cells measure 17 μm (s.d. 2·5), 9–20 μm wide. Asexual conceptacles are characteristically depressed with a short wide conical pore. Conceptacle floors are flat or following undulations of previous cell rows (Pl. 17, fig. 8). Conceptacles measure 459 μm (s.d. 63), 330–600 μm wide and 98 μm (s.d. 36), 40–180 μm high. Smaller crystocarpic conceptacles are also present (Pl. 17, fig. 9) with depressed chambers with a long pore nearly as high as the conceptacles are wide. Conceptacles measure 156 μm (s.d. 26), 140–210 μm wide and 38 μm (s.d. 17), 20–60 μm high.

Remarks. The perithallial tissue of *L. bahrijense* is not significantly different from that of *L. albanense* and without conceptacles these two species cannot be separated. This species is similar in some respects to *Lithophyllum barbarense* Lemoine described from the Oligocene of Algeria (Lemoine

1939). There are no photographs of this species and only one conceptacle is known (450 × 160 μm). The hypothallium of *L. barbarense* is always truly coaxial and the cells are larger than those of *L. bahrijense*. In addition the hypothallium and the crust thicknesses are greater in *L. bahrijense* and it always occurs as distinctive finely branched spheroidal rhodoliths a form unknown in *L. barbarense*.

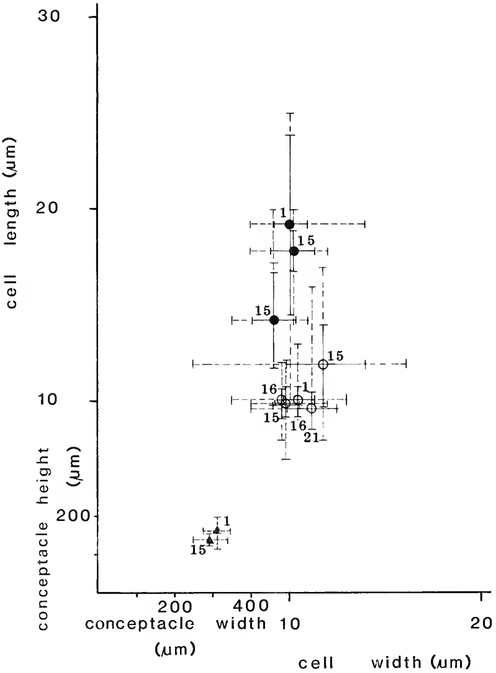
Occurrence. L. bahrijense is found occasionally in rhodoliths of the Crustose Pavement and Rhodolith Pavement facies. The characteristic rhodoliths in which it is found are multispecific with *L. bahrijense* overgrowing or being grown over by *M. commune* and *Lithoporella melobesioides*. Monospecific rhodoliths are found at the type locality in the Rhodolith Pavement facies.

Lithophyllum mgarrense n.sp.

Plate 16, figs. 5, 6; text-fig. 9

1982 *Lithophyllum* sps. 'a', Bosence and Pedley.

Holotype. BM V.60930 in concentric lamina rhodolith from the Crustose Algal Marl facies, locality 15 (Bosence and Pedley, 1982). *Times of Malta* map grid ref. 410 746.



TEXT-FIG. 9. *Lithophyllum mgarrense*: Hypothallial, perithallial, and conceptacle measurements. (Symbols as for text-figs. 2–4.)

Derivation. Named after nearby town of Mgarr, Malta.

Description. L. mgarrense occurs as crusts and columns (6·5 mm (s.d. 2·5), 4–9 mm wide and up to 9 mm high) within rhodoliths. The coaxial hypothallium is thin (60 μm (s.d. 8), 50–70 μm) and often weakly developed and poorly preserved. Cells are rectangular and measure 19 μm (s.d. 5·2), 12–20 μm long and 11 μm (s.d. 1·9), 8–15 μm wide. The perithallium (up to 850 μm thick in crusts) has distinctive thick walled filaments which diverge in fan-shaped zones, particularly around conceptacles (Pl. 17, fig. 5). Perithallial cells in crusts are square and measure 10 μm (s.d. 0·8), 7–12 μm long and 10 μm (s.d. 0·8), 7–13 μm wide. Columnar tissue is zoned (183 μm (s.d. 35), 150–220 μm thick at the apex) and cells are more elongate and variable in length (16 μm (s.d. 4·6), 10–25 μm long and 11 μm (s.d. 1·4), 8–15 μm wide) than crust cells. The unipored conceptacles are oval with either a raised or flat floor. They measure 301 μm (s.d. 40), 260–370 μm wide and 152 μm (s.d. 23), 126–210 μm high and have short wide pores. Conceptacles are commonly roofed with a distinctive row of elongate perithallial cells (Pl. 17, fig. 5).

Remarks. L. mgarrensis has similar ranges of cell sizes as *Lithophyllum uvaria* (Michelin) Lemoine but the latter species has a thicker hypothallium and the perithallium is arranged in rows. Conceptacles are unknown in *L. uvaria*. The distinctive perithallium of *L. mgarrense* is similar to that of *Lithophyllum duplex* Maslov but the latter species has larger cells and characteristic bulbous pored conceptacles.

Occurrence. L. mgarrense is common in branching rhodoliths of the Crustose Algal Marl and Algal Debris Wackestone facies. It also occurs in the Rhodolith Pavement facies and at the top of the Ghajn Znuber Beds. Its commonest habit is to overgrow concentric laminar cores of *M. commune* with crusts and then branches. The occurrence of *L. mgarrense* in the above facies suggests it had a preference for relatively quiet water conditions.

cf. *Lithophyllum prelichenoides* Lemoine

Plate 18, fig. 1; text-fig. 10

1917 *Lithophyllum prelichenoides* Lemoine, p. 262; text-figs. 8–9.

Description. Laminar crusts and dividing leafy crusts of hypothallial and perithallial tissue. Distinctive thick (300 μm (s.d. 79), 800–400 μm) coaxial hypothallium and thin (120 μm (s.d. 47), 80–200 μm) multistromatic perithallus (Pl. 18, fig. 1). Hypothallial cells rectangular, measuring 22 μm (s.d. 3·2), 15–30 μm long and 12 μm (s.d. 2·4), 9–19 μm wide. The perithallial cells which are arranged in filaments are often poorly preserved and measure 19 μm (s.d. 1·7), 16–22 μm long and 16 μm (s.d. 3·9), 10–22 μm wide. No conceptacles are present.

Remarks. Due to the absence of conceptacles no definite generic assignment can be made for this coralline. The size and structure of the hypothallium and perithallium is very similar to those of *L. prelichenoides*. However, the hypothallial cells are smaller (22–38 μm × 10–20 μm) and the perithallial cells larger (7–15 μm × 7–10 μm) than is normal for this species (Lemoine 1939).

Occurrence. As crusts in multispecific rhodoliths. One specimen from the Rhodolith Pavement facies and one from the Crustose Pavement facies.

Sub-family MASTOPHOROIDEAE (Svedelius 1911); Setchell 1943

Genus LITHOPORELLA (Foslie 1904); Foslie 1909

Lithoporella melobesioides (Foslie); Foslie

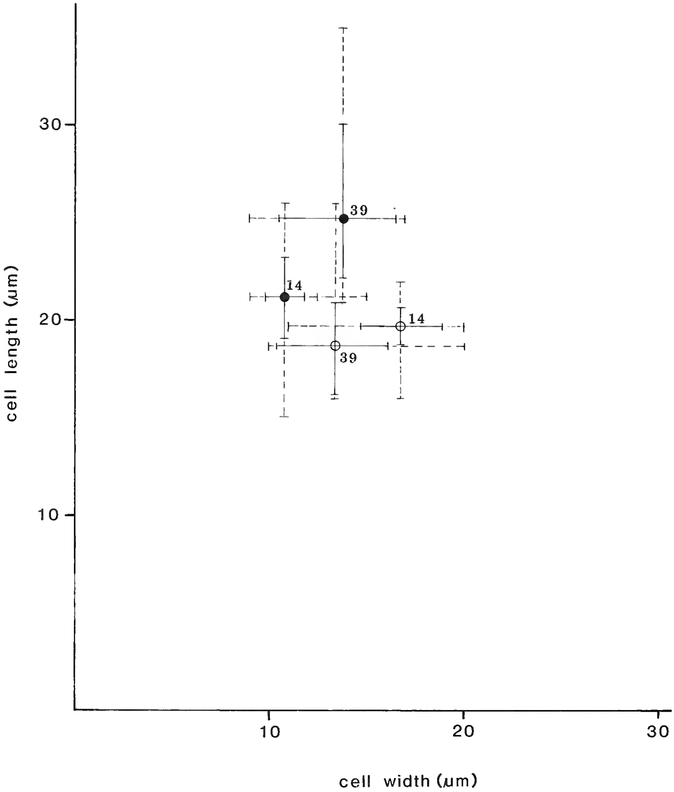
Plate 18, fig. 2; text-fig. 11

1904 *Mastophora* (*Lithoporella*) *melobesioides* Foslie *in* Weber van Bosse and Foslie 1904, pp. 73–77, text-figs. 30–32.

1939 *Melobesia* (*Lithoporella*) *melobesioides* (Foslie); Lemoine, pp. 108–110, text-figs. 78–79.

1949 *Lithoporella* (*Melobesia*) *melobesioides* (Foslie); Johnson and Ferris, p. 196, pl. 37, figs 4–5; pl. 39, fig. 2.

Description. Monostromatic crusts of hypothallium with successive layers forming crusts up to 500 μm thick.



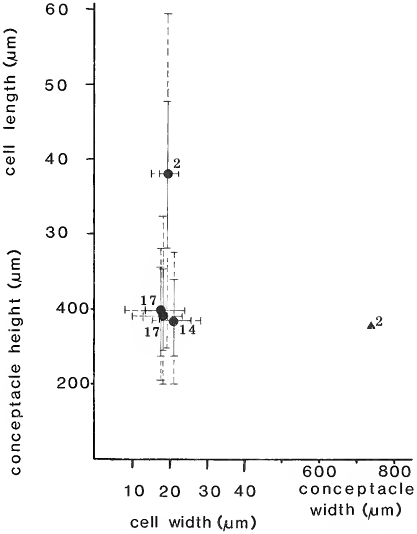
TEXT-FIG. 10. Cf. *Lithophyllum prelichenoides*: Hypothallial and perithallial cell measurements. (Symbols as for text-figs. 2–4.)

Cells often arranged in imbricate patterns with variable cell lengths (text-fig. 11, pl. 18, fig. 2). Cells measure 37 μm (s.d. 23), 15–120 μm long and 18 μm (s.d. 4·5), 8–29 μm wide. One large semicircular conceptacle is present 730 μm wide and 350 μm high. This conceptacle has preserved spherical spores with diameters in section of 45 μm (s.d. 28), 30–105 μm.

Occurrence. L. melobesioides is common as crusts within rhodoliths from all biostrome facies. It is frequently intergrown with crusts of *M. commune. L. melobesioides* is also found as encrusting sheets in the framework of the Crustose Pavement facies. Because of its simple morphology it is never a framework constructor in the manner of *M. commune* as outlined below.

MESOPHYLLUM COMMUNE—OCCURRENCE, FRAMEWORK CONSTRUCTION, AND FUNCTIONAL MORPHOLOGY

M. commune is abundant in all facies of the Coralline Algal Biostrome. In each facies this alga produces different growth forms in response to different environmental conditions. In the quiet water Crustose Algal Marl facies crusts of *M. commune* grow over the sediment surface; a mode of life unusual for crustose corallines (Adey and MacIntyre 1973). This habit is proven by growth responses by the algae to substrate irregularities. Bifurcations and occasional turning of these crusts give rise to leafy rhodoliths (Bosence and Pedley 1982). Large discoidal rhodoliths originating from crusts are found in the Algal Debris Wackestone facies. In addition, open branched rhodoliths of *M. commune* occur in the Crustose Algal Marl facies and denser branched forms in the higher energy Algal Debris Wackestone facies. *M. commune* forms laminar, concentric, and columnar cores to most rhodoliths from the Rhodolith Pavement and Algal Branch Packstone facies. These rhodoliths are overgrown by species of *Lithophyllum*, *Lithothamnium*, and *Lithoporella melobesioides*.



TEXT-FIG. 11. *Lithoporella melobesioides*: Cell lengths and widths and conceptacle measurement. (Symbols as for text-figs. 2–4.)

The most striking occurrence of *M. commune* is in the construction of the *in situ* framework in the Crustose Pavement facies (Pl. 18, figs. 3–6). The frameworks are up to 4·5 m thick, covering areas measured in 10,000s of square metres (text-fig. 1). They had an original relief of around 10–20 cm above the sea bed. The sedimentological features and associated fauna of the Crustose Pavement facies is described in Bosence and Pedley (1982). I describe here the morphological details of framework construction and their adaptive significance.

Framework construction

The construction of the framework in the Crustose Pavement facies is basically a combination of foliaceous crust growth, crust divisions, crust fusion (Pl. 18, figs. 3–6), and vertical branch growth (Pl. 18, fig. 4). However, in detail there are a variety of ways in which this is achieved.

(a) *Normal crust division* (text-fig. 12A). Crusts may divide through rejuvenation of previously dormant perithallial meristem to form a surface ridge which grows upwards into an overgrowing crust. The resulting new crust is identical in structure to the original crust and continues growth in the same direction as the underlying crust.

(b) *Reverse crust division* (text-fig. 12B). Divided crusts as in (a) above but the new crust grows in the opposite direction.

(c) *Crust fusion* (Pl. 18, fig. 5; text-fig. 12C). A downward growing crust can fuse on to an underlying crust. Two such examples are shown in Pl. 18, fig. 5 and text-fig. 12C, together with a short vertical branch. Either the upper downward growing, or the lower crust can heal the junction with additional perithallial tissue. The right-hand example has been fused mainly by perithallial tissue from the downward growing crust. The inverted left-hand crust has been fused by perithallial tissue derived from the basal crust.

(d) *Crust bridging* (text-fig. 12D). Bridging between over and underlying crusts can occur with a combination of crust division and crust fusion described above. Text-fig. 12D shows a vertically growing crust of perithallium growing on to the basal hypothallium of an overgrowing crust.

(e) *Enforced crust division* (text-fig. 12E). Divisions and redirected crust growth occur where a crust grows up against an obstruction. The hypothallial meristem ceases division against the obstruction and growth continues through rejuvenation of adjacent perithallal meristem to form an upward growing crust with hypo- and perithallal tissue identical to the original crust.

(f) *Crust overgrowth* (text-fig. 12F). When crusts (presumed to be dead) are overgrown by successive crusts the upper one may grow up and away from its substrate. Similarly juvenile crusts from spore settlement on old crusts may grow away from the substrate with a foliaceous habit.

(g) *Crusts—branch frameworks* (Pl. 18, fig. 4). Distinctive frameworks are also constructed by branches arising from horizontal crusts which are then subsequently overgrown by crusts. Further growth alternates between crusts and branches. Branches usually originate directly above previous branch tips giving the impression of continuous branch growth. Sections indicate that branches originate from raised areas where crusts overgrow previous branches.

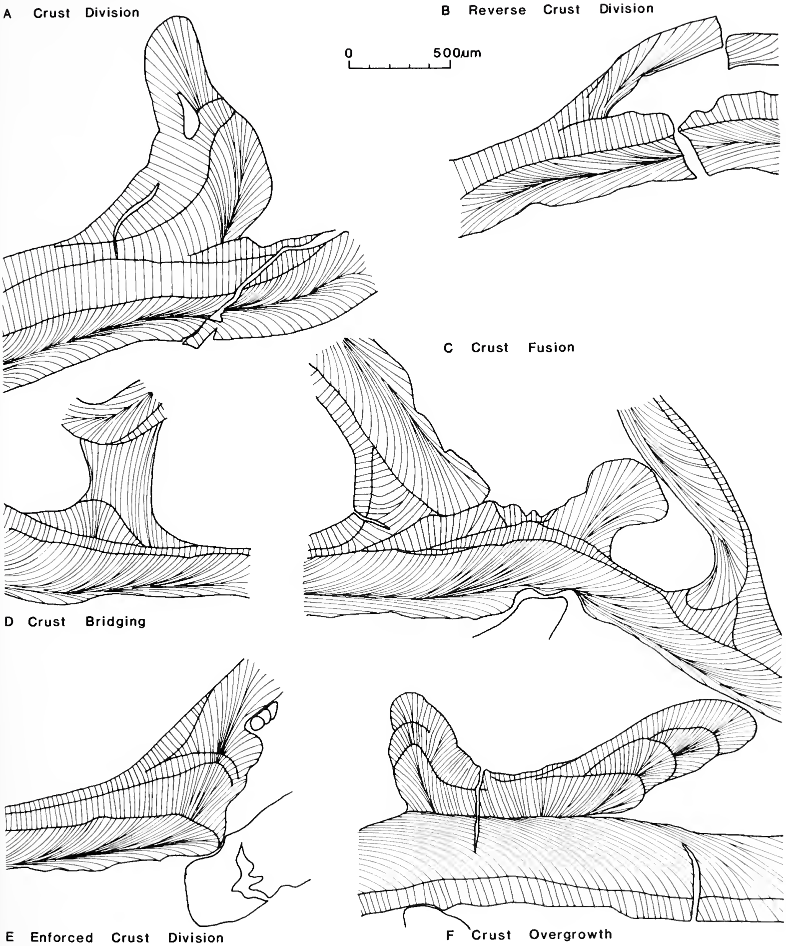
Discussion

This variety of crust fusions and division has not, to my knowledge, been described before for one species of fossil or recent coralline. The foliaceous habit of *M. commune* together with its constructional abilities clearly enabled it to become a successful frame-building species in the Miocene.

The morphologies exhibited by Recent frame-building corallines are being investigated by the author (e.g. Bosence 1981), but preliminary examination of material collected from south-west England and W. H. Adey's material at the Smithsonian Institution indicate possible Recent analogues.

The closest analogue for *M. commune* appears to be *Mesophyllum lichenoides* (L) Lemoine. Specimens from intertidal and shallow subtidal rocky shores at Kimmeridge Bay, Dorset, exhibit small-scale frameworks (up to 10 cm across and 1–2 cm thick). In the Mediterranean this species occurs at greater depths as an important constructor in the 'coralligène bioceonose' (Laborel 1961) which is also used as an analogue for the Coralline Algal Biostrome of Malta.

M. lichenoides exhibits the same foliaceous growth as *M. commune* and crust division, crust fusion, enforced crust division, crust bridging, and crust overgrowth can all be recognized (Pl. 18, figs. 7, 8). Similar leafy frameworks are constructed by *Lithophyllum expansion* Phillippi from Naples and



TEXT-FIG. 12A–F. Framework construction by *Mesophyllum commune* (for details see text). Outlines and growth zones in heavy lines. Filaments (lines of cells) indicating direction (divergence) and sequence of growth in fine lines. Note post depositional fracturing of framework (12B, F) and foraminifer in 12E. Sketches from camera lucida drawings of thin sections.

Neogoniolithon notarissi Delfour from Bibane, Tunisia (Coll. W. H. Adey), which both show crust division, fusion, bridging, and overgrowth. None of these species, however, combine branches in their frameworks.

Few authors have discussed the adaptive strategies exhibited by corallines when competing for hard substrate space. Steneck (1978) considers competition to be important because overgrowth is commonly seen. Competitive growth along growth ridges (Pl. 17, fig. 10) may also be added as evidence for space competition. Steneck (1978) discusses the roles of crust thickness and growth rates in producing a competitive hierarchy for crustose corallines from Maine. He has shown these to be important in explaining relative abundance of crusts from rocky substrates. The development of a foliaceous growth habit above the substrate is clearly an additional growth strategy which would compete successfully with closely adhering crusts. In addition to shading the underlying crusts overgrowth creates a cavity which collects debris and becomes infested with filamentous epiphytes (Pl. 18, fig. 7). One constraint on foliaceous growth is the increased skeletal strength required to support the overhang. The species described above have, in all probability, evolved this range of fusions and divisions to give strength to the foliaceous growth form and which gives rise to a framework. In addition, Adey and Adey (1973) mention that *M. lichenoides* is unusual in that it increases its calcified cell wall thickness within the thallus possibly to support a foliaceous growth form.

A comparison may be made with Jacksons's (1979) morphological strategies proposed for sessile marine invertebrates. The closely adhering crustose corallines would classify as 'sheets' and the foliaceous corallines as 'plates'. The advantages of the plate strategy are considered to be isolation from the deleterious 'substratum associated processes' at a cost of increased commitment to support structures and damage by strong water movements.

In conclusion, there are arguments that suggest that the origin of a foliaceous coralline framework lies in space competition on hard substrates. Many corallines compete for space by growing a thick crust which will overtop neighbours or by growing faster than their neighbours (Steneck 1978). However, some corallines have evolved a more successful strategy to compete for space by crust division and overgrowth of neighbour. The cost to these corallines is in the construction of a thallus to support the overhangs. *Mesophyllum* has achieved this through a diverse array of crust divisions and fusions in *M. commune* and *M. lichenoides* and possibly by increased calcification in *M. lichenoides*. The result of this growth strategy is the construction of a foliaceous framework so well exemplified by *M. commune*.

Similar leafy frameworks are at present undescribed from the Tertiary but are reported by Babič and Zupanič (1981) from the Palaeocene of Yugoslavia and are present in Eocene reefs of Catalana, Spain.

DISCUSSION

Biogeography

The crustose coralline flora from the Coralline Algal Biostrome, Malta, is most similar to Miocene floras from Algeria described by Lemoine (1939) (8 out of 11 species co-occurrences). Similarities also exist with floras from the Miocene of Egypt (5 out of 11 co-occurrences) (Souya 1963), southern U.S.S.R. (5 out of 11 co-occurrences) (Maslov 1956), and Corsica (4 out of 11 co-occurrences) (Orszag-Sperber and Poignant 1972). Comparisons with other areas can only be made with the wide-ranging species; *Lithoporella melobesioides* and *Lithophyllum prelichenoides*. There are no similarities with Miocene floras of the Vienna Basin described by Conti (1946).

On a world-wide scale the Maltese floras show no similarities (apart from the wide-ranging *Lithoporella melobesioides*) with Miocene limestones of Pacific Reefs described by Johnson (1957, 1961) and Johnson and Ferris (1949). The possible closure of the Mediterranean Pacific connection at around the Oligocene/Miocene boundary is discussed by Adams (1981).

Climate and water depth

The genera from the Miocene of Malta are today found in waters from the tropics to temperate waters (Adey 1970). Tropical to subtropical climates are, however, indicated by the presence of small patch reefs of *Montastrea* and *Porites*, within the biostrome together with locally abundant *Halimeda* plates. In these climates a flora dominated by *Mesophyllum* is typical of water depths of 60–80 m (Adey and Boykins, in press). Comparison has been made with the 50–130 m 'Coralligène de Plateau' (Pérès 1967) of the present-day Mediterranean (Bosence and Pedley 1982).

TABLE 1. Occurrences of coralline taxa in facies of the Miocene Coralline Algal Biostrome

Facies Taxa per cent	Ghajn Znuber Beds	Crustose Algal Marl	Algal Debris Wackestone	Rhodolith Pavement	Algal Branch Packstone	Crustose Pavement	Algal Crust Packstone	Total occurrences of taxa
Archaeolithothamnium affine				2		2		2
A. intermedium					4			1
Lithothamnium magnum				3		2	7	4
L. praefructiculosum					4	9		5
Mesophyllum commune	57	43	36	38	43	45	43	80
M. koritzae			14					3
Lithophyllum albanense	14	19		27	30	14	29	41
L. bahrijense				2		4		3
L. mgarrense	7	19	36	6				14
Cf. *L. prelichenoides*				2		2		3
Lithoporella melobesioides	22	19	14	20	17	21	21	36
Total occurrences in facies	15	21	14	61	23	44	14	192

Distribution of flora in Biostrome

The occurrence of corallines in the biostrome facies is shown in Table 1. The differences in sample sizes precludes a statistical analysis of the diversity and comparisons of floras from each facies. The facies with the greatest numbers of species are the Rhodolith Pavement and Crustose Pavement facies. These two facies contain the greatest volume of *in situ* material and therefore probably represent the richest original floras. The range of taxa in the Rhodolith Pavement facies occurs in multispecific rhodoliths. Species numbers are increased by ecological succession within rhodoliths with inner laminar cores of *M. commune* and *Lithoporella melobesioides* and outer layers with species of *Lithophyllum* and *Lithothamnium*. In the Crustose Pavement facies the corallines of the framework (*M. commune*, *Lithoporella melobesioides*, and *Lithophyllum albanense*) are added to those of rhodoliths occurring along erosion surfaces within the framework.

In general, the floras from each facies are similar and dominated by *M. commune*, *L. melobesioides*, and *L. albanense*. The facies are characterized more by the algal growth forms than by species composition. The one exception is *Lithophyllum mgarrense* which occurs mainly in quieter water sediments.

Acknowledgements. This work arose from an initial investigation of the sedimentology and palaeoecology of the Coralline Algal Biostrome on Malta in conjunction with H. M. Pedley (Polytechnic of North London). I thank him for introducing me to the sections on the Maltese Islands. W. H. Adey and R. S. Steneck of the National Museum of Natural History, Washington, kindly showed me collections of Recent corallines. Funding for the field-work was awarded by NERC and is gratefully acknowledged. I also wish to thank Messrs. T. Easter, O. Green, and D. Norman from Goldsmiths's for technical and secretarial help.

REFERENCES

ADAMS, C. G. 1981. An outline of Tertiary Palaeogeography. In *The evolving earth*, 221-235. British Museum (NH): Cambridge University Press.

ADEY, W. H. 1970. A revision of the Foslie Crustose Coralline Herbarium. *Det. Kong. Norske Vidensk. Sels.* **1,** 1-46.

—— and ADEY, P. J. 1973. Studies of the biosystematics and ecology of the epilithic crustose corallinaceae of the British Isles. *Br. phycol. J.* **8,** 343-407.

—— and BOYKINS, W. T. (in press). The crustose coralline algae of the Hawaiian Archipelago. *Smithson. Contr. Mar. Sci.*

—— and MACINTYRE, I. G. 1973. Crustose coralline algae: a re-evaluation in the geological sciences. *Bull. geol. Soc. Am.* **84,** 883-903.

BABIČ, L. and ZUPANIČ, J. 1981. Various pore types in a Palaeocene reef, Banija, Yugoslavia. *In* TOOMEY, D. (ed.). European fossil reef models. *Soc. Econ. Pet. Min. Spec. Pub.*, no. 30, 473-482.

BOSENCE, D. W. J. 1981. Internal structures and fabrics of coralline algal ridges, St. Croix. A preliminary report. IV. *Int. coral reef symp. Phillipines*, p. 7 (Abstr.).

—— and PEDLEY, H. M. 1979. Palaeoecology of a Miocene coralline algal bioherm, Malta. *Bull. Cent. Rech. Explor.-Prod. Elf-Aquitaine*, **3,** 463-470.

—— —— 1982. Sedimentology and palaeoecology of a Miocene coralline algal biostrome from the Maltese Islands. *Palaeoclimat. Palaeogeog. Paleoecol.* **37,** 9-43.

CAPEDER, G. 1900. Contribuzione allo studio dei *Lithothamnion* terziari. *Malpighia*, **14,** 172-182.

CONTI, S. 1946. Le Corallinacee del calcare Miocenico (Leithakalk) del Bacino di Vienna. *Pub. Inst. geol. Univ. Geneva*, ser. A. *Palaeontologia*, quad. 1-2, 31-68.

HOWE, M. 1919. Tertiary calcareous algae from the islands of St. Bartholomew, Antigua and Anguilla. *Carnegie Inst. Wash.* **291,** 11-19.

JACKSON, J. B. C. 1979. Morphological strategies of sessile animals. *In* LARWOOD, G. and ROSEN, B. R. (eds.). *Biology and systematics of colonial organisms*, 499-555. Academic Press.

JOHNSON, J. H. 1957. Geology of Saipan-Mariana Islands, calcareous algae. *U.S. Geol. Surv. Prof. paper*, **280C,** 209-243.

—— 1961. Fossil algae from Eniwetok, Funafuti and Kita-Daito-Jima. Ibid. **260Z,** 907-950.

—— and FERRIS, B. J. 1949. Tertiary coralline algae from the Dutch East Indies. *J. Paleont.* **23,** 193-198.

LABOREL, J. 1961. Le concrétionnement algal 'coralligène' et son importance géomorphologique en Méditerranée. *Rec. trav. sta. mar. Endoume.*, Fasc. **37,** 37-60.

LEMOINE, P. 1917. Corallinacées fossiles de la Martinique. *Geol. Soc. France bull.* **7,** 256-279.

—— 1924. Contributions à l'étude des corallinacées fossiles. VII Mélobésidées miocenes, recueillies par M. Bourcant en Albanie. Ibid. **23,** 275-283.

—— 1926. Révision des Mélobésidées tertaires d'Italie décrites par M. Capeder. *Congr. Sci. Sav.* (1925) *Sect. Sci. C.R.* 241-259.

—— 1939. Les algues calcaires fossiles de l'Algérie. Matériaux pour la carte géologique de l'Algérie, sér. 1. *Pal.* **9,** 1-128.

MASLOV, V. P. 1956. Fossil Algae of the USSR *Akad. Nauk. SSSR Geol. Inst. Trudy.* **160,** 1-301. [In Russian.]

ORSZAG-SPERBER, F. and POIGNANT, A. F. 1972. Corallinacées du Miocène de la plaine orientale Corse. *Rev. Micropal.* **15,** 115-124.

PEDLEY, H. M. 1978. A new lithostratigraphical and palaeoenvironmental interpretation of the coralline limestone formations (Miocene) of the Maltese Islands. *Overseas Geol. Miner. Resourc.* **54,** 17 pp.

PÉRÈS, J. M. 1967. The Mediterranean benthos. *Oceanogr. mar. Biol. Annu. Rev.* **5,** 449-533.

POIGNANT, A. F. 1979. Determination générique des corallinacées Mesozoïque et Cénozoïques. *Bull. Cent. Rech. Explor.-Prod. Elf-Aquitaine*, **3** (2), 757-765.

RAINERI, R. 1924. Alghe fossili mioceniche di Cirenaica. *Nuova Notarisia*, **35,** 5-23.

SAMSONOFF-ARUFFO, C. (1917*a*). Di alcune alghe calcaree provenienti dall'isola di Malta. Nota 1. *Atti Acad. Naz. Lincie Rc.* **11,** 564-569.

—— (1917*b*). Di alcune alghe calcaree provenienti dall'isola di Malta. Nota 11. Ibid. **11,** 610-616.

SOUYA, F. J. 1963. On the calcareous algae (Melobesioideae) of Gebel Ghana (Cairo-Suez road) with a local zonation and some possible correlations. *J. Paleont.* **37,** 1204-1216.

STENECK, R. S. 1978. Factors influencing the distribution of crustose coralline algae (Rhodophyta, corallinaceae) in the Damariscotta River Estuary, Maine. M.Sc. thesis, University of Maine.

WEBER VAN BOSSE, A. and FOSLIE, M. 1904. The corallinaceae of the Siboga—Expedition. *Siboga Exped. Monog.* **41.** London.

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SILURIAN CHEIRURID TRILOBITES FROM GOTLAND

by LARS RAMSKÖLD

ABSTRACT. Trilobites of the family Cheiruridae are described from the Silurian of Gotland, Sweden. Nineteen species (fourteen named formally, of which six are new) are assigned to seven genera (one new). The generic composition of the fauna shows affinities with East Baltic, Bohemian, British, and Canadian faunas. None of the species is known with certainty outside Gotland. The presence of six stratigraphically successive species of *Deiphon* is noteworthy, but no phylogenetic lineage can be established. *Radiurus* gen. nov. includes the type species *R. phlogoideus* sp. nov. from the Llandovery of Gotland, together with *Cheirurus estonicus* Männil, 1958. Other new species described are *Didrepanon gutnicum*, *Deiphon sphaericum*, *Deiphon brevispina*, *Deiphon ellipticum*, and *Deiphon snodensis*.

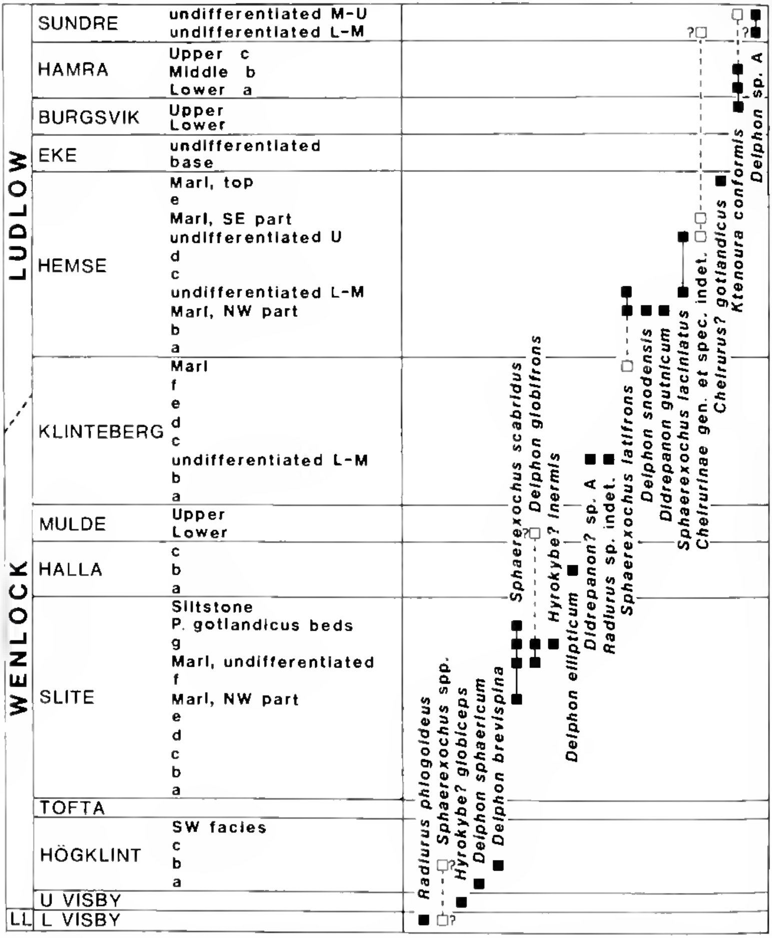
DURING the last decade, several Silurian trilobite faunas including cheirurids have been described from various parts of the world. Lane (1971) revised the British Cheiruridae, the Wenlock species of which were reviewed by Thomas (1981), and additional Scottish Llandovery material was studied by Clarkson and Howells (1981). Holloway (1980) described several North American species, Canadian Arctic faunas have been reviewed by Perry and Chatterton (1977, 1979), and Australian cheirurids have been described by Chatterton and Campbell (1980). A number of these authors made reference to or comparisons with Gotland species, although the basis for such comparisons was rather vague since the material has not been revised since the study by Lindström (1885). This paper, which comprises a study of all known Gotland material of the family, is intended to provide a modern basis for comparative studies. The excellent preservation of the Gotland material allows detailed studies to be made of most features of cheirurid morphology.

A cheirurid was first described from Gotland by Hisinger (1837), although he identified it as the Ordovician species *Pilekia speciosus* (Dalman, 1827). Angelin (1851, 1854) then included several Gotland cheirurids in his monographic study of Scandinavian trilobites, and these were revised by Lindström (1885) who also described additional Gotland species. Following Lindström's paper, very little additional work has been done on the group, although the same author included a cheirurid (now recognized as *Ktenoura conformis*) in his study of the visual system of trilobites (1901). Some Gotland species were mentioned by Warburg (1925) in comparative discussions of Ordovician species, and Whittard (1934) redescribed *Deiphon globifrons* Angelin. More recently, Lane (1971) revised the generic allocation of some Gotland cheirurids.

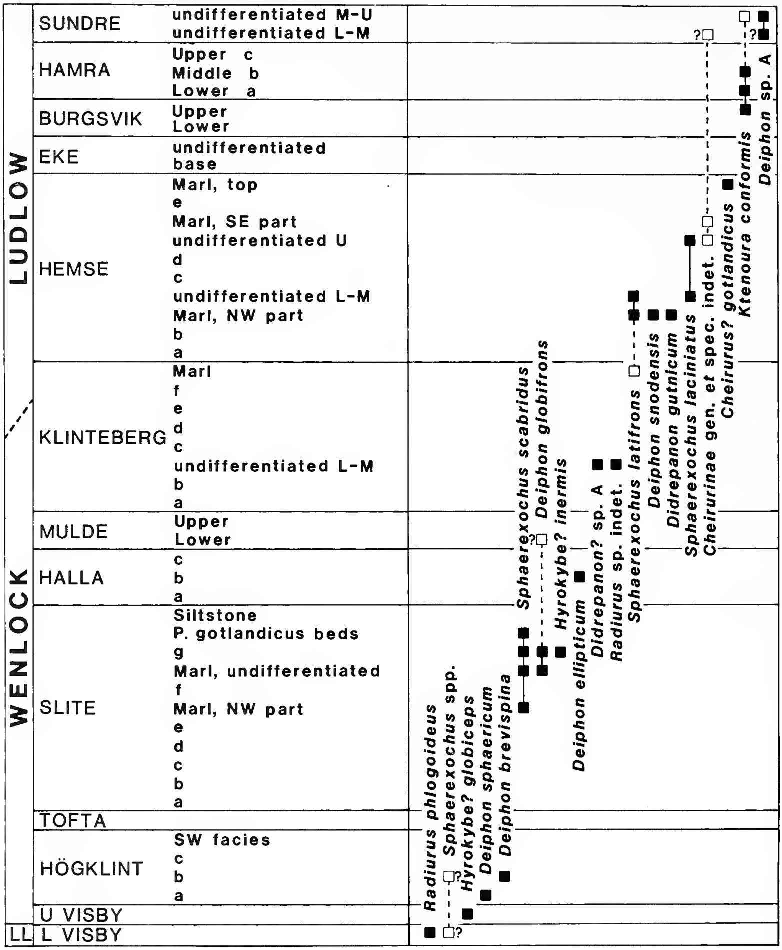
STRATIGRAPHY AND LOCALITIES

Numerous workers have described aspects of the stratigraphy of Gotland for well over one hundred years. Most accounts are in Swedish, but an excellent review in English is given by Laufeld (1974*a*, pp. 7–13). The classification used here (text-fig. 1) is essentially that of Hede (e.g. 1921, 1925). It should be emphasized that this classification is composite in the sense that some boundaries were based on biostratigraphical criteria and others on lithostratigraphical features, Hede's main intention being to distinguish mappable units. It is now understood (e.g. Martinsson 1967, fig. 2; Laufeld and Bassett 1981, pp. 26, 27) that most of Hede's units are not synchronous, but become younger from south-west to north-east along the outcrop. Laufeld and Jeppson (1976, fig. 4) made a useful attempt to describe the lateral variations within Hede's units, which in a graphic way illustrates the complexity of the stratigraphy.

[Palaeontology, Vol. 26, Part 1, 1983, pp. 175–210, pls. 19–28.]



TEXT-FIG 1. Occurrence of Cheiruridae in the different stratigraphical units of Gotland. Solid squares represent specimens assigned definitely to a taxon and open squares represent compared forms. A square with a question mark indicates that the horizon is uncertain. The stratigraphical column is a practical way of illustrating the distribution of the species within the mapped units, and is not necessarily a reflection of the chronological appearance and disappearance of various taxa. Diagram modified from Laufeld (1974*a*, p. 124).



TEXT-FIG. 1. Occurrence of Cheiruridae in the different stratigraphical units of Gotland. Solid squares represent specimens assigned definitely to a taxon and open squares represent compared forms. A square with a question mark indicates that the horizon is uncertain. The stratigraphical column is a practical way of illustrating the distribution of the species within the mapped units, and is not necessarily a reflection of the chronological appearance and disappearance of various taxa. Diagram modified from Laufeld (1974*a*, p. 124).

The system of reference localities introduced by Laufeld (1974*b*) has been followed here wherever possible. However, much of the material is from old museum collections with locality data that are too vague to permit this. Locality names followed by numbers are defined in Laufeld (1974*b*) and Larsson (1979). Three new localities are described here in conformity with this system.

GISLE 2, 632505 164979 (CJ 3446 2396) *c.* 5,800 m SSW of Fide church. Topographical map-sheet 5 I Hoburgen SO & 5 J Hemse SV. Geological map-sheet Aa 152 Burgsvik. Ditch exposure along the main road, immediately south-west of the intersection of the small road from the windmill *c.* 210 m south-west of point 8.76 south of Burgsvik. Hamra Beds, unit a.

MOJNER 3, 639959 167789 (CJ 6824 9609) *c.* 1,550 m east of Boge church. Topographical map sheet 6 J Roma NV & NO. Geological map-sheet Aa 169 Slite. Ditch exposure immediately north of the main road, *c.* 500 m south-west of point 3.70 south of Slite. The ditch runs in line with the west side of the open field south of the road. Slite Beds, Slite Marl.

VALBYTTE 4, 636921 164079 (CJ 2888 6865) *c.* 1,575 m south of Västergarn church. Topographical map-sheet 6 I Visby SO. Geological map-sheet Aa 160 Klintehamn. Shore exposure on the south-east shore of the small bight *c.* 100 m west of the main road, and *c.* 200 m west of the large barn (not marked on topographical map-sheet) east of the road. At low water levels there are exposures some metres outside the shore-line proper. Slite Beds, Slite Marl.

SYSTEMATIC PALAEONTOLOGY

The suprageneric classification is that of Lane (1971), except where otherwise stated. The terminology is essentially that of Harrington *et al.* (*in* Moore 1959, p. O117), and Lane (1971, p. 7). Lateral glabellar lobes and furrows are labelled as by Jaanusson (1956, p. 37). The term 'preoccipital depression' (in Deiphoninae) is explained in Holloway and Campbell (1974, pp. 418, 419). 'Eye socle' (in *Deiphon*) is the part of the fixed and free cheek between visual surface and subocular furrow. 'Width ratio fixed cheek : occipital ring' is the maximum distance between the axial furrow–posterior border furrow intersection and the lateral margin of the fixed cheek, divided by the transverse width of the occipital ring. 'Ankylosed articulating half-ring' is a purely descriptive term, with no phylogenetic or ontogenetic implications. In measurements and photographs a dorsal view indicates orientation with a vertical posterior margin of the occipital ring, or, in pygidia, a vertical anterior axial ring.

Specimen numbers with the prefix Ar belong to Naturhistoriska Riksmuséet, Stockholm. Specimens in the Type Collection of the Geological Survey of Sweden are prefixed SGU. Unless stated otherwise, the material illustrated in the plates comprises external exoskeletons. All specimens were painted with matt black opaque and coated lightly with ammonium chloride prior to photography. Dorsal views are shown unless stated otherwise in the plate explanations.

Family CHEIRURIDAE Hawle and Corda, 1847

Diagnosis. See Thomas 1981, p. 57.

Subfamily CHEIRURINAE Hawle and Corda, 1847

Genus CHEIRURUS Beyrich, 1845

Type species. *Cheirurus insignis* Beyrich, 1845, from the Liteň Formation (Wenlock), Svatý Jan pod Skalou, Czechoslovakia; subsequently designated by Barton 1916.

Diagnosis. See Lane 1971, p. 11.

Cheirurus? *gotlandicus* (Lindström, 1885)

Plate 19, figs. 1–10; text-fig. 2

v* 1885 *Chirurus gotlandicus* Lindström, p. 45, pl. 12, figs. 9, 10.
1971 *Cheirurus gotlandicus* Lindström; Lane, p. 11.

Lectotype. Selected here, Ar29785, internal mould of cranidium, Pl. 19, fig. 2; figured Lindström 1885, pl. 12, fig. 9; from Lau, probably uppermost Hemse Beds.

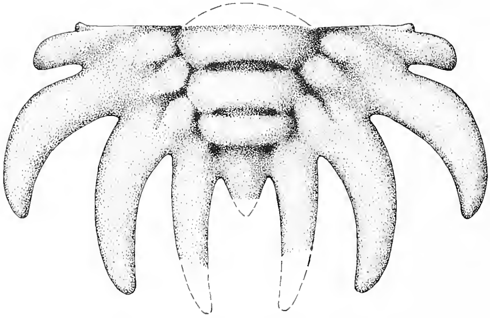
Material. All specimens appear to be from the uppermost Hemse Beds, Lau parish, mostly from Gannor 1–3 (= Lau Canal); in total five cranidia, one free cheek, one hypostome (paralectotype Ar29786), one thorax, and three pygidia.

Diagnosis. Glabella weakly convex, widening very gently anteriorly. S3 and S2 almost transverse, reaching more than two-fifths across glabella, connected medially by distinct depressions. Width ratio fixed cheek : occipital ring 0·9–1·0 : 1. Pygidium with a large anterolateral process, three pairs of spines, and a terminal mucronation.

Description. Frontal lobe slightly inflated, part of glabella behind rather flat (tr., sag.). L3 parallel-sided to widening slightly abaxially, L2 widening adaxially. Basal lobes subtriangular, circumscribed, inner angles separated by tongue-shaped posterior part of median lobe. S3 and S2 subparallel, directed very gently backwards. In some specimens S2 is shallow and constricted close to axial furrow (Pl. 19, fig. 7*a–c*). S1 narrow and occupied by S1 apodeme for two-thirds of its length, then running more obliquely backwards to meet occipital furrow. This is constricted abaxially with apodemal pit, medially curved in an arch, being narrow but distinct. Small median tubercle sometimes present on occipital ring. Axial furrow with deep anterior pit opposite S3. Preglabellar furrow absent on median third of frontal lobe.

Fixed cheek narrow, barely as wide as occipital ring. Free cheek small, subtriangular. Posterior cephalic margin convex backwards. Posterior border very narrow (exsag.) adaxially, a little wider lateral to fulcrum. Genal spine short. Posterior border furrow very distinct, constricted adaxially, shallowing laterally. Lateral border narrow (tr.), equal in width to posterior border. Lateral border furrow shallow, less distinct than posterior border furrow.

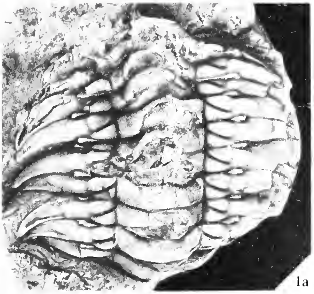
Eye fairly small, extending from opposite slightly posterior to S3 to opposite S2. Palpebral rim narrow, convex. Palpebral furrow distinct along palpebral rim and just posterior to eye. Posterior branch of facial suture



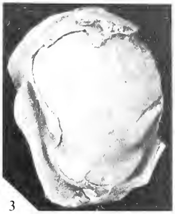
TEXT-FIG. 2. *Cheirurus*? *gotlandicus* (Lindström, 1885). Reconstruction of pygidium, based on Ar29792, Ar29793, and Ar30805. × 3.

EXPLANATION OF PLATE 19

Figs. 1–10. *Cheirurus*? *gotlandicus* (Lindström, 1885). Hemse Beds, uppermost part. Lau Canal (1, 3–9), Lau (2), the beach at Lau fishing harbour (10). 1*a*, *b*, Ar29796, thorax, dorsal view and enlargement of pleurae, *a* × 3, *b* × 5. 2, lectotype Ar29785, cranidium, internal mould, figured Lindström 1885, pl. 12, fig. 9, × 2. 3. Ar29786, hypostome, mainly internal mould, figured Lindström 1885, pl. 12, fig. 10, × 3. 4, Ar30805, small pygidium, ventral view, × 6. 5, Ar29793, partial pygidium, × 2. 6, Ar29791, cranidium showing pathological? deformation of right cheek, × 3. 7*a–c*, Ar29794, cranidium, mainly internal mould, dorsal, oblique dorsal, and oblique anterolateral views, *a*, *b* × 3, *c* × 2. 8, Ar29795, cranidium, enlargement showing granulation, × 7. 9*a*, *b*, Ar29790, cranidium and displaced free cheek, continuous S2 due to distortion, *a*, dorsal view, × 3, *b*, free cheek, × 5. 10, Ar29792, pygidium, internal mould, × 2.


1a


2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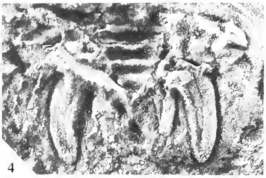
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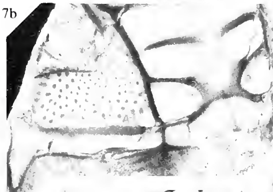
5


7b

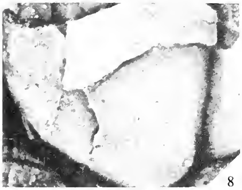

9b


6


1b


7c


7a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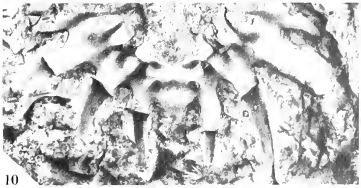
9a


10

RAMSKÖLD, *Cheirurus*?

turns sharply backwards just after meeting lateral border. Frontal lobe of glabella with evenly spaced, rather large granules (Pl. 19, fig. 8). Lateral lobes with no visible granulation. Lateral borders very finely and densely granulated. Field of cheek, including lateral border furrow, finely and densely pitted.

Rostral plate unknown. Hypostome with middle body fairly convex (tr., sag.), narrowing backwards. Middle furrow wide and shallow, continuous across middle body, very shallow medially. Anterior border furrow wide and shallow laterally. Anterior wing large. Lateral border narrow and convex (tr.), narrowest opposite posterior lobe of middle body. Shoulder rather pronounced, with posterior end marked by incurving of lateral margin. Lateral border furrow shallowing slightly posteriorly, but still distinct when merging with equally distinct posterior border furrow. Posterior border not preserved. Middle body with very fine and dense granulation, as on borders. Middle body with numerous pits dorsally.

Thorax of at least ten (probably eleven) segments. Axis wide, just slightly narrower (tr.) than pleural portions. On each segment abaxial to the deep pleural furrow is a rounded swelling, lateral to this is an indistinct median ridge with three to four equally spaced, faint tubercles.

Pygidium incompletely known. Axis narrowing backwards, composed of three rings and a terminal piece. A pair of pits is present laterally in each of the inter-ring furrows. Anterior pleural furrow deep, middle pleural furrow firmly impressed to indistinct. Interpleural furrows deep, widening and shallowing distally, reaching pygidial margin. Axial furrow distinct adjacent to anterior and middle rings, indistinct adjacent to posterior ring. Anterolateral process large, elongate transversely, end blunt. Anterior pair of spines long, hook-like, curving almost through 90°; middle pair equal in size to anterior one, curving backwards to an exsagittal direction; both pairs with blunt ends. Posterior pair almost exsagittally directed, possibly converging slightly backwards, more slender than the other spines, length not known. Terminal mucronation short and wide. Doublure narrow, with embayment anterior to terminal mucronation. Surface of pygidium, including doublure, covered with very dense and fine granulation.

Discussion. This species differs in several respects from other species of *Cheirurus*. The shape of S3 and S2 and the presence of a large anterolateral process on the pygidium are features in which it shows some similarity to *Didrepanon*, but it is otherwise very different from that genus. The cephalic features seem to represent a step towards the Lower Devonian Cheirurinae (e.g. *Crotalocephalus*) which have continuous S3 and S2 furrows and a rather narrow (tr.) cephalon. However, the pygidium with its large anterolateral process is different from all known Cheirurinae, and the systematic position of *C.*? *gotlandicus* is regarded here as uncertain.

Genus DIDREPANON Lane, 1971

Type species. Didrepanon falcatum Lane, 1971, from the upper Silurian (?lower Ludlow), Sedgley, West Midlands, Great Britain; by original designation.

Diagnosis. See Lane 1971, p. 21.

Didrepanon gutnicum sp. nov.

Plate 20, figs. 1–9; Plate 21, figs. 4–6; text-fig. 3

Name. Latin *gutnicus*, meaning inhabitant of Gotland.

Holotype. Ar51328, a pygidium, Pl. 21, fig. 4*a*, *b*, from Snoder 2; Hemse Marl, north-west part, Hemse Beds.

EXPLANATION OF PLATE 20

Figs. 1–9. *Didrepanon gutnicum* sp. nov. Hemse Marl, north-west part, Hemse Beds. Petesvik (5, 9), Snoder 2 (1, 2, 4, 6–8), Visne myr (3). 1, paratype Ar51293, partial left thoracic pleura, ×3. 2, paratype Ar51292, small hypostome, ×5. 3*a–c*, Ar29789, partial cranidium, dorsal view, enlargement of cheek, and enlargement of glabella, *a* ×3, *b*, *c* ×7. 4, paratype Ar51291, partial free cheek, ventral view showing doublure, ×3. 5, Ar29695a, latex cast of ventrally exposed cranidium, ×2. 6, paratype Ar51330, free cheek, ×3. 7*a*, *b*, paratype Ar51331, partial cranidium, dorsal view and enlargement of granulation, *a* ×2, *b* ×6. 8*a–c*, paratype Ar51329, cranidium, dorsal, lateral, and oblique anterolateral views, all ×3. 9, Ar29695b, partial pygidium, ×2.

PLATE 20


1

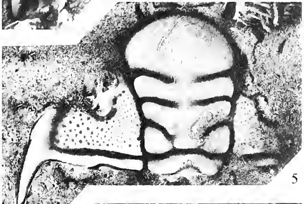

2


3b


3c

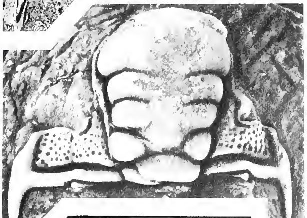

3a


4


5


6


7b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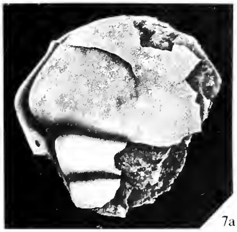
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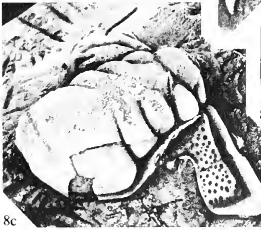
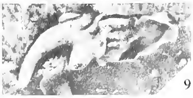

8c


8b


9

RAMSKÖLD, *Didrepanon*

Paratypes. From the type locality, Ar51290–51293, Ar51329–51336; from Snoder 1, Ar51287–51289. Other material referred to this species, although poorly preserved: Fardhem parish—drainage ditch in Visne myr (may include Gerete 1), Ar29789. Hablingbo parish—Petesvik, Ar29695a–b; Hablingbo kanal, Ar29784; Nissevik, Ar29726. All material is from the Hemse Marl, north-west part, Hemse Beds.

Diagnosis. Cheeks wide; width ratio fixed cheek : occipital ring 1·5 : 1, pygidium with very curved, widely separated, blunt spines.

Description. Cephalon short (sag.) and wide, length to width ratio about 1 : 1·9. L3 widening slightly abaxially, L2 widening adaxially. Basal lobes subtriangular, inner angles separated by tongue-shaped posterior part of median lobe. S3 and S2 reaching more than two-fifths across glabella, connected medially by wide, shallow depressions. S1 deep and narrow to half its length, then shallows and runs more obliquely backwards to meet occipital furrow. This is deep abaxially for the same distance as S1, then shallowing but still fairly deep and narrow, running in an arch medially. Axial furrow quite narrow and distinct, with deep anterior pit. Preglabellar furrow absent on median one-third of frontal lobe.

Fixed cheek wide (tr.) and short, broadening a little laterally. Free cheek subtriangular. Posterior border convex, narrow (exsag.), slightly wider lateral to fulcrum. Posterior border furrow slightly constricted adaxially, widening and shallowing laterally before narrowing slightly close to genal angle. Genal spine as long as length (exsag.) of fixed cheek behind eye, pointed. Lateral border twice as wide as posterior border, defined by fairly wide and shallow border furrow which narrows and deepens forwards. Doublure narrow, flat, smooth, flexed dorsally.

Eye large, extending from opposite mid L3 to almost opposite S1 (left eyes in Pl. 20, figs. 3*a* and 8*a* posteriorly dislocated due to fractures). Eye socle low, well defined by subocular furrow. Palpebral furrow distinct along palpebral rim and posterior to eye. Field of cheek of low convexity, densely pitted. Frontal lobe of glabella with granules of varying size with microgranulation in between. Granulation posterior to frontal lobe very sparse. Lateral border and genal spine very densely and finely granulated. Muscle attachements on frontal lobe visible only on internal moulds, consisting of two anteriorly diverging rows of pits with scattered pits between.

Rostral plate unknown. Hypostome lacking anterior border furrow medially. Middle furrow with deeper distal portions reaching less than one-quarter across middle body, very shallow medially. Anterior wing with indistinct median furrow. Lateral border furrow distinct, deeper than posterior border furrow. Lateral border gently convex (tr.), narrow, shoulder opposite mid length of anterior lobe of middle body. Posterior border short (sag.). Lateral and posterior margins meet at about 110°, posterior margin straight. Entire hypostome covered with microgranulation, slightly coarser on lateral borders. Middle body with numerous scattered, irregularly formed, shallow pits. Dorsal surface of middle body with equally numerous fairly large pits, seemingly not corresponding to any structures on ventral surface.

Thorax known only from proximal pleural fragments. In shape they are typical of the Cheirurinae.

Pygidium known mainly from ventral side. Axis tapering backwards, composed of three rings and a terminal piece. Anterior ring short medially, long (exsag.) laterally with swellings directed forwards. Middle and posterior rings progressively smaller, posterior ring poorly defined posterolaterally. Anterior inter-ring furrow with a distinct ankylosed articulating half-ring, middle inter-ring furrow with a similar, but smaller and less distinct, structure. Axial furrow deep adjacent to anterior ring and distinct opposite middle ring. Four pairs of apodemes present, corresponding to deep pits in the axial furrows. Anterior pleural furrow deep, middle furrow less distinct. Interpleural furrows deep adaxially, faint close to pygidial margin. Anterior and middle pairs of spines long, subequal in size, curving posterolaterally, converging distally; middle pair more gently curved. Both pairs

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EXPLANATION OF PLATE 21

Figs. 1–3. *Didrepanon*? sp. A. Klinteberg Beds, Klinteberget. 1, Ar46983, cranidium, internal mould, figured Hisinger 1837, pl. 39, fig. 9, refigured Angelin 1854, pl. 39, fig. 14, × 1. 2, SGU 1352, cranidium internal mould, × 1·5. 3, Ar29803, glabella, mainly internal mould, × 2.

Figs. 4–6. *Didrepanon gutnicum* sp. nov. Hemse Marl, north-west part, Hemse Beds. Snoder 1 (6), Snoder 2 (4, 5). 4*a*, *b*, holotype Ar51328, pygidium, ventral and posteroventral views, × 2. 5, paratype Ar51288, pygidium, ventral view, × 2. 6, paratype Ar51287, large hypostome, × 2.

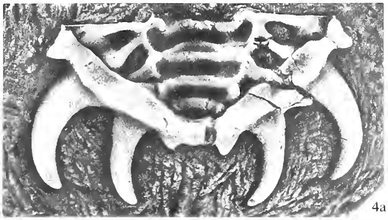
Fig. 7*a–c*. *Ktenoura conformis* (Angelin, 1854). Hamra Beds, Geistermyr kanal. Ar29788, partial exoskeleton, *a*, dorsal view, note fragmentary hypostome and rostral plate on right pleurae, *b*, anterolateral view, *c*, enlargement of cheek, *a*, *b* × 2·5, *c* × 7.

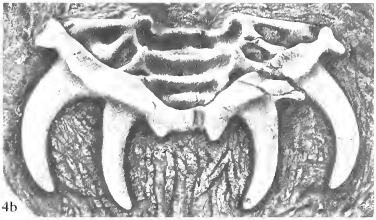
PLATE 21


1


2


3


4a


4b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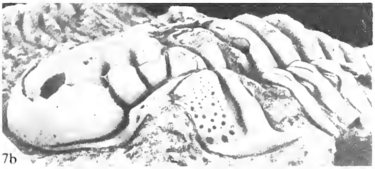
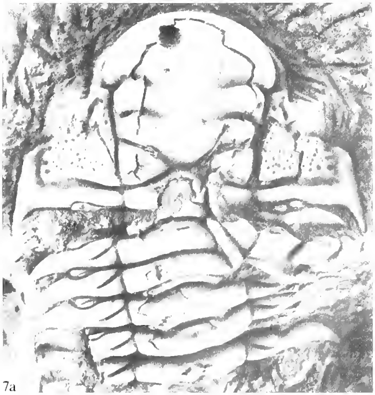

7b

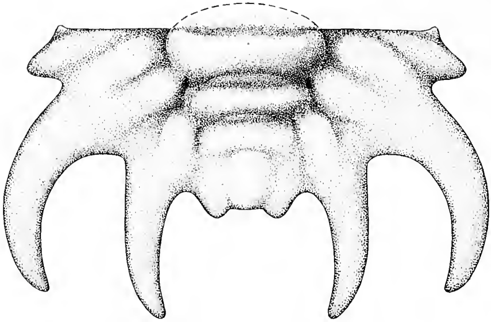

6


7c


7a

RAMSKÖLD, *Didrepanon*, *Ktenoura*

curve gently upwards distally, and are widely separated, with furcations wide and rounded proximally. Posterior pair of spines short, blunt, subtriangular. Anterolateral process short, subtriangular, slightly posterior to transversely directed, separated from anterior pleural ridge by an oblique, shallow furrow. Doublure with a posteromedian semicircular embayment. Ventral surface of spines and outer part of doublure finely and densely granulated. Dorsal surface with dense granulation on spines and borders, less dense on pleural ridges.



TEXT-FIG. 3. *Didrepanon gutnicum* sp. nov. Reconstruction of pygidium, based mainly on Ar51288. × 3.

Discussion. D. gutnicum differs from the type species in its larger size, smaller anterolateral processes, distinct ankylosed articulating half-ring, and much more widely spaced, more curved spines. *D. quenstedti* (Barrande, 1846) from the lower Ludlow of Bohemia has S3 and S2 more firmly impressed medially, a less curved posterior branch of facial suture, narrower lateral borders in the cephalon, and more slender, pointed, and less curved pygidial spines. (Cephalic features as figured by Přibyl and Vaněk 1964, pl. 1, fig. 7.)

Didrepanon? sp. A

Plate 21, figs. 1–3

v. 1837 *Calymene*? *speciosus* Dalm.; Hisinger, p. 6, pl. 39, fig. 9, *non* Dalman 1827
v. 1854 *Chirurus speciosus* His. [*sic*]; Angelin, p. 78, pl. 39, fig. 14, *non* Dalman 1827.
v. *non*. 1885 *Chirurus speciosus* His.; Lindström, pl. 12, fig. 11 [= *Radiurus phlogoideus* sp. nov.].
1971 *Didrepanon*? *speciosum* (Hisinger, 1837) Lane, p. 21.

Material. Hisinger (1837) and Angelin (1854) figured the same cranidium, Ar46983; refigured here Pl. 21, fig. 1. As noted by Lindström (1885, p. 44) this specimen is not related to *Calymene*? *speciosus* Dalman, 1827. Three more cranidia are known, Ar46982, Ar 29803, SGU 1352. All specimens stated to be from Klinteberget, Klinteberg Beds. Some similar specimens were collected in the 1840s by Marklin and labelled 'Burgsvik'. The lithology, however, which is not otherwise found in the Burgsvik area, is similar to that of the Klinteberget specimens, and suggests that the labelling is a mistake. These specimens are not figured, but would add no significant details.

Discussion. The course of S3 and S2 together with the general shape of the specimens suggest that this species belongs to *Didrepanon*. The only pygidium recorded from the Klinteberg Beds at Klinteberget belongs to *Radiurus* (see p. 190), but it is unlikely that the material referred here to *D*.? sp. A is related to the specimen. *D*.? sp. A is distinguished from *D. gutnicum* by its shorter and wider glabella and narrower cheek, giving a width ratio fixed cheek : occipital ring of only 1·2 : 1, as compared to 1·5 : 1. It is also characterized by the incurved anterolateral margin of the frontal lobe and basal lobes that are better defined adaxially. *D.*? sp. A is very similar to *D.* sp. A of Lane (1971, pl. 7, fig. 22) from the British Wenlock. It seems to differ only in having broader and deeper lateral glabellar and axial furrows. The absence of pygidia, however, hampers further comparison.

Genus KTENOURA Lane, 1971

Type species. Ktenoura retrospinosa Lane, 1971; from the Much Wenlock Limestone Formation and Coalbrookdale Formation, Dudley, West Midlands, Great Britain; by original designation.

Diagnosis. See Lane 1971, p. 31.

Ktenoura conformis (Angelin, 1854)

Plate 21, fig. 7; Plate 22, figs. 1–16

v. 1851 Angelin, pl. 21, fig. 3 [illustration only, without name].
v.* 1854 *Chirurus conformis* Angelin, pp. 32, 79, pl. 39, fig. 15*a*.
v.1885 *Chirurus conformis* Ang.; Lindström, p. 45, pl. 13, figs. 13, 14.
v.1901 *Chirurus speciosus* His.; Lindström, p. 50, pl. 4, fig. 1.
?1933 *Cheirurus bicuspidatus* Bouček, pp. 5, 6, pl. 1, figs. 1–6.

Lectotype. Selected here, Ar29787, a fragmentary cranidium from Hamra Beds at Hoburgen, Pl. 22, fig. 1; figured Lindström 1885, and stated by him to be the original of Angelin 1851 and 1854. It is clear from Angelin's description that he had access to more material (which cannot be identified); the specimen he figured is therefore chosen as lectotype.

Additional material. Fragmentary material is common in the lower Hamra Beds. Localities: Grötlingbo parish—Uddvide stapelhage; east of Sallmunds allmänning; south of the south house of Sallmunds. Öja parish—Gisle 2. Sundre parish—Hoburgen 2; Kättelviken 1; Majstre 1; road ESE of the lighthouse at Hoburgen; west side of the southernmost point at Hoburgen. Vamlingbo parish—Geistermyrs kanal; Grumpevik; Snäckvik; Vallmyrs kanal. One specimen is from the Burgsvik oolite, Burgsvik Beds, from an unknown locality.

Diagnosis. Posterior border furrow wide, shallow, eye opposite L3 and S2, width ratio fixed cheek : occipital ring 0·9–1·0 : 1. Pygidium with ankylosed articulating half-ring in anterior inter-ring furrow, pleural furrows on both anterior and middle pleural ridges, and three pairs of spines reaching progressively further back.

Description. Frontal lobe strongly vaulted, middle and posterior part of glabella convex (tr.) and gently convex to flat (sag.). L3 widening very gently abaxially, L2 widening adaxially. Basal lobes subtriangular, circumscribed. S3 and S2 subparallel, curving slightly backwards, reaching one-third to a little more across glabella. S1 very deep and narrow from close to axial furrow to two-fifths its length, where it shallows and runs more obliquely backwards to meet the occipital furrow; this is constricted abaxially behind S1, then turns forwards in an arch, being wider and shallower between the inner angles of basal lobes. Occipital ring with a small median tubercle (Pl. 22, fig. 2). Axial furrow deepest where met by S3, shallowing backwards. Preglabellar furrow absent on median one-third of frontal lobe.

Cheeks subtriangular, gently convex (tr., exsag.). Posterior cephalic margin straight. Posterior border narrow (exsag.) adaxially, 1·5 times as wide lateral to fulcrum. Posterior border furrow constricted adaxially, curving laterally and slightly forwards while becoming broader and shallower, narrowing close to genal angle. Genal spine pointed, equal in length to sagittal length of occipital ring. Lateral border wider than posterior border, narrowing slightly forwards with increasing convexity. Lateral border furrow wide near genal angle, narrowing anteriorly.

Eye small, extending from opposite S3 to slightly behind S2. Palpebral rim strongly convex, palpebral furrow distinct. Field of cheek coarsely pitted, pits larger and more widely spaced closer to lateral border furrow, which is itself pitted. Genal spines, lateral borders, posterior edge of posterior border, and frontal lobe close to anterior margin very finely and densely granulated; larger, widely spaced granules on entire glabella, more dense on frontal lobe. On well-preserved specimens two diverging rows of pits can be seen on frontal lobe, as well as numerous pore-openings (Pl. 22, fig. 10).

Rostral plate (Pl. 21, fig. 7*a*) wide (tr.), very short. Hypostome with middle furrow deep abaxially, very shallow to indistinct medially. Anterior border furrow distinct, with anterior border very short medially. Lateral border furrows wide and deep anteriorly, shallower behind middle furrows, continuing as a fairly deep posterior border furrow. Posterior margin straight. Entire surface very finely and densely granulated, granules smaller and more numerous posteriorly. Irregular, shallow pits of varying size are scattered over the middle body. Interior surface of middle body with coarse pits, larger anteriorly.

Number of thoracic segments unknown. First segment with narrower (tr.) pleurae than succeeding segments. Pleurae with a few median tubercles distally; anterior and posterior edges of pleurae lateral to fulcra densely granulated.

Pygidium with three rings and a terminal piece in axis. Inter-ring furrows long medially, constricted and deep abaxially; anterior furrow with a very distinct ankylosed articulating half-ring. Axial furrow shallow but distinct adjacent to anterior ring, very weak to absent posteriorly. Anterior and middle pleural ridges with oblique pleural furrows, the anterior one longer and deeper. Interpleural furrows very deep adaxially, shallowing distally, not reaching pygidial margin. Anterior pair of spines stoutest and longest, spine separated from well-developed anterolateral process by a marginal notch and a distinct, oblique furrow. Middle and posterior pairs of spines subequally stout and long, posterior pair reaching furthest back. Doublure with posteromedian embayment. Surface of pygidium, including doublure, finely granulated, densest on the spines.

Discussion. The range of variation in pygidial morphology is great in this species. However, even pygidia from the same locality exhibit these differences, which are therefore considered to be intraspecific. A few poorly preserved cranidia from Holmhällar 1, Hamra parish, might also belong to this species, which would extend its vertical distribution into the Sundre Beds. *K. conformis* differs from the type species in having longer (exsag.) fixed cheeks with more anteriorly situated eyes, wider posterior border furrows, a pygidium with a smaller anterior pair of spines, the middle and posterior pair reaching progressively further back than the anterior pair, longer (sag.) inter-ring furrows with an ankylosed articulating half-ring in the anterior one, and a distinct furrow on the middle pleural ridge. *K. bicuspidata* (Bouček, 1933) from the upper Wenlock–Ludlow Kopanina Beds of Bohemia is apparently closely related to *K. conformis*, but seems to differ in the pygidium by having more radially disposed spines, less distinct apodemal pits, and by lacking a middle pleural furrow. However, the figured material is rather poorly preserved, and it is possible that it is conspecific with the Gotland species.

Genus RADIURUS gen. nov.

Name. Latin *radius*, ray, radial, and greek *oura*, tail; referring to the radially disposed pygidial spines.

Type species. Radiurus phlogoideus sp. nov; from the Lower Visby Marl (uppermost Llandovery), Norderstrand, Visby, Gotland.

Other species. Cheirurus estonicus Männil, 1958; *R.* sp. (see below); *Cheirurus*? sp. of Norford 1981 (pygidium only).

EXPLANATION OF PLATE 22

Figs. 1–16. *Ktenoura conformis* (Angelin, 1854). Hamra Beds. 1, lectotype Ar29787, cranidium, Hoburgen, figured Angelin 1851, pl. 21, fig. 3; pl. 39, fig. 15, refigured Lindström 1885, pl. 13, figs. 13, 14, × 3. 2, Ar29741, glabella, Sundre, × 3. 3, Ar29703, partial cephalon, Uddvide stapelhage, × 3. 4, Ar29707, cranidium with two thoracic segments, Uddvide stapelhage, × 3. 5, Ar51299, free cheek, Kättelviken 1, × 5. 6*a*, *b*, SGU 1356, pygidium, dorsal view and enlargement of granulation, west side of southernmost point at Hoburgen, *a* × 3, *b* × 5. 7, Ar29731, pygidium, Vallmyrs kanal, × 3. 8, SGU 1357, hypostome, road ESE of the lighthouse at Hoburgen, × 3. 9, Ar51337, small hypostome, Hoburgen 2, × 4. 10, Ar51326, partial cranidium showing granulation, fine pore-openings and one of the two diverging rows of pits, Kättelviken 1, × 4. 11, Ar29696, hypostome, Uddvide stapelhage, × 2·5. 12, Ar29799, ventral view of pygidium, Vallmyrs kanal, × 3. 13, Ar29747, pygidium showing well-developed middle pleural furrows, Uddvide stapelhage, × 3. 14, Ar46973, hypostome, internal mould, Grumpevik, × 3. 15, Ar51301, ventral view of pygidium, Kättelviken 1, × 3. 16, SGU 1358, pygidium, Hoburgen, × 3.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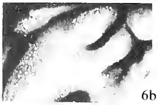
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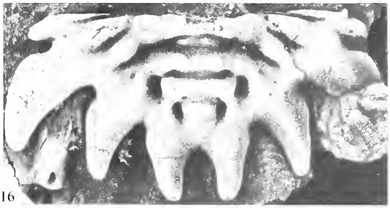
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RAMSKÖLD, *Ktenoura*

Diagnosis. Cheirurinae with entire anterior border and preglabellar furrow. S3 and S2 reaching one-third to three-eighths across glabella. Pygidium with three pairs of radially disposed, equally spaced spines of subequal size.

Remarks. *Radiurus* is the only Silurian Cheirurinae having a complete anterior border and preglabellar furrow. It is also easily distinguished by its pygidial features. Lane (1971, pp. 76–79) saw *R. estonicus* as being close to an ancestor of several Silurian and Devonian Cheirurinae. The undifferentiated pygidium in *Radiurus* is certainly a likely morphological feature for such an ancestor, but to deal further with that problem is beyond the scope of this study.

Radiurus phlogoideus sp. nov.

Plate 23, figs. 2–5; text-fig. 4

v. 1885 *Chirurus speciosus* His.; Lindström, p. 44 [*pars*], pl. 12, fig. 11, *non* Hisinger 1837.

Name. Greek *phlogos*, flame; referring to the shape of the pygidial spines.

Holotype. Ar29779, a cranidium, from the Lower Visby Marl, Norderstrand, Visby; Pl. 23, figs. 2*a*, *b*.

Paratypes. Ar29742–29744, Ar29759–29778, Ar29780–29781; cranidia, seven hypostomes and one pygidium, all from the type locality.

Diagnosis. Glabella strongly convex. Anterior border entire, short. Preglabellar furrow entire, distinct. Width ratio fixed cheek : occipital ring 1·3 : 1. Pygidium with spines closely spaced, at least middle pair pointed, axis with a pair of tubercles on each ring, ankylosed articulating half-ring present in anterior inter-ring furrow.

Description. Frontal lobe strongly convex, forming widest part of glabella. Portion of glabella behind frontal lobe gently convex (sag.), in large specimens less convex (sag., tr.). L3 parallel-sided to widening slightly abaxially. Basal lobes slightly inflated independently, rather poorly delimited medially on external moulds, circumscribed on internal moulds. S3 and S2 deep, narrow (exsag.). S1 deep and constricted from axial furrow to half its length. Occipital furrow deep and narrow behind S1, then shallower in an arch medially. Occipital ring with a very small median tubercle. Axial furrow rather narrow, with anterior pit opposite S3. Preglabellar furrow unbroken, but shallower medially. Anterior border short and convex (sag.), a little longer anterolaterally (Pl. 23, fig. 6).

Posterior portion of fixed cheek broadening abaxially. Posterior border short (exsag.) adaxially, broadening lateral to fulcrum. Posterior border furrow narrow, distinct, shallower close to genal angle. Genal spine fairly long, pointed, directed backwards and slightly outwards. Lateral border known from fixed cheek only, wider than posterior border, narrowing anteriorly. Lateral border furrow narrow, distinct.

EXPLANATION OF PLATE 23

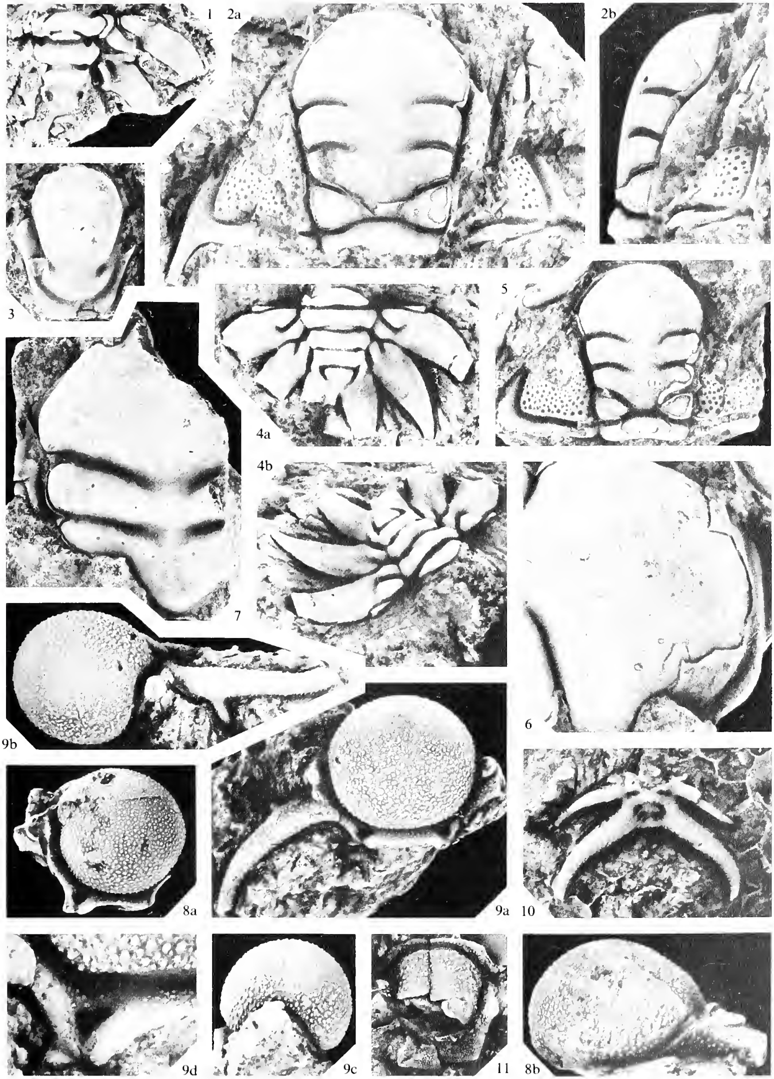
Fig. 1. *Radiurus* sp. indet. Ar29804, pygidium, internal mould, Klinteberg Beds, Klinteberget, × 3.

Figs. 2–6. *Radiurus phlogoideus* gen. et sp. nov. Lower Visby Beds, Norderstrand. 2*a*, *b*, holotype Ar29779, cranidium, internal mould, dorsal and lateral views, × 3. 3, paratype Ar29775, hypostome, internal mould, × 3. 4*a*, *b*, paratype Ar29766, pygidium, dorsal and oblique anterolateral views, × 4. 5, paratype Ar29780, cranidium, mainly internal mould, × 3. 6, paratype Ar29764, cranidium, mainly internal mould, showing preglabellar furrow and anterior border, × 5.

Fig. 7. Cheirurinae gen. et. sp. indet. Ar29724, partial cranidium, internal mould, ?Sundre Beds, Klev, Hoburgen, × 2.

Figs. 8–10. *Deiphon sphaericum* sp. nov. Possibly Högklint Beds. Visby–Lickershamn (8, 9), Lickershamn (10). 8*a*, *b*, paratype Ar6165, partial cephalon, oblique dorsal and anterolateral views, *a* × 4, *b* × 6. 9*a–d*, holotype Ar6162, cranidium, dorsal, anterolateral, lateral views, and enlargement showing L1 area, *a–c* × 4, *d* × 10. 10, paratype Ar6153, pygidium, figured Whittard 1934, pl. 15, fig. 12, × 4.

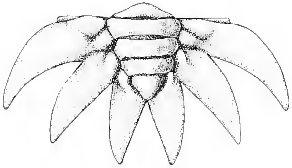
Fig. 11. *Deiphon brevispina*? sp. nov. Ar51269, hypostome, Högklint Beds, unit b, dump at Visby harbour, × 4.



RAMSKÖLD, *Radiurus* gen. nov., *Deiphon*

Eye extending from opposite mid L3 to opposite mid L2. Palpebral furrow distinct posteriorly, less so anteriorly. Anterior branch of facial suture curves around frontal lobe close to axial and preglabellar furrows. Posterior branch runs from eye straight to gently convex forwards in a slightly anterior direction to meet lateral border opposite S2, then curves backwards across border.

Surface sculpture on entire glabella consists of rather widely spaced granules. Cheek excluding borders densely pitted, pits larger laterally and also present in lateral border furrow. Anterior and lateral borders and genal spines covered with microgranulation.



TEXT-FIG. 4. *Radiurus phlogoideus* gen. et sp. nov. Reconstruction of pygidium, based on Ar29766. ×4.

Rostral plate unknown. Hypostome with middle furrow deep and wide laterally, distinct one-quarter to almost one-third distance across middle body, very shallow medially. Anterior border furrow absent medially. Lateral border furrows deep and distinct, continuing around posterior lobe as an equally distinct posterior border furrow. Lateral borders with distinct shoulders posterior to antennular notches, narrowing backwards. Posterior border convex (sag.), slightly broader than lateral borders. Posterior margin straight. Middle body with granulation similar to that of glabella. Borders with microgranulation. Dorsal surface of middle body with numerous pits.

Thorax of unknown number of segments. Axial ring with elevated middle portion, making it subtriangular in section. Segments otherwise typical for subfamily.

Pygidium with axis of three rings and a terminal piece. The rings are equally long (sag.), with a pair of tubercles on each, less distinct on anterior ring. Terminal piece posteriorly reaching median furcation. Anterior inter-ring furrow with a distinct, short, ankylosed articulating half-ring. Middle and posterior inter-ring furrows short (sag.), with lateral apodemal pits. Axial furrow distinct adjacent to anterior and middle rings, weak adjacent to posterior ring. Anterior and middle pleural ridges with deep and narrow pleural furrows. Interpleural furrows very deep proximally, shallowing distally, but still firmly impressed when reaching pygidial margin. At least middle pair of spines pointed, posterior pair probably slightly shorter than anterior and middle pair. Spines separated by equally sized, pointed furcations. Surface sculpture of microgranulation.

Discussion. This species differs from *R. estonicus* (Männil, 1958), from the upper Llandovery of Estonia, in having a more expanding-forwards glabella, eyes placed closer to axial furrows, longer (tr.) S3 and S2, and closer spaced, more curved pygidial spines. The terminal shape of the spines is not considered a difference since Männil's reconstruction of the pygidium is based on a specimen with all terminal parts apparently lost, and the Gotland specimen has only one complete spine. The hypostome figured by Lindström (1885) as '*Chirurus speciosus* His.' is typical of *R. phlogoideus* and is from the type locality.

Radiurus sp. indet.

Plate 23, fig. 1

Material. Ar29804, a fragmentary pygidium, stated to be from Klinteberget, Klinteberg Beds.

Discussion. A comparison of this single specimen with *R. phlogoideus* is difficult because the only known pygidium of the latter has the exoskeleton preserved, whereas the Klinteberget specimen is an internal mould. However, *R.* sp. indet. has more widely spaced spines, in particular the posterior pair is widely separated. Apart from this, all major features of *R. phlogoideus* seem to be present, including the pairs of tubercles on the axial rings, so that an assignment to *Radiurus* can be confirmed. Norford (1981, pl. 9, fig. 7) figured a very similar pygidium as *Cheirurus*? sp. His specimen, from the Llandovery of Canada, differs from the Klinteberget specimen by its smaller middle and posterior axial rings and less inflated pleural ridges. The figured cephalon associated by Norford with this pygidium does not, however, fit the definition of *Radiurus*, and may in fact not be related to the pygidium.

CHEIRURINAE gen. et sp. indet.

Plate 23, fig. 7

Material. Ar29724–29725, a fragmentary cranidium, from Klev, north of Hoburgen, Sundre parish, probably Sundre Beds.

Discussion. This large specimen shows similarities both to *Didrepanon* and *Cheirurus*? *gotlandicus* in having the S3 and S2 connected medially by depressions. Two other, indeterminate cranidia (Ar29727 from Linde klint, south side, Linde parish, Hemse Beds, upper part; and Ar29802 from Alva parish, Hemse Marl, south-east part, Hemse Beds) also exhibit the same features. However, the relationships of these specimens cannot be evaluated until further material is available.

Subfamily DEIPHONINAE Raymond, 1913

Diagnosis. See Holloway 1980, p. 39, and Thomas 1981, p. 60.

Genus DEIPHON Barrande, 1850

Type species. Deiphon Forbesi Barrande, 1850, from the Liteň Formation (upper Wenlock), Lištice, near Beroun, Czechoslovakia; by original designation.

Diagnosis. Cheeks spinose, curving outwards, backwards, and downwards, with upturned tips. Ventrally on fixed cheek there is a small spine close to facial suture. Free cheek small, with doublure as large as dorsal area. Eye small, surrounded by convex rim, placed close to axial furrow on anterior part of spinose cheek. Thorax of nine segments, fulcra close to axial furrows and spinose pleurae not in contact with each other. Pygidium with axis of four rings, the small posterior two set in an oval depression. Two pairs of lateral spines, the posterior of which is the stouter, running transversely or obliquely backwards, distally recurved; and a posterior pair of short, ventrally directed spines.

Remarks. The diagnosis given by Lane (1971, p. 59) has been modified mainly to allow for the presence of the third pair of spines.

Discussion. Only *D. globifrons*, the most completely known species, is described fully here. Differences in the other species are brought out in comparative diagnosis.

Deiphon globifrons Angelin, 1854

Plate 24, figs. 6–13; Plate 25, figs. 1–4, 6–8, 11

*1854 *Deiphon globifrons* Angelin, p. 66, pl. 34, figs. 7, 7*a*.
v. 1934 *Deiphon forbesi* var. *globifrons* (Ang.); Whittard [*pars*], pp. 510–513, pl. 15, figs. 4–11, *non* fig. 12 [= *D. sphaericum* sp. nov.].

Neotype. Selected here, Ar51271, a cranidium, Pl. 24, fig. 12*a*, *b*, from Valbytte 1, Sanda parish, Slite Marl, Slite Beds.

Remarks. The specimen figured by Angelin (1854, locality given as 'Gotland') cannot be located, and there is no trace of other possible syntypes. Unfortunately, Angelin's figures are rather poor, and it is difficult to recognize diagnostic features. However, *D. globifrons* is by far the most common *Deiphon* on Gotland, and it seems likely that Angelin's concept of the species included the taxon as described here. In addition, the name has been widely used, and should be retained for stability. A neotype is therefore chosen from the specimens from Valbytte 1, the locality which has yielded the largest and best-preserved material of this species.

Additional material. Two records of *D. globifrons* are known from the Slite Beds, unit g (quarry by the windmill at Fårösund, and Lännaberget 2), otherwise the species is restricted to the Slite Marl (apparently to the upper part), where in some areas it is not uncommon. The known localities are: Bunge parish—the shore at Boviken; the shore at Fårösund village; the quarry by the old windmill *c.* 600 m south-west of Fårösund harbour; *c.* 200 m south-east of Hägur; ditch section on Ekenäs (Grundudden). Fårö parish—Braidaursvik 1; Friggars 1; Haganäs 1; Lansa; Ryssnäs; Gåsmorahammar, the shore 3 m a.s.l.; drainage ditch close to south shore of Eketräsk. Follingbo parish—locality unknown. Hejdeby parish—locality unknown. Othem parish—Lännaberget 2. Sanda parish—Valbytte 1; Valbytte 4. Stenkumla parish—Myrse 1.

Diagnosis. Spinose cheeks stout, sigmoidally curved in lateral profile, curving upwards distally through 90°. Secondary spines long and stout. Glabellar granulation unimodal, medium sized, coarser towards glabellar margins. Lateral borders of hypostome narrow, middle body large. Thorax with slender pleurae. Pygidium with second pair of spines curving to point straight back, or converge very slightly backwards.

Description. Glabellar bulb almost spherical, in large specimens with a tendency to become somewhat flattened anteromedially. Basal lobes present as ridges lateral to the preoccipital depression, merging with cheeks laterally. Occipital furrow rising from deep, circular occipital apodemal pit, fading into preoccipital depression. S1 longer (exsag.) than occipital furrow, rising from S1–S2 apodemal pit to merge with preoccipital depression. Occipital ring very convex (tr., exsag.), about half as wide as widest part of glabella. Axial furrow shallow adjacent to occipital ring, deepening into occipital apodemal pit before shallowing adjacent to L1, then deepening again into the very deep and fairly wide (tr.) elongate S1–S2 apodemal pit (apodemes visible on Pl. 24, fig. 9*c*), before shallowing half-way between L1 and eye, being very broad and shallow towards eye. Preglabellar furrow evenly distinct, gently arched upwards medially.

Fixed cheek posteriorly band-like, short (exsag.), curving anterolaterally to meet spinose portion behind the eye. A small, subtriangular articulating flange is separated off by an oblique, distinct furrow. The flange is wider (tr.) than cheek in front, and is laterally flexed first ventrally, then adaxially, through 180°. Spinose cheek stout, curving posterolaterally and downwards. Secondary spine situated almost immediately lateral to facial suture, cheek inflated dorsal to this. Posterior area of secondary spine and spinose cheek flattened medially to this. Spinose cheek distally circular and proximally oval in section.

Eye with reniform to oval visual surface. Subocular furrow wide and rounded in profile. Posterior branch of facial suture cuts eye socle at less than half the distance from anterior end. Glabella densely granulated, granules smallest and densest on central portion, and successively larger towards glabellar margins, largest posteromedially. Small specimens have relatively fewer, larger, and more equally sized granules (Pl. 24, fig. 11; Pl. 25, fig. 6). Granulation on cheeks intermediate in size, dense to rather widely spaced, on occipital ring very fine.

Rostral plate (Pl. 24, fig. 9*c*) twice as long laterally as sagittally. Hypostome with short anterior border. Anterior border furrow wide medially, narrowing and deepening laterally. Lateral border furrow deep anteriorly, shallowing and widening posteriorly, continuous with the very wide (sag.) and shallow posterior border furrow. Anterior wing (Pl. 24, fig. 13*d*) with median furrow deep and constricted adaxially, widening laterally into an oval, depressed area centrally on wing (corresponding to wing process). Anterior border of wing

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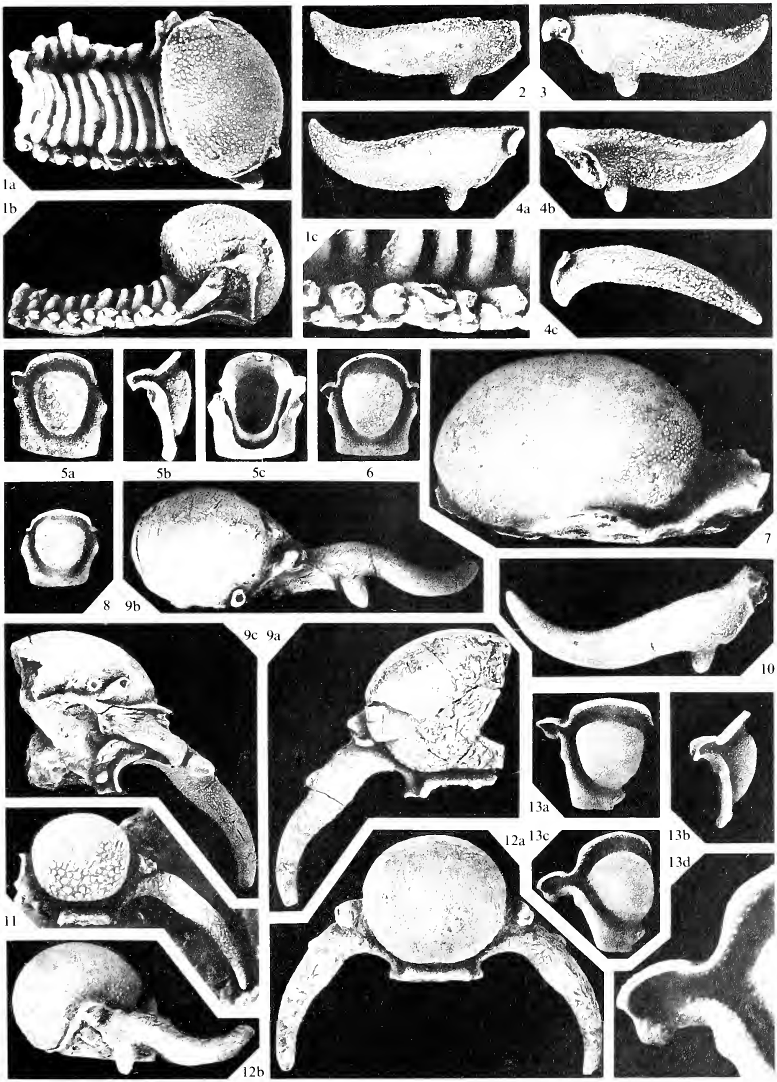
EXPLANATION OF PLATE 24

Figs. 1–5. *Deiphon brevispina* sp. nov. Högklint Beds, unit b. Västös. 1*a–c*, holotype Ar6156, partial exoskeleton, dorsal and lateral views, and enlargement of thoracic segments, *a*, *b* × 4, *c* × 10. 2, holotype Ar6159, right spinose cheek, anterior view, × 4. 3, holotype Ar6158, left spinose cheek, anterior view, × 4. 4*a–c*, paratype Ar6160, right spinose cheek, anterior, posterior, and dorsal views, all × 4. 5*a–c*, paratype Ar6157, hypostome, figured Whittard 1934, pl. 15, fig. 7a, b, ventral, lateral, and dorsal views, all × 4.

Figs. 6–13. *Deiphon globifrons* Angelin, 1854. Slite Marl, Slite Beds. Valbytte 1 (6, 8, 9, 11, 12), Haganäs 1 (7, 10, 13). 6, Ar51274, hypostome, × 3. 7, Ar51281, partial cranidium, posterior view, × 4. 8, Ar51275, small hypostome, × 4. 9*a–c*, Ar51272, partial cephalon, dorsal, anterolateral, and ventral views, showing free cheek and rostral plate, all × 2·5. 10, Ar51298, spinose cheek, × 4. 11, Ar51273, small cranidium, note coarse granulation and long preoccipital depression, × 5. 12*a*, *b*, neotype Ar51271, worn cranidium, dorsal and lateral views, both × 2·5. 13*a–d*, Ar51276, hypostome, ventral, lateral, oblique lateral views, and enlargement of anterior wing, *a–c* × 3, *d* × 8.

PLATE 24



RAMSKÖLD, *Deiphon*

very narrow, lateral border narrow, overhanging part of central depression, posterior border protruding posterolaterally, narrowing adaxially, then merging with lateral hypostomal border. This is evenly raised, widening posteriorly, with a distinct shoulder which is larger in small specimens (Pl. 24, fig. 8). Posterior border fairly wide, gently convex (sag.), margin straight to slightly convex. Doublure present posterior to wing furrow, inner margin follows a course corresponding to inner margins of borders. Shoulders continue on doublure as ridges directed obliquely posteromedially. Rostral plate with granulation at least laterally. Anterior hypostomal border with an irregular row of small granules, continuing on to wing. Lateral and posterior borders finely and densely granulated. Middle body with larger, more widely spaced granules.

Thorax of unknown number of segments. Pleurae unfurrowed, very slender, adaxially oval and distally circular in section, pointed. Pleurae finely granulated.

Pygidium with anterior pair of spines slender, directed slightly backwards from the transverse direction. Second pair stout, curved backwards, much stouter and diverging at greater angle in large specimens (Pl. 25, figs. 1, 4), pointed tips directed straight back or converging slightly (Pl. 25, fig. 8). Inter-ring furrows very shallow medially, ankylosed articulating half-ring in the anterior one. Beneath posterior margin is a posterior pair of short, blunt spines, hooked backwards (Pl. 25, figs. 2, 11), reaching behind posterior margin. Surface of pygidium, at least behind anterior inter-ring furrow, finely and densely granulated.

Discussion. This is the largest *Deiphon* known, attaining a glabellar diameter of 14 mm or more. There are some differences between specimens from Valbytte 1 and those from Haganäs 1 (i.e. between the west and the east part of the Slite Marl). The latter have less sigmoidally curved spinose cheeks (Pl. 24, fig. 10) with less prominent swellings and slightly shorter secondary spines, and possibly the granulation is denser (Pl. 24, fig. 7). No other differences have been found, and they are considered to be of intraspecific nature.

In the Gotland species of *Deiphon*, mainly the cheeks and the granulation are of taxonomic value. Possibly, differences in the pygidium would also be helpful, but unfortunately it is rarely found. Each species recognized here is distinguished by a complex set of characters. There are no obvious chronological trends in these features, and the phylogenetic relationships between the species are uncertain. Some important comparative features are listed in Table 1. The two most closely related species appear to be *D. snodensis* and the type species. However, *D. forbesi* (figured Whittard 1934, pl. 15, figs. 1–3; and Horný and Bastl 1970, pl. 15, fig. 8) has even more slender spinose cheeks, denser granulation, and nodular L1.

Deiphon cf. *globifrons* Angelin, 1854

(Not figured)

Remarks. From Djupvik, Eksta parish, two fragmentary cranidia (Ar6170–6171) are known,

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EXPLANATION OF PLATE 25

Figs. 1–4, 6–8, 11. *Deiphon globifrons* Angelin, 1854. Slite Marl (1–4, 6–8), Slite Beds, unit g (11). 1, Ar6154, worn pygidium, Fårö, figured Whittard 1934, pl. 15, fig. 11, ×3. 2, Ar51294, partial pygidium, lateral view showing posterior spine, Valbytte 1, ×6. 3, Ar51279, thoracic segment, Haganäs 1, ×3. 4, Ar51277, pygidium, ventral view, Haganäs 1, ×3. 6, Ar51314, smallest known cranidium, note long preoccipital depression, Valbytte 4, ×6. 7, Ar51280, thoracic segment, Haganäs 1, ×3. 8, Ar51310, pygidium with unusually long spines, ventral view, Valbytte 4, ×4. 11, SGU 1359, pygidium with unusually short spines, ventral view, quarry by the windmill *c.* 600 m south-west of Fårösund harbour, ×3.

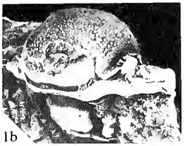
Figs. 5, 9, 10, 12–16. *Deiphon ellipticum* sp. nov. Halla Beds, unit b. Hörsne 5 (9, 12, 15), Hörsne Canal (5, 10, 13, 14, 16). 5, paratype SGU 1361, partial cranidium, ×6. 9*a*, *b*, paratype Ar51296, thoracic segment, dorsal and anterior views, note faint pleural furrow, both ×8. 10, paratype SGU 1362, small cranidium, ×5. 12*a*, *b*, paratype Ar51295, hypostome, ventral, and lateral views, both ×6. 13, paratype SGU 1363, hypostome, ×6. 14*a–d*, holotype SGU 1360, partial exoskeleton, *a*, *b*, dorsal and anterior views, *c*, *d*, enlargements of granulation and pygidium, *a*, *b* ×5, *c*, *d* ×10. 15, paratype Ar51297, smallest cranidium known, ×6. 16*a–d*, paratype SGU 1364, cephalon, dorsal, lateral, anterolateral, and anterior views, all ×4.

ERRATUM

The printer apologizes that plates 25 and 26 have been transposed; but they do carry the correct numbering and captions.

PLATE 26


1a

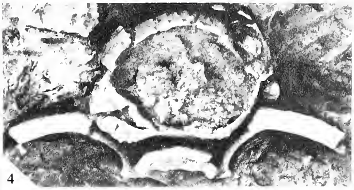

1b


1c


2


3a


3b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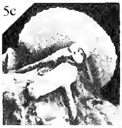
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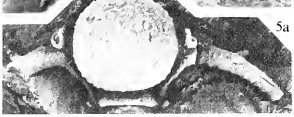
6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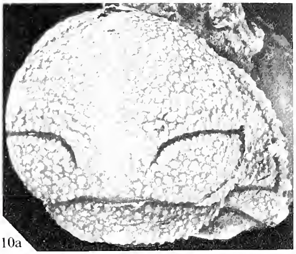
7


8


9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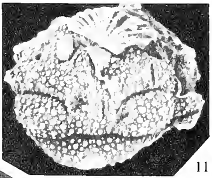
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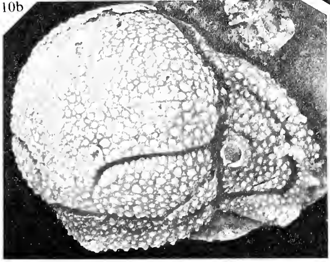
12a


13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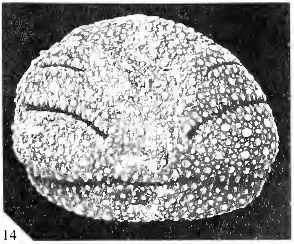
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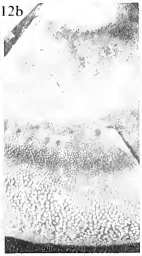
12b

RAMSKÖLD, *Deiphon*, *Sphaerexochus*, *Hyrokybe*?

TABLE 1. Comparison of some morphological features of taxonomic value in *Deiphon*. The Gotland species are listed in upwards chronological order. Four major non-Gotland species are included for comparison; the type species *D. forbesi* Barrande, 1850; the British *D. barrandei* Whittard, 1934; the Canadian *D. braybrooki* Perry and Chatterton, 1979; and the American *D. longifrons* Whittard, 1934.

SPECIES	AGE	SPINOSE CHEEK	SECONDARY SPINE	DOMINANT GLABELLAR GRANULATION	
				DENSITY	SIZE
D. sp. A	**U Ludlow**	**medium?**	**slender?**	**sparse**	**coarse unimodal**
D. snodensis	**L Ludlow**	**very slender**	**very long slender**	**very sparse**	**very coarse unimodal**
D. ellipticum	**U Wenlock**	**medium**	**long slender**	**dense**	**fine unimodal**
D. globifrons	**Wenlock**	**stout**	**long stout**	**dense**	**medium unimodal**
D. brevispina	**L Wenlock**	**very stout**	**short stout**	**medium**	**medium bimodal**
D. sphaericum	**L Wenlock**	**medium**	**long slender**	**medium**	**medium bimodal**
D. forbesi	**Wenlock**	**very slender**	**shape uncertain**	**sparse**	**coarse bimodal**
D. barrandei	**Wenlock**	**stout**	**rel. short rel. stout**	**sparse**	**coarse unimodal**
D. braybrooki	**Wenlock**	**rel. stout**	**long slender**	**medium**	**medium bimodal**
D. longifrons	**Wenlock**	**medium**	**very long rel. stout**	**medium**	**medium bimodal**

showing close affinities with *D. globifrons*. However, the lithology in these specimens is atypical of the Mulde Marl at Djupvik, and they may in fact be from the Slite Marl.

Deiphon sphaericum sp. nov.

Plate 23, figs. 8–10

v. 1934 *Deiphon globifrons* Angelin; Whittard [*pars*], pl. 15, fig. 12, *non* Angelin, 1854.

Name. Referring to the shape of the glabella.

Holotype. Ar6162, a cranidium, Pl. 23, fig. 9*a–c*, from unknown locality close to shore between Visby and Lickershamn.

Paratypes. From Visby–Lickershamn, Ar6161–6169, Ar6153. Vattenfallsprofilen 1, SGU 1353. Unspecified quarry south of Visby, SGU 1354. Norra Svältan Lickershamn, SGU 1355. The stratigraphic range is uncertain. Some material seems to be from the Högklint Beds, and specimens labelled Visby–Lickershamn could come from the Lower or Upper Visby Marl. Of the material from the Vattenfallet section (see Jaanusson, Laufeld and Skoglund 1979, pp. 117, 118) only the specimen from 10·7 to 10·8 m a.s.l. (lowermost Högklint Beds) can possibly be assigned to this species. The fragmentary state of the other specimens precludes a definite assignment to any species.

Diagnosis. Glabellar bulb almost spherical, barely wider than long. Basal lobe ridge-like, merging laterally with cheek. Preoccipital depression short (sag.), rather shallow. Occipital ring slightly over half as wide (tr.) as maximum width of glabella. Band-like portion of fixed cheek short (exsag.), spinose portion emerging behind mid length of glabellar bulb, of moderate stoutness, with no swellings. Secondary spine long, slender, pointed, distance to facial suture approximately equal to its own diameter. Eye with anterior edge opposite mid length of glabellar bulb. Glabellar granulation bimodal, larger granules interspersed by a greater number of minute granules, especially antero-medially, where large granules are few. Spinose cheeks with rather sparse and coarse granulation. Pygidium behind anterior inter-ring furrow sparsely and coarsely granulated.

Deiphon brevispina sp. nov.

Plate 24, figs. 1–5

v. 1885 *Deiphon Forbesi* Barr.; Lindström, p. 51, pl. 13, figs. 9, 10; pl. 16, figs. 18–20, *non* Barrande, 1850.

Name. Latin *brevis*, short, and *spinus*, spine: referring to the rather short spinose cheeks.

Holotype. Ar6156, Ar6158, Ar6159; all parts belonging to the same specimen, a damaged individual lacking pygidium, partly figured Lindström 1885, pl. 13, figs. 9, 10; from ditch section at Västös, Hall parish, Högklint Beds, unit b; Pl. 24, figs. 1–3.

Paratypes. Ar6157, a hypostome, and Ar6160, a spinose cheek; from the type locality.

Specimens questionably assigned. Ar51269–51270, from dump at Visby harbour, Högklint Beds, unit b (Pl. 23, fig. 11).

Diagnosis. Basal lobe present as a low swelling, apparently not merging laterally with cheek. Occipital ring approximately half as wide (tr.) as widest part of glabella. Band-like portion of fixed cheek short (exsag.), spinose portion very stout, rather short, flat to concave posteriorly on proximal half, very high dorsoventrally, proximally reniform and distally oval in section, with short, upturned terminal part. Secondary spine short, stout, and blunt, situated very close to facial suture. Glabellar granulation bimodal, very similar to that of *D. sphaericum*, but denser and more markedly bimodal on spinose cheeks. Hypostome with rather small middle body, wide borders, and long (sag.) anterior border furrow. Thoracic pleural spines slender, circular in section close to fulcra.

Discussion. The glabella is slightly compressed anteroposteriorly, which makes it difficult to deduce its original shape. The Västös hypostome may also have belonged to the holotype, as judged from its size and preservation. (Account has not been taken of hypostome Ar51269 in the diagnosis.)

Deiphon ellipticum sp. nov.

Plate 25, figs. 5, 9, 10, 12–16

1855 *Deiphon Forbesi* Barr.; Lindström [*pars*], p. 51 [type locality mentioned], *non* Barrande, 1850.

Name. The specific name *ellipticum* was used on labels written by the nineteenth-century collector G. Liljevall, apparently as a working name, but it has never been published. The name refers to the shape of the glabella.

Holotype. SGU 1360, cranidium, six thoracic segments and pygidium, Pl. 25, fig. 14*a–d*, from Hörsne kanal, Hörsne parish, Halla Beds, unit b.

Paratypes. Ar51295–51297, SGU 1361–1397; thirty-seven cranidia and cephala, two hypostomes, one thoracic segment; all from the type locality (in Laufeld 1974*b*, divided into Hörsne 1–Hörsne 5).

Diagnosis. Glabellar bulb oval; length to width ratio about 5:6, low dorsoventrally. Occipital ring more than half as wide (tr.) as maximum width of glabella. Basal lobe in shape of a small swelling connected by a ridge lateral to cheek. Axial furrow apparently curving laterally abaxial to this ridge and fading lateral to S1–S2 apodemal pit. Band-like portion of fixed cheek short (exsag.). Spinose portion of medium stoutness, without swellings, proximally oval and distally circular in section, curving upwards distally through about 45°. Secondary spine long, slender, pointed, distance to facial suture equal to its own diameter. Glabellar granulation dense, fine, regarded as unimodal although a few minute granules are scattered over the glabella, granules larger and more widely spaced close to glabellar margins. Hypostome fairly wide and short, with short (sag.) anterior border furrow. Thoracic pleurae elliptical in section, with a hint of a transverse pleural furrow on anterior one-third of proximal part. Pygidium finely and densely granulated.

Discussion. This is the Gotland species closest to the Canadian Wenlock *D. braybrooki* Perry and Chatterton, 1979. It differs mainly in having a more oval and less inflated glabella, more slender spinose cheeks, and less divergent pygidial spines. In addition, *D. braybrooki* has a coarser glabellar granulation which is equal all over, whereas in the Gotland species the granulation is much finer anteromedially, a difference that cannot be due to the different modes of preservation. The granulation of the Canadian species is also markedly bimodal, especially on the spinose cheeks. See also Table 1.

Deiphon snodensis sp. nov.

Plate 26, figs. 3–5

Name. After the type locality.

Holotype. Ar51284, a cranidium, Pl. 26, fig. 5*a–c*, from Snoder 2, Sproge parish, Hemse Marl, north-west part, Hemse Beds.

Paratypes. Ar51285–51286, both cranidia from the type locality.

Diagnosis. Glabellar bulb with length to width ratio 1:1. Basal lobe ridge-like, merging with cheek laterally. Occipital ring approximately half as wide (tr.) as maximum width of glabella. Band-like portion of fixed cheek long (exsag.), with only faintly concave lateral margin. Spinose cheek very slender with base opposite widest part of glabella, straight in lateral view for at least as long as diameter of glabella, without swellings, flattened posteriorly on proximal part. Secondary spine very long, slender, pointed, distance to facial suture equal to its own diameter. Glabella with very coarse,

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EXPLANATION OF PLATE 26

Figs. 1, 2. *Deiphon* sp. A. 1*a–c*, Ar51565, cephalon, mainly internal mould, collected by Professor H. Alberti (Göttingen), anterior, anterolateral views, and enlargement of eye, Holmhällar 1, Sundre Beds, middle to upper part, *a*, *b* ×4, *c* ×10. 2, Ar29815, partial cranidium, Klev, Hoburgen, probably Sundre Beds, lower to middle part, ×4.

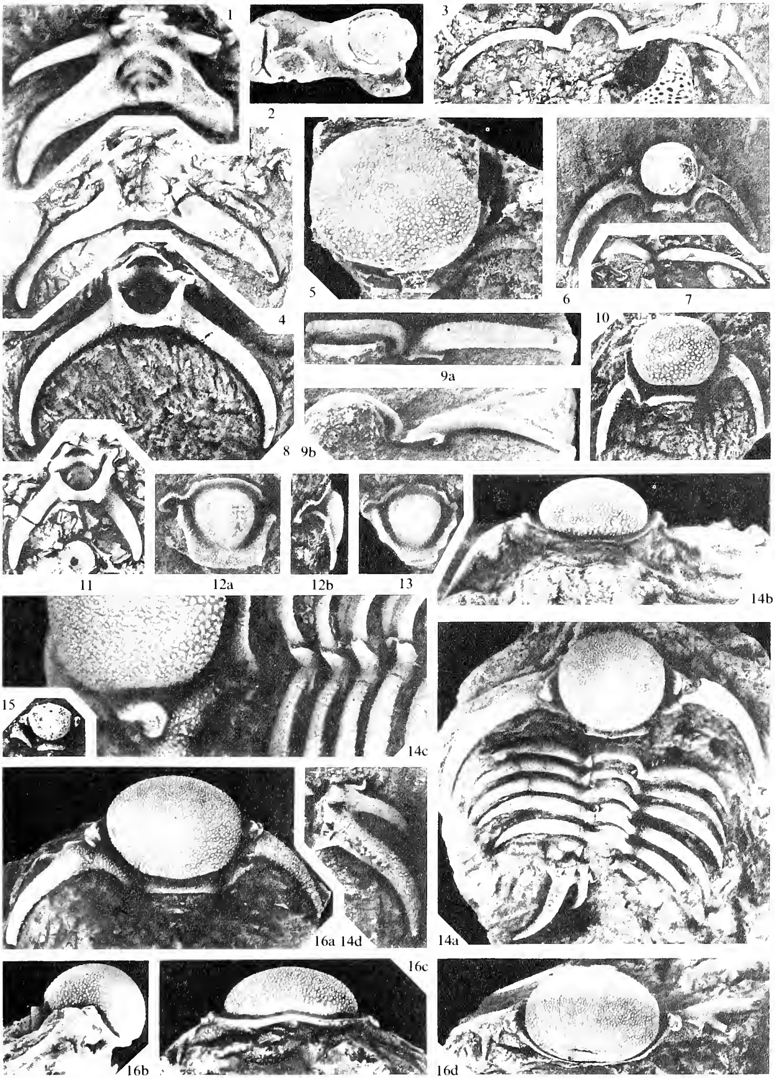
Figs. 3–5. *Deiphon snodensis* sp. nov. Hemse Marl, north-west part, Hemse Beds, Snoder 2. 3*a*, *b*, paratype Ar51285, cranidium with right free cheek, dorsal and ventral views, both ×4. 4, paratype Ar51286, crushed cranidium, ×4. 5*a–c*, holotype Ar51284, cranidium, dorsal, anterior, and lateral views, all ×4.

Figs. 6, 8, 9, 12, 13. *Sphaerexochus scabridus* Angelin, 1854. Slite Marl (8, 9, 12, 13), Slite Beds, unit g (6). 6, Ar30042, cranidium, internal mould, anterior view showing rostral plate, Samsugn, ×5. 8, Ar51313, left free cheek, Mojner 3, ×3. 9, Ar51304, left free cheek, ventral view, lacking anterior part of doublure, Valbytte 1, ×3. 12*a*, *b*, Ar51302, left free cheek with unusually shallow lateral border furrow, dorsal view and enlargement of granulation, *a* ×3, *b* ×6. 13, Ar51323, right free cheek, Valbytte 1, ×3.

Figs. 7, 10, 11. *Hyrokybe*? *globiceps* (Lindström, 1885). Upper Visby Beds. 7, SGU 1399, glabella, Själsö, ×4. 10*a*, *b*, lectotype Ar29810, partial cephalon, Visby area, figured Lindström 1885, pl. 13, fig. 11, dorsal and dorsolateral views, both ×4. 11, Ar29811, cranidium, Visby area, ×5.

Fig. 14. *Hyrokybe*? *inermis* (Lindström, 1885). Holotype G238, compressed glabella, Slite Beds, unit g, Slite, ×4.

PLATE 25



RAMSKÖLD, *Deiphon*

widely and evenly spaced unimodal granulation, equally sized and spaced anteromedially. Spinose cheek with coarse, widely spaced granulation.

Discussion. Of the Gotland species of *Deiphon* this differs most from the others (see Table 1). It has one feature in common with the only other known Ludlow species, *D.* sp. A—namely, the granulation that is equal in size and density all over the glabella within each species. However, in *D.* sp. A the granulation is less coarse and much denser.

Deiphon sp. A

Plate 26, figs. 1, 2

Material. Ar29815, a cranidium from Klev, Hoburgen, Sundre parish, probably Sundre Beds, lower to middle part; Ar30185, a glabella from Holmhällar, Vamlingbo parish; Ar51555–51565, cephala and cranidia collected at Holmhällar 1, Sundre Beds, middle to upper part, by Professor H. Alberti (Göttingen).

Discussion. These specimens are not described here since most of the important taxonomic features are lacking. However, it is clear that the material does not belong to any described species. An interesting feature is that several of the specimens have the rostral plate, free cheeks, and hypostome *in situ*, although the thorax is obviously separated from the cephalon. The material shows that *Deiphon* survived well into the Ludlow.

Deiphon sp. indet.

(Not figured)

Remarks. From the topmost strata (of uncertain stratigraphical level in Halla or Klinteberg Beds) on the island of Lilla Karlsö several glabellae (Ar6136–6148; mainly internal moulds) are known, seemingly not belonging to *D. globifrons* or *D. ellipticum* (the species closest in age).

Subfamily ACANTHOPARYPHINAE Whittington and Evitt, 1954

Genus HYROKYBE Lane, 1972

Type species. *Hyrokybe pharanx* Lane, 1972, from the ?Wenlock (?Llandovery) of Kronprins Christians Land, north-east Greenland; by original designation. (For discussion of age see Perry and Chatterton 1977, p. 287.)

Remarks. When erecting this genus, Lane (1972, p. 359) placed it in the Sphaerexochinae, but noted the similarity between *Hyrokybe* and a cranidium referred to *Youngia uralica* Tschernyschew, 1893, by Weber (1951). Dr. B. D. E. Chatterton has kindly informed me that he is working on new Canadian Llandovery material which includes several forms referrable to *Youngia* and *Hyrokybe*. Both genera most probably belong to the Acanthoparyphinae. The main differences lie in the development of the cephalic spines and in the shape of the pygidium. Several species hitherto referred to *Youngia* will be reassigned to *Hyrokybe*, among them *Youngia copelandi* Perry and Chatterton, 1979. No pygidia that can be referred either to *Youngia* or *Hyrokybe* are known from Gotland, but cephalic features in the Gotland species previously assigned to *Youngia* suggest that they should be referred provisionally to *Hyrokybe*, pending the publication of the Canadian material.

Hyrokybe? *globiceps* (Lindström, 1885)

Plate 26, figs. 7, 10, 11

v.* 1885 *Youngia globiceps* Lindström, p. 50, pl. 13, fig. 11.
v. 1979 *Youngia* sp.; Jaanusson *in* Jaanusson *et al.*, pp. 117, 118.

Lectotype. Selected here, Ar29810, an incomplete cephalon, Pl. 26, fig. 10*a–b*, figured Lindström 1885, pl. 13, fig. 11; from the Upper Visby Marl in the Visby area.

Additional material. From 'Visby' (exact localities not known), Ar29811–29812 (these are probably Lindström's two additional specimens, i.e. paralectotypes). Vattenfallsprofilen 1, 9·6 m a.s.l., SGU 1398. Själsö, SGU 1399.

The beach at Kneippbyn, SGU 1400. This species is probably restricted to the Upper Visby Marl, although the Själsö specimen may be from the Lower Visby Marl.

Diagnosis. Glabella with S1 not reaching occipital furrow, S2 and S3 weak, reaching respectively one-third and one-fifth across glabella. Occipital ring with a small, ?short median spine. Genal spine situated close to genal angle; short, spinose tubercles present laterally on fixed cheek. Border furrows very narrow. Eye immediately adjacent to axial furrow, extending from opposite mid L1 to slightly anterior to S1. Cephalic tuberculation dense, coarse.

Description. Glabella with sagittal length (excluding occipital spine) equal to maximum width, which is reached across L1 and L2. L3 and L2 equally long (exsag.), L2 the widest (tr.). L1 1·7 times as long as L2, slightly independently inflated. S2 slightly more distinct than S3. S1 deep and narrow, directed slightly backwards, reaching two-fifths across glabella, medially flexed backwards, ending at mid length (exsag.) of L1. Occipital furrow transverse behind L1, then curves a little anteriorly, and again transverse for the medial one-fifth, where it is slightly broader and shallower than laterally. Occipital ring with a small spine-base medially on posterior margin. Axial furrow deep and narrow, preglabellar furrow (Pl. 26, fig. 10*b*) narrowest (sag.) medially, where it is gently arcuate.

Cheeks small. Posterior border broadening laterally, with a large spine-base close to genal angle. Lateral border of even width. Posterior border furrow evenly deep and narrow, merging with similar lateral border furrow, which is interrupted one-quarter way (of furrow length) from genal angle by a strong sutural ridge. Anterior to this ridge the furrow is shallower, close to axial furrow it ends against anterior sutural ridge.

Palpebral lobe diminutive. Anterior branch of facial suture runs from eye very close to axial furrow. Posterior branch running laterally and slightly forwards from eye until meeting lateral border, flexed backwards across the border. Surface of entire cephalon except furrows covered with more or less spinose tubercles, many of which are perforated, and granules of varying size. On posterior part of lateral margin are a few elongated tubercles; just posterior to the facial suture is a small spine (Pl. 26, fig. 10*b*). Rostral plate, hypostome, thorax, and pygidium unknown.

Discussion. *H.*? *globiceps* differs from the type species in having much denser and coarser tuberculation, better developed S2, S3 present, narrower axial and border furrows, a more laterally situated genal spine, and in having an occipital spine. A comparison with species now assigned to *Youngia* but which will be reassigned to *Hyrokybe* is hampered by the lack of pygidia. However, *Y. douglasi* Lamont, 1948 (see Clarkson and Howells 1981), from the upper Llandovery of Scotland, appears to be very similar, but is stated to lack an occipital spine. *Y. copelandi* Perry and Chatterton, 1979, from the Canadian Wenlock, has L1 circumscribed. *Y. uralica* Tschernyschew, 1893, from the lower Ludlow of the Urals, lacks an occipital spine.

Hyrokybe? *inermis* (Lindström, 1885)

Plate 26, fig. 14

v.* 1885 *Youngia inermis* Lindström, pp. 50, 51, pl. 13, fig. 12.

Holotype. Specimen in the Palaeontological Institution, University of Uppsala, no. G238, a glabella, from the 'upper limestone at Slite' (= Slite Beds, unit g).

Discussion. This is the only known specimen of the species, although Lindström (1885, p. 51) considered two other fragmentary cranidia to be possible varieties. These latter specimens are too fragmentary to be recognized even at generic level. Most of the features listed by Lindström as diagnostic for *H.*? *inermis* can be explained by the fact that the specimen is considerably flattened, and hence should be excluded from the diagnosis. A single distinguishing feature remains—namely, the lack of an occipital spine. *H.*? *inermis* is too poorly known to be compared properly with other species, but seems to be close to *Y. douglasi* Lamont, 1948, and *Y. uralica* Tschernyschew, 1893.

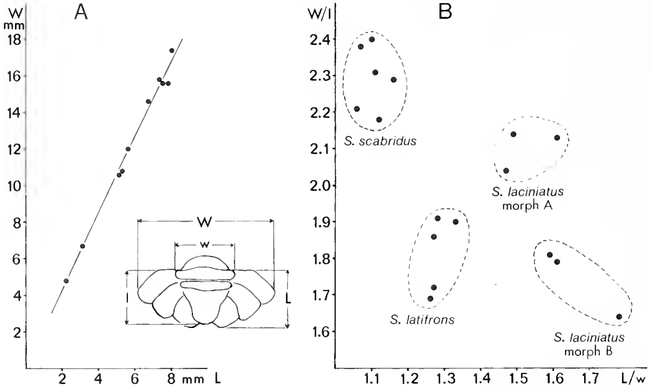
Subfamily SPHAEREXOCHINAE Öpik, 1937

Genus SPHAEREXOCHUS Beyrich, 1845

Type species. By monotypy; *Spaerexochus* [*sic*] *mirus* Beyrich, 1845, from the Liteň Formation (upper Wenlock), Lištice, near Beroun, Czechoslovakia.

Diagnosis. See Lane 1971, p. 53.

Discussion. Some confusion has arisen concerning some Silurian *Sphaerexochus*. Dean (1971, pp. 29, 30) considered the British material to be specifically distinct from *S. mirus*, and described it as *S. brittanicus*, but noted that either the species is highly variable, or the material may consist of more than one species. Thomas (1981, pp. 61–63) found no consistent differences between British and Bohemian material, and synonymized *brittanicus*, and other species, with *mirus*, on the basis of overlapping variation in pygidial morphology. Variation in pygidial length–breadth proportions was stated as being due mainly to ontogeny, small individuals having a relatively wider pygidium.



TEXT-FIG. 5. *A*, *Sphaerexochus scabridus*; pygidial length plotted against pygidial width ($W = 2{\cdot}20L^{0{\cdot}978}$, $r = 0{\cdot}998$). *B*, plot of some parameters of the pygidium in the Gotland species of *Sphaerexochus*. (Material; *A*: Ar51305–51307, Ar51338–51343, SGU 1402. *B*: Ar29857–29858, Ar29862, Ar29866, Ar29882, Ar29934, Ar30072, Ar51305–51306, Ar51338–51344, SGU 1402.)

However, plots for *S. scabridus* (text-fig. 5A) show isometric pygidial growth already from very small individuals, which probably holds for other *Sphaerexochus* as well. Both the Bohemian and British material almost certainly consist of more than one species. Figured Bohemian pygidia can be placed in two groups, one with 'long and narrow' pygidia (width : length ratio close to 1·8 : 1; Beyrich 1846, pl. 1, fig. 8*c*; Barrande 1852, pl. 42, figs. 22, 23; Barrande 1872, pl. 7, fig. 3; Shaw 1968, pl. 14, fig. 25; Thomas 1981, pl. 16, fig. 6), and one with 'wide and short' pygidia (width : length ratio 2·0–2·1 : 1; Thomas 1981, pl. 16, figs. 8, 10). Similarly, the British material can be divided into two such groups (Thomas 1981, pl. 16, fig. 7; and pl. 16, figs. 1, 5, 9, 11, 12, ?14, respectively). The first group (ratio 1·8 : 1) is very close to *S. latifrons* morph A, and the second (ratio 2·0–2·1 : 1) is very close to *S. scabridus*, and the respective forms may very well be conspecific. A thorough study of all Bohemian material is necessary to solve these problems. In the meantime, *S. mirus* and *S. brittanicus* are regarded here as specifically distinct, and occurring both in Bohemia and Britain. *S. latifrons* may prove to be a junior synonym of *S. mirus*, if this is shown to be dimorphic, and *S. brittanicus* is possibly a junior synonym of *S. scabridus*. *S. laciniatus* is well separated from the species discussed above.

Similarly to Bohemia and Britain, the Gotland material of *Sphaerexochus* is heterogenous.

However, apart from the isolated specimens referred to *S.* spp. below, the material falls into three groups, one from the Slite Beds and two from the Hemse Beds. This grouping based on morphology is supported by the stratigraphical occurrences. Unfortunately, most specimens are isolated glabellae or cranidia. As pointed out by *i.a.* Holloway (1980, p. 38), cephalic features alone are mostly insufficient for specific identification of *Sphaerexochus*. More material may therefore well make it possible to distinguish more than one species in some groups. The presence of dimorphism in at least two of the groups is also a complicating factor. For these reasons, and those outlined above, no detailed comparisons can be carried out at present between Gotland and non-Gotland species. To facilitate future studies, the diagnoses given here are detailed, although some features may prove to be generically rather than specifically diagnostic. Additional shared features are deep vincular furrows, accommodating the shortened first thoracic segment, and a small median occipital tubercle.

Sphaerexochus scabridus Angelin, 1854

Plate 26, figs. 6, 8, 9, 12, 13; Plate 27, figs. 1–11

1851	Angelin, pl. 22, fig. 9 [illustration only, without name].
*1854	*Sphaerexochus scabridus* Angelin, p. 37, pl. 33, fig. 1; pl. 38, figs. 14, 14*a*.
v. *non* 1885	*Sphaerexochus scabridus* Angelin; Lindström, pl. 15, fig. 26 [= *S. laciniatus* Lindström].

Neotype. Selected here, SGU 1402, a pygidium, from Alby 2, Rute parish, Slite Marl, Slite Beds, Pl. 27, fig. 10*a–d*. Angelin's original specimens cannot be located, and are considered lost (two cranidia and a pygidium were figured, locality given only as 'Gotland'). No other possible syntypes can be traced. The neotype, which agrees closely with Angelin's figure, is for diagnostic reasons a pygidium.

Material. At present all specimens from Slite Beds are referred to *S. scabridus*. Localities: Slite Beds, unit g: Follingbo parish—Stora Vede 1. Lokrume parish—drainage ditch near Lokrume (= Tomase 1?). Othem parish—Lännaberget 2; Samsugn. Slite Marl (including '*Pentamerus gothlandicus* beds'): Boge parish—Mojner 3; Tjälder. Bäl parish—Gane 2. Bunge parish—the beach at Fårösund; the beach 1 km south of Fårösund harbour. Dalhem parish—Nygårds 1. Eksta parish—Stora Karlsö. Eskelhem parish—drainage ditch south of the south farm at Valdarve. Fårö parish—Brajdaursvik 1; the beach NNW of Ryssnäs. Follingbo parish—Follingbo 6; Follingbo 7; Follingbo 8; the well near the borehole west of Rosendal. Hejdeby parish—Hajdungs 1. Hörsne parish—Bara 1. Othem parish—the beach at Slite; the beach by the shooting-range north of Länna. Roma parish—the large drainage ditch at Roma. Rute parish—Alby 2; the beach of Fardume träsk 225 m south of *a* in Fardume. Sanda parish—Valbytte 1; Valbytte 3; Valbytte 4; drainage ditch close to Klintehamn; drainage ditch 500 m WNW of L. Varbos. Västergarn parish—locality unknown.

Diagnosis. S3 and S2 very weak, S2 1·3 times as long (tr.) as S3. Occipital ring 0·6–0·7 times as wide (tr.) as widest part of glabella. Fixed cheek with about the same area as L1. Part of cheek between eye and posterior border furrow considerably longer (exsag.) than posterior border (in adult specimens). Posterior margin of cheek convex in large specimens, almost straight in small ones, where a small, blunt spine (Pl. 27, fig. 2*c*) is also present three-quarters of the way from axial furrow. Lateral border furrow deep in some specimens (Pl. 26, figs. 8, 13), shallow in others (Pl. 26, fig. 12). Palpebral furrow continuing anteriorly from eye parallel to facial suture until ending in a series of pits opposite L3.

Entire cephalon except doublure finely and densely granulated, granules almost in contact with each other, slightly coarser on anterolateral part of lateral border. Fixed cheek with a few scattered, irregular pits, area between axial furrow and anterior branch of facial suture with a few similar pits, free cheek with pits mainly beneath eye socle, sometimes also in lateral border furrow (Pl. 26, fig. 12).

Rostral plate (Pl. 26, fig. 6) with fine pitting anteromedially (on internal mould). Hypostome with anterior border at least on the lateral quarter, but possibly absent medially. Middle furrow very weak, reaching about one-quarter across middle body. Anterior wing small (Pl. 27, fig. 7 right side), cylindrical, blunt tip. Middle body and borders covered with very small granules.

Axis and pleurae of thoracic segments extremely finely and densely granulated.

Pygidium wide and short, width : length ratio 2·1–2·2 : 1 (text-fig. 5A). Terminal piece short, inflated and rounded posteriorly with subhemispherical to pyramid-shaped termination. Remnants of a third inter-ring furrow present as deep notches laterally at midlength on terminal piece. Anterior pleural ridge with a short but distinct, almost transverse pleural furrow midway between axial furrow and flexure. Pleural ridges rounded convex in profile. Interpleural furrows evenly rounded in section. Terminal piece and posterior pair of spines elevated considerably above plane of anterior and middle pleural ridges. Spines in shape of subsemicircular lobations of margin, occasionally short, broad and hook-like (Pl. 27, figs. 3, 5). Surface including doublure very densely and finely granulated.

Discussion. A few pygidia (Pl. 27, figs. 3, 5) from Slite Beds, unit g, show a rounded spinose margin, but are otherwise similar to the neotype. Also, at Valbytte 1 two types of free cheeks occur, with either a deep (Pl. 26, figs. 8, 13) or a shallow border furrow (Pl. 26, fig. 12). Whether these cases indicate dimorphism or two separate species is indeterminate at present.

Sphaerexochus latifrons Angelin, 1854

Plate 27, figs. 12–17; Plate 28, figs. 1–6

v. 1851 Angelin, pl. 22, figs. 10 [illustration only, without name].
*1854 *Sphaerexochus latifrons* Angelin, pp. 37, 75, pl. 38, fig. 15.
v. 1885 *Sphaerexochus latifrons* Angelin; Lindström, pp. 46, 47, pl. 14, fig. 17.

Discussion. The cranidium (Ar30060) figured by Angelin in 1851 (and to which the 1854 description refers) is very fragmentary (Pl. 27, fig. 15), and only one of the features listed in the diagnosis below is preserved, the pointed anteroventral corner of L1. However, Angelin's (1854) illustration of the pygidium is distinctive, and the species has always been interpreted in accordance with this pygidium. Unfortunately, it cannot be located, and no locality was given. The alternative to referring material from strata presumably equivalent to those from which Angelin's cranidium came (stated by Lindström 1885, p. 47, to be from Östergarn [Hemse Beds]) to *S. latifrons* would be to consider the species a *nomen dubium*, and to erect a new species for the Hemse Beds material. Since material from this interval is rather variable, and it is possible that more than one species is present, the material is referred here as a whole to Angelin's species until further specimens are available for study. A lectotype (by necessity the 1851 cranidium) is not formally established here for the above reasons.

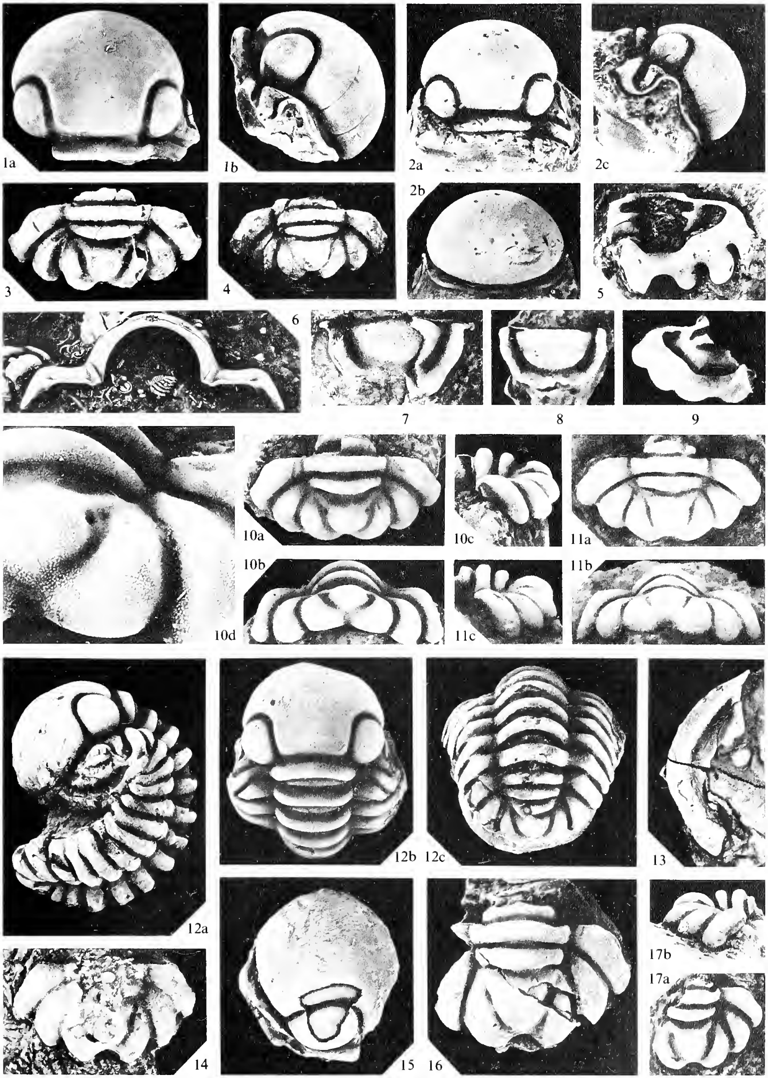
Material. All specimens are from the Hemse Marl of the Hemse Beds. Localities: Fardhem parish—Visne myrs kanal (may include Gerete 1). Hablingbo parish—drainage ditch west of Hablingbo railway station; Lukse 1; Petesvik. Havdhem parish—Kvinnegårde; Nissevik. Hemse parish—dump at Frigges 2 km north-east of Hemse; Likmide 1. Linde parish—Amlings 1; Rangsarve 1. Östergarn parish—unknown locality. Sproge parish—Eske 1; Snoder 1; Snoder 2.

EXPLANATION OF PLATE 27

Figs. 1–11. *Sphaerexochus scabridus* Angelin, 1854. Slite Marl (1, 4, 6–11), Slite Beds, unit g (2, 3, ?5). Alby 2 (10), Follingbo 8 (6), Lännaberget 2 (2), Rosendal (1), Slite (3, 5), Valbytte 1 (4, 8, 9, 11), Valbytte 4 (7). 1*a*, *b*, SGU 1401, cranidium, dorsal and lateral views, ×1·5. 2*a–c*, Ar51312, small cranidium, dorsal, anterior, and lateral views, note short genal spine, ×4. 3, Ar51315, pygidium, spinose form, ×3. 4, Ar51306, smallest known pygidium, ×6. 5, Ar30187, pygidium, spinose form, ventral view, ×2. 6, Ar51311, first thoracic segment, posterior view, ×2. 7, Ar51309, hypostome, partly internal mould, ×3. 8, Ar51308, hypostome, ×2. 9, Ar51307, pygidium, ventral view, ×2. 10*a–d*, neotype SGU 1402, pygidium, dorsal, posterior, lateral views and enlargement of granulation, note short transverse pleural furrow, *a–c* ×2, *d* ×6. 11*a–c*, Ar51305, small pygidium, dorsal, posterior, and lateral views, ×5.

Figs. 12–17. *Sphaerexochus latifrons* Angelin, 1854. All except fig. 15 from Hemse Marl, north-west part, Hemse Beds. 12*a–c*, Ar30067, complete exoskeleton, lateral view, cephalon, and pygidium, showing aberrant pygidial axis with three rings, Hablingbo, ×2. 13, Ar51322, partial left free cheek, Eske 1, ×3. 14, Ar51316, pygidium, morph A, Snoder 1, ×1·5. 15, Ar30060, partial cranidium, ?Östergarn, figured Angelin 1851, pl. 22, fig. 10, ×1·5. 16, Ar30063, pygidium, morph A, figured Lindström 1885, pl. 14, fig. 17, Visne myr, ×1·5. 17*a*, *b*, Ar51324, pygidium, morph A, Likmide 1, ×2.

PLATE 27



RAMSKÖLD, *Sphaerexochus*

Diagnosis. S3 slightly shorter than S2 (tr.), both very faint. L1 with a rather pointed anteroventral corner. Occipital ring about 0·6 times as wide as maximum width of glabella. Fixed cheek with smaller area than L1. Part of cheek between eye and posterior border furrow as long (exsag.) as posterior border. Lateral border furrow deep. Palpebral furrow continues anteriorly from eye parallel to facial suture and ends opposite S3 in a series of pits. Surface sculpture with smaller and more widely spaced granules than in *S. scabridus*, so that the surface is dominated by smooth intergranule area. Fixed cheeks with a few pits, free cheek with pits beneath eye socle.

No granulation observed on thorax.

Pygidium with width:length ratio about 1·8:1, dimorphic. Morph A bulbous, morph B flatter. Morph A (Pl. 27, figs. 12, 14, 16, 17; Pl. 28, figs. 3–5) with a swollen terminal piece with blunt end, deep and wide interpleural furrows, swollen pleural ridges, and pleural spines forming subsemicircular lobes on margin. Morph B (Pl. 28, figs. 1, 6) with a subtriangular terminal piece with pointed end, narrow and shallow interpleural furrows, low, flat pleural ridges, and a very gently lobated margin. Both morphs have faint notches slightly anterior to midlength laterally on terminal piece, more pronounced on morph A. Very faint anterior pleural furrows may be present (Pl. 28, fig. 5). Surface with denser granulation than on cranidium, but still with granules clearly separate.

Discussion. This is a definite case of pygidial dimorphism. The morphs are found together, morph B less frequent. No dimorphism is observed in the cranidia. Some specimens, e.g. from Visne myr, differ in detail (Pl. 28, fig. 2) from the main bulk of the material, which is from Snoder 1 and 2 and from Eske 1.

Sphaerexochus laciniatus Lindström, 1885

Plate 28, figs. 7–17

v.* 1885 *Sphaerexochus laciniatus* Lindström, pp. 47, 48, pl. 13, figs. 2–6.
v. 1885 *Sphaerexochus scabridus* Angelin; Lindström, pl. 15, fig. 26, *non* Angelin, 1854.

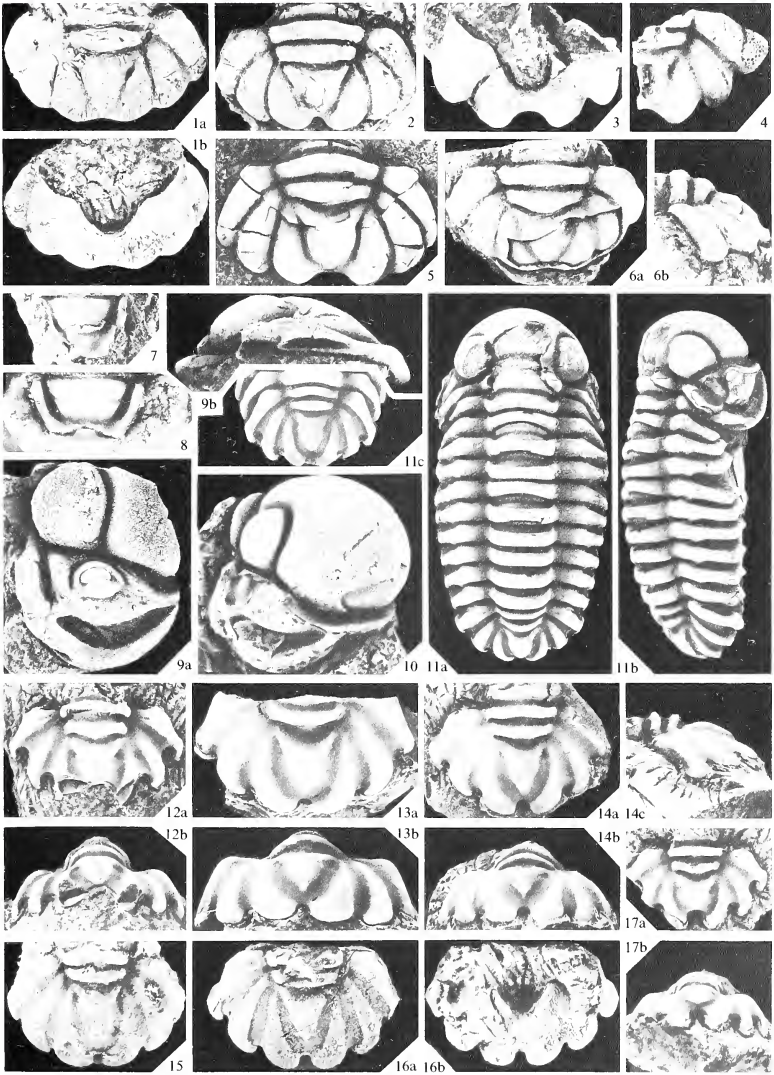
Lectotype. Selected here, Ar30072, complete exoskeleton, Pl. 28, fig. 11*a–c*; figured Lindström, 1885, pl. 13, figs. 2–6, stated by him to be from Kyrkviken, Fårö (Slite Marl), but this is questioned here, since material indistinguishable from this specimen occurs only in the Hemse Beds. The other material included in this species by Lindström is all from the Hemse Beds, but no specimens can be identified.

Additional material. This species is restricted to the limestone areas in the Hemse Beds (lower to upper part), where it is common in the south-western outcrops. Localities: Ardre parish—Ljugarn. Etelhem parish—Etelhem backar; Hageby träskbackar; Sigvalde 1; Tänglings hällar. Linde parish—Linde klint; Sandarve kulle. Lojsta parish—Tornklint; Asa träskbacke. Lye parish—Mannegårde.

EXPLANATION OF PLATE 28

Figs. 1–6. *Sphaerexochus latifrons* Angelin, 1854. Hemse Marl, north-west part, Hemse Beds. 1*a*, *b*, Ar51317, pygidium, morph B, dorsal and ventral views, Snoder 1, ×2. 2, Ar30065, pygidium, morph B?, Visne myr, ×2. 3, Ar51321, partial pygidium, morph A, ventral view, Eske 1, ×2. 4, Ar51320, partial pygidium, morph A, Eske 1, ×2. 5, SGU 1403, crushed and flattened pygidium, morph A, Amlings, ×2. 6*a*, *b*, Ar51318, pygidium, morph B, dorsal and lateral views, Snoder 1, ×2.

Figs. 7–17. *Sphaerexochus laciniatus* Lindström, 1885. Hemse Beds, middle to upper part. Linde Klint (8, 12–17), Sandarve kulle (7, 9, 10), unknown locality (11). 7, Ar30112, hypostome, partly internal mould, ×3. 8, Ar29831, hypostome, internal mould, ×3. 9*a*, *b*, Ar51325, partial cephalon, lateral and oblique ventral views, ×4. 10, Ar30059, cephalon, figured Lindström 1885, pl. 15, fig. 26, ×4. 11*a–c* lectotype Ar30072, complete exoskeleton, dorsal, lateral views, and pygidium, morph A, figured Lindström, 1885, pl. 15, figs. 2–6, ×2. 12*a*, *b*, Ar29857, pygidium, morph A, internal mould, dorsal and posterior views, ×2. 13*a*, *b*, Ar29860, pygidium, morph B, internal mould, dorsal and posterior views, ×2. 14*a–c*, Ar29858, pygidium, morph B, internal mould, dorsal, posterior, and lateral views, ×2. 15, Ar29866, pygidium, morph B, ×2. 16*a*, *b*, Ar29882, pygidium, morph B, dorsal and ventral views, ×2. 17*a*, *b*, Ar29862, pygidium, morph A, internal mould, dorsal and posterior views, ×2.



RAMSKÖLD, *Sphaerexochus*

Diagnosis. S3 and S2 indicated only by break in granulation, S2 1·5 times as long (tr.) as S3. Occipital ring about 0·6 times as wide as maximum width of glabella. Fixed cheek with smaller area than L1. Part of cheek between eye and posterior border furrow slightly longer or equal in length (exsag.) to posterior border. Lateral border narrow. Lateral border furrow deep and fairly wide. Palpebral furrow and rim short (exsag.), ending opposite S2, with one or two pits anterior to this. Cranidium and free cheeks with fine and dense granulation, intermediate in size and density, closer to *S. scabridus* than to *S. latifrons*. Fixed cheek with very few pits, cheek beneath eye with sparse, scattered pits.

Hypostome with very short (sag., exsag.) anterior border, and distinct, continuous anterior border furrow. Middle furrow distinct laterally, fading out one-quarter across middle body (on internal mould). Posterior border with elevated crescent-shaped central area, posterior margin notched medially. Preserved parts of middle body and lateral borders (Pl. 28, fig. 7) with fine and dense granulation, posterior border smooth.

Thorax with maximum pleural length (tr.) reached in sixth segment. Faint, short (tr.) pleural furrows on all segments midway between axial furrow and flexure.

Pygidium long and narrow, dimorphic, width:length ratio 1·6–1·8:1 depending on morph. Axis long and very narrow. Pleural ridges and interpleural furrows angular and sharply delimited. Short (tr.) pleural furrow on anterior pleural ridge. Morph A (Pl. 28, figs. 11, 12, 17) relatively wider, with inflated, elevated, blunt terminal piece, very deep interpleural furrows and pleural ridges that are gently convex in section, ending in fairly long, hooked spines, separated by wide furcations. Morph B (Pl. 28, figs. 13–16) with flat, pointed terminal piece, very shallow interpleural furrows, and flat pleural ridges that end in short, gently hooked spines, separated by narrow furcations. Both morphs with notches anterior to midlength laterally on terminal piece.

Discussion. As with *S. latifrons*, there is no doubt that this species exhibits pygidial dimorphism. More than fifty pygidia have been studied, and the two morphs occur together. A is more common than B. The peculiar shape of the very sharply delimited pleural ridges and interpleural furrows, as well as general proportions and the hooked spines, are shared by the spine-bearing specimens in *S. dimorphus* Perry and Chatterton, 1977, but not by the non-spinose ones.

Sphaerexochus spp.

(Not figured)

Material. Ar29928–29931, three pygidia and a glabella, stated to be from the Lower Visby Marl, 'Visby'; Ar30079–30080, a pygidium and a cranidium, stated to be from Högklint Beds, 'Visby'.

Remarks. These specimens are all poorly preserved. Most pygidia are indistinguishable from *S. scabridus*, and it is not improbable that the horizons given on the nineteenth-century museum labels are wrong, since reference to 'Visby' at that time could indicate a locality quite far from Visby. This supposition is supported by the fact that most of the specimens are water-worn, and were thus found on the beach, and may have been transported quite a distance. However, they are included here to indicate the possible stratigraphical range of the genus on Gotland.

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REFERENCES

ANGELIN, N. P. 1851. *Palaeontologia Svecica.* I: *Iconographia crustaceorum formationis transitionis*, Holmiae. Fasc. 1, 1–24, pls. 1–24.

—— 1854. *Palaeontologia Scandinavica.* I: *Crustacea formationis transitionis.* Lund. Fasc. 2, 21–92, pls. 25–41.

BARRANDE, J. 1846. *Notice préliminaire sur le Systême Silurien et les trilobites de Bohême.* Leipsic. i–vi, 97 pp.

—— 1850. [Bohemian trilobites.] *Ber. Mitt. Freunden naturw. Wien*, **7,** 4–7, 2 text-figs. (unnumbered).

—— 1852. *Systême Silurien du centre de la Bohême. 1ère partie: Recherches paléontologiques*, vol. 1. *Crustacés: Trilobites.* Prague and Paris. i–xxx, 935 pp., 51 pls.

—— 1872. Ibid. *Supplément au vol. 1.* Prague and Paris. xxx, 647 pp., 35 pls.

BARTON, D. C. 1916. A revision of the Cheirurinae, with notes on their evolution. *Wash. Univ. Stud. scient. Ser.* **3** (4), 101–152, one chart.

BEYRICH, E. 1845. *Ueber einige böhmische Trilobiten.* Berlin. 47 pp., 1 pl.

—— 1846. *Untersuchungen über Trilobiten. Zweites Stück.* Berlin. 37 pp., 4 pls.

BOUČEK, B. 1933. O nových trilobitech českého gotlandienu. část. 1. *Věst. st. geol. Úst. čsl. Repub.* **9,** 171–179, pls. 1, 2.

CHATTERTON, B. D. E. and CAMPBELL, K. S. W. 1980. Silurian trilobites from near Canberra and some related forms from the Yass Basin. *Palaeontographica* (A), **167,** 77–119, pls. 9–24.

CLARKSON, E. N. K. and HOWELLS, Y. 1981. Upper Llandovery trilobites from the Pentland Hills, Scotland. *Palaeontology*, **24,** 507–536.

DALMAN, J. W. 1827. Om paleaderna, eller de så kallade trilobiterna. *K. svenska Vetensk-Akad. Handl.* [for 1826], 113–152, 226–294, pls. 1–6.

DEAN, W. T. 1971. The trilobites of the Chair of Kildare Limestone (Upper Ordovician) of eastern Ireland. *Palaeontogr. Soc.* [*Monogr.*], (1), 1–60, pls. 1–25.

HARRINGTON, H. J. 1959. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part O, Arthropoda 1.* Geol. Soc. Amer. and Univ. Kansas press. i–xix, 560 pp., 415 figs.

HAWLE, I. and CORDA, A. J. C. 1847. *Prodrom einer Monographie der böhmischen Trilobiten.* Prague. 176 pp., 7 pls. [Also 1848, *Abh. K. Böhm. Ges. Wiss.* **5,** 117–292, pls. 1–7.]

HEDE, J. E. 1921. Gottlands silurstratigrafi. *Sver. geol. Unders.* C **305,** 100 pp.

—— 1925. Beskrivning av Gotlands silurlager. *In* MUNTHE, H., HEDE, J. E. and VON POST, L. Gotlands geologi. Ibid. C **331,** 130 pp.

HISINGER, W. 1837. *Lethaea Svecica seu petreficata Sveciae, iconibus et characteribus illustrata.* Holmiae. 124 pp., 36 pls.

HOLLOWAY, D. J. 1980. Middle Silurian trilobites from Arkansas and Oklahoma, U.S.A. *Palaeontographica* (A), **170,** 1–85, pls. 1–20.

HORNÝ, R. and BASTL, F. 1970. *Type specimens of fossils in the National Museum, Prague, Volume 1. Trilobita.* Prague. 354 pp., 20 pls.

JAANUSSON, V. 1956. On the trilobite Genus *Celmus* Angelin, 1854. *Bull. geol. Instn. Univ. Uppsala*, **36,** 35–49.

—— LAUFELD, S. and SKOGLUND, R. (eds.) 1979. Lower Wenlock faunal and floral dynamics, Vattenfallet section, Gotland. *Sver. geol. Unders.* C **762,** 294 pp.

LAMONT, A. 1948. Scottish Dragons. *Quarry Mgrs' J.* **31,** 531–535, pl. 1.

LANE, P. D. 1971. British Cheiruridae (Trilobita). *Palaeontogr. Soc.* [*Monogr.*], 95 pp., 16 pls.

—— 1972. New trilobites from the Silurian of north-east Greenland, with a note on trilobite faunas in pure limestones. *Palaeontology*, **15,** 336–364, pls. 59–64.

LARSSON, K. 1979. Silurian tentaculitids from Gotland and Scania. *Fossils Strata*, **11,** 180 pp.

LAUFELD, S. 1974*a*. Silurian Chitinozoa from Gotland. Ibid. **5,** 130 pp.

—— 1974*b*. Reference localities for palaeontology and geology in the Silurian of Gotland. *Sver. geol. Unders.* C **705,** 172 pp.

—— and BASSETT, M. G. 1981. Gotland: the anatomy of a Silurian carbonate platform. *Episodes*, **2,** 23–27.

—— and JEPPSSON, L. 1976. Silicification and bentonites in the Silurian of Gotland. *Geol. För. Stockh. Förh.* **98,** 31–44.

LINDSTRÖM, G. 1885. Förteckning på Gotlands siluriska crustacéer. *Öfvers. K. Vetensk-Akad. Förh. Stockh.* **6,** 37–100, pls. 12–16.

—— 1901. Researches on the visual organs of the Trilobites. *K. svenska Vetensk-Akad. Handl.* **34,** 1–86, 6 pls.

MÄNNIL, R. 1958. Trilobites of the families Cheiruridae and Encrinuridae from Estonia. *Geoloogia-Inst. Uurim.* **3,** 165–212, pls. 1–6. [In Russian; with Russian, Estonian, and English summaries.]

MARTINSSON, A. 1967. The succession and correlation of ostracode faunas in the Silurian of Gotland. *Geol. För. Stockh. Förh.* **89,** 350–386.

NORFORD, B. S. 1981. The trilobite fauna of the Silurian Attawapiskat Formation, northern Ontario and northern Manitoba. *Bull. geol. Surv. Can.* **327,** 15 pp., 11 pls.

ÖPIK, A. A. 1937. Trilobiten aus Estland. *Acta Comment. Univ. tartu.* (A), **32** (3), 1–163, pls. 1–26. [*Pub. Geol. Inst. Univ. Tartu,* **52.**]

PERRY, D. G. and CHATTERTON, B. D. E. 1977. Silurian (Wenlockian) trilobites from Baille-Hamilton Island, Canadian Arctic Archipelago. *Can. J. Earth Sci.* **14,** 285–317, 7 pls.

—— —— 1979. Wenlock trilobites and brachiopods from the Mackenzie Mountains, north-western Canada. *Palaeontology,* **22,** 569–607, pls. 68–76.

PŘIBYL, A. and VANĚK, J. 1964. Několik poznámek ke klasifikaci rodu *Cheirurus* Beyrich (Trilobita). *Čas. národ. Mus.* **133** (2), 93–95, pl. 1. [In German, with Czech summary.]

RAYMOND, P. E. 1913. Subclass Trilobita, pp. 692–729. *In* EASTMAN, C. R. (ed.). *Text-book of paleontology.* London. (2nd edn.), vol. 1. 839 pp., 1594 figs.

SHAW, F. C. 1968. Early Middle Ordovician Chazy Trilobites of New York. *Mem. N.Y. St. Mus. nat. Hist.* **17,** 1–163, pls. 1–24.

THOMAS, A. T. 1981. British Wenlock trilobites. Part 2. *Palaeontogr. Soc.* [*Monogr.*], 57–99, pls. 15–25.

TSCHERNYSCHEW, A. 1893. [The fauna of the Lower Devonian on the western slope of the Urals.] *Trudȳ geol. Kom.* **4** (3), 1–221, pls. 1–14. [In Russian, with German summary.]

WEBER, V. N. 1951. [Upper Silurian trilobites of the U.S.S.R.] *Trudȳ vses. nauchno-issled. geol. inst.* **2,** 1–55, pls. 1–6. [In Russian.]

WHITTARD, W. F. 1934. A revision of the trilobite genera *Deiphon* and *Onycopyge. Ann. Mag. nat. Hist.* (10), **14,** 505–533, pls. 15, 16.

WHITTINGTON, H. B. and EVITT, W. R. 1954. Silicified Middle Ordovician trilobites. *Mem. geol. Soc. Am.,* no. **59,** 1–137, pls. 1–33.

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Note added in proof. Since the completion of the paper, I have collected additional cheirurid material on Gotland. *Deiphon sphaericum* sp. nov. occurs in Högklint Beds, unit a, at Ireviken 1, Stenkumla parish, which confirms the stratigraphical position suggested in text-fig. 1. From the upper Eke Beds at Lau backar 1, Lau parish, there are a few cheirurinid cranidia and hypostomes that can be assigned almost certainly to *Ktenoura conformis,* and the vertical range of this species is thus extended downward.

THE CARBONIFEROUS CORAL *PALAEACIS* IN IRELAND

by JOHN R. NUDDS

ABSTRACT. The tabulate coral *Palaeacis* Haime, 1857 is common in North America, but in Europe only two indigenous species occur, both in Ireland. *P. smythi* Hudson, 1966 is distinguished from *P. axinoides* Smyth, 1929 by having only two corallites and a non-adherent corallum. *P.* sp. nov. has a conical corallum with a single corallite. These species have limited stratigraphical ranges in the Courceyan and basal Chadian stages and are useful zonal indices.

PALAEACIS, usually regarded as a tabulate coral, was founded posthumously by Haime in Milne-Edwards (1857, p. 9) for small wedge-shaped colonial corals from the Lower Carboniferous of North America. Many additional species have since been discovered in North America (see below), but only six species occur elsewhere; two of these are from Ireland.

North America

Haime's genus was based on a single species, *P. cuneiformis*, from the Lower Carboniferous of Indiana (see Milne-Edwards 1860, p. 171). Soon afterwards Meek and Worthen (1860) referred four similar corals also from the Lower Carboniferous of Indiana and Illinois to *Sphenopoterium*, but the identity of these (*S. cuneatum*, *S. enorme*, *S. obtusum*, and *S. compressum*, plus *S. enorme* var. *depressum* described in 1866) with *Palaeacis* (and indeed of *P. cuneiformis* with *S. cuneatum*) was proved by von Seebach (1866, p. 306), who himself described *P. cymba* (1866, p. 309) and *P. umbonata* (1866, p. 309) from the Lower Carboniferous of Iowa. (Kunth (1869, p. 188) later showed these to be synonyms of *S. obtusum*.)

Additional American species have been described from the Lower Carboniferous (Mississippian) by Miller (1892, p. 614) from Indiana (*P. cavernosa*), by Weller (1909, p. 277) from Missouri (*P. bifidus*), by Girty (1910, p. 190) from Arkansas (*P. carinata*), by Snider (1915, p. 70) from Oklahoma (*P. cuneata*), and by Easton (1944, p. 56) from Missouri (*P. conica*). Upper Carboniferous (Pennsylvanian) species have been described by Moore and Jeffords (1945, pp. 195–197) from Texas (*P. testata* and *P. walcotti*) and by Jeffords (1955, p. 11) from New Mexico (*P. kingi*).

Other North American records are summarized by Jeffords (1955, p. 9), who considered that *S. depressum* was synonymous with *S. enorme*, that *S. compressum* was synonymous with *S. obtusum*, and that *P. cuneata* was synonymous with *P. carinata*. Finally, Conkin, Bratcher and Conkin (1976, p. 4; 1978, p. 4) considered that *P. cavernosa* was synonymous with *S. obtusum*.

Europe

American species were discovered in Europe by Perceval (1876, p. 267), who recorded *P. cuneiformis* from the Lower Carboniferous of Bristol. The first European species referred to *Palaeacis* were Kunth's (1869, p. 185) record of *Ptychochartocyathus laxus* Ludwig (1866, pp. 189, 231) from the Lower Carboniferous of Hausdorf, Silesia, and de Koninck's (1872, p. 159) record of *Hydnopora cyclostoma* Phillips (1836, p. 202) from the Lower Carboniferous of Tournai, Belgium, and Northumberland. These species, now considered synonymous, were, however, rejected from *Palaeacis* by Hinde (1896, p. 446) and referred to *Microcyathus*.

Etheridge (1873, pp. 86, 97) described *P. compressa* var. *irregularis* from the Lower Carboniferous of Lanarkshire, but later (Etheridge and Nicholson 1878, p. 210) doubted its affinities.

[Palaeontology, Vol. 26, Part 1, 1983, pp. 211–225, pl. 29.]

Etheridge and Nicholson (1878, p. 224) described *P. cyclostoma koninckii* from the Lower Carboniferous of Tournai, Belgium, but this also now belongs to *Microcyathus*.

Hinde (1896, p. 440) described *P. humilis* from the Lower Carboniferous of Lancashire and Devon, which was also rejected from *Palaeacis* by Smyth (1929, p. 133) and placed in *Microcyathus* (see Jeffords 1955, p. 10).

The only indigenous European species of *Palaeacis* are therefore those from the Lower Carboniferous of County Wexford, Ireland, described by Smyth (1929, p. 126) as *P. axinoides* and by Hudson *in* Hudson, Clarke and Sevastopulo (1966, p. 257) as *P. axinoides smythi*.

Africa, Australasia, and Asia

The genus was recognized in Africa by Termier and Termier (1950, p. 81), who described *P. mauretanicus* from the Lower Carboniferous of Mauretania.

In Australasia Hill (1934, p. 100) discovered the American species, *P. cuneiformis*, from the Lower Carboniferous of Queensland, and Gerth (1921, pp. 120–122) described two indigenous species, *P. regularis* and *P. tubifer*, from the Permian of Timor Island.

Finally, Chudinova (1976, p. 33) recently discovered *Palaeacis* in Russia and described *P. formosa* from the Middle Carboniferous of the southern Verkhoyansk region, northern Siberia.

IRISH RECORDS OF *PALAEACIS*

The first records from Ireland were by de Koninck (1872, p. 158), Etheridge and Nicholson (1878, p. 221), Roemer (1883, p. 517), and Hinde (1896, p. 446), who all listed specimens from 'Hook Point' [= Hook Head], County Wexford, as *P. obtusa* (Meek and Worthen 1860). Smyth (1929, p. 126), after a detailed study of Hook Head material, however, referred the Irish specimens to a new species, *P. axinoides*, which has since been recorded from the Donegal Syncline by George and Oswald (1957, p. 172), and from a borehole at Ballyvergin, County Clare, by Hudson and Sevastopulo (1966, p. 296). I have traced only one of George and Oswald's specimens (HM C7739a, b), which is *Microcyathus cyclostoma* (Phillips).

Smyth (1929, p. 132) also described *Palaeacis* from two particular horizons at Hook Head which differed by possessing only two corallites. Hudson *in* Hudson, Clarke and Sevastopulo (1966, p. 257) found a similar two-corallite form at Feltrim Quarry, County Dublin, and referred these to a new subspecies, *P. axinoides smythi*. Hudson (1966, p. 256) also described a one-corallite specimen from Feltrim Quarry as *Palaeacis* sp. nov.

In addition to these published occurrences *P. axinoides* has recently been recorded from boreholes at Scagh (near Nenagh), County Tipperary (Irish Nat. Grid Ref. R830733) (I. D. Somerville, pers. comm. 1981). Knocktopher, County Kilkenny (Irish Nat. Grid Ref. S538376) (G. Ll. Jones, pers. comm. 1981), and Pallaskenry (near Askeaton), County Limerick (Irish Nat. Grid Ref. R415534) (G. Ll. Jones, pers. comm. 1981). *P. smythi* has recently been collected at Newtown Castle (near Callan), County Kilkenny (Irish Nat. Grid Ref. S464437) (G. Ll. Jones, pers. comm. 1981), Charlestown, County Kilkenny (Irish Nat. Grid Ref. S605177) (M. L. Keeley, pers. comm. 1979), and from a borehole at Moate, County Westmeath (Irish Nat. Grid Ref. N271490). Finally, *P.* sp. has been recorded from a number of boreholes near Silvermines, County Tipperary (Irish Nat. Grid Ref. R840712, R835712) (I. D. Somerville, pers. comm. 1981).

The Irish specimens mentioned herein are reposited in the Geological Museum of Trinity College, Dublin (TCD), the National Museum of Ireland, Dublin (NMI), the British Museum (Natural History), London (BM), and the Hunterian Museum, Glasgow (HM).

Stratigraphical occurrence

Because no formal chronostratigraphical division of the British and Irish Courceyan Stage has been agreed, the stratigraphical occurrence of *Palaeacis* in Ireland is reviewed using the informal chronostratigraphical subdivisions introduced by Sevastopulo (1979). 'Courceyan 1' is coextensive with the VI Miospore Subzone of Clayton *et al.* (1978); 'Courceyan 2' is defined by the base of the PC

Miospore Zone and has its upper limit at the extinction of siphonodellid conodonts; 'Courceyan 3' is equivalent to the *Polygnathus communis carina* Conodont Zone of Groessens (1977); 'Courceyan 4' is equivalent to the *Scaliognathus anchoralis* Conodont Zone and extends to the base of the Chadian.

P. axinoides. Smyth's (1929, 1930) records of *P. axinoides* from Hook Head span much of the marine succession which is entirely Courceyan in age. Text-fig. 1 shows Smyth's lithostratigraphical divisions, the revised nomenclature of Sleeman *et al.* (1974), and their relationship with the Courceyan subdivisions referred to above, based on palynological and conodont work at Hook Head by Higgs (1975), Clayton *et al.* (1977), and Johnston and Higgins (1981).

Smyth's lowermost record (as *Palaeacis* sp.), from the Grey Sandstone Group (1930, p. 539), corresponds to the upper part of the Houseland Sandstone Member of the Porter's Gate Formation (text-fig. 1*a*, *b*), and this horizon lies near the base of Courceyan 2 (text-fig. 1*c*). Smyth (1930, pp. 539, 540) also recorded the species from the succeeding Fish Shales and *Michelinia favosa* Beds, which are equivalent to Sleeman's (1974) Lyraun Cove Shale Member of the Porter's Gate Formation, and the lower part of the Hook Head Formation respectively (text-fig. 1*a*, *b*). The succeeding Bullockpark Bay Dolomite Member is devoid of fossils, but *P. axinoides* makes its last appearance at Hook Head (Smyth 1930, p. 541) 12 m below the top of the Supra Dolomite Beds (= upper part of the Hook Head Formation) (text-fig. 1*a*, *b*), which lies within Courceyan 3 (text-fig. 1*c*).

The borehole specimens are consistent with this range: that from Knocktopher occurs 1·7 m above the base of the Lyraun Cove Shale Member (text-fig. 1*b*, *c*) in Courceyan 2 (G. Ll. Jones, pers. comm. 1981); that from Pallaskenry occurs 12 m above the base of the Ringmoylan Shales, which are approximately equivalent to the Lyraun Cove Shales (G. Ll. Jones, pers. comm. 1981); those from Ballyvergin occur 4 m below and 12 m above the 'Ballyvergin Shale', which, according to conodont evidence of Clayton *et al.* (1980, pp. 85–89), would lie within Courceyan 2 and 3 respectively; finally, that from Scagh also occurs in Courceyan 2, 1 m below the 'Ballyvergin Shale' (I. D. Somerville, pers. comm. 1981).

P. smythi. Smyth's (1929, p. 132; 1930, p. 542) records of *P. axinoides* from the *Chonetes* Beds, at the top of the Hook Head Formation (text-fig. 1*a*, *b*), are shown herein to belong to *P. smythi*. This species therefore appears at Hook Head soon after the last appearance of *P. axinoides* in the upper part of Courceyan 3 (text-fig. 1*c*).

The specimen from Charlestown occurs in the Iverk Limestone Member, which is also Courceyan 3 (M. L. Keeley, pers. comm. 1979), that from Newtown Castle is from the Mallardstown Member, which is either Courceyan 3 or 4 (G. Ll. Jones, pers. comm. 1981), while that from the Moate borehole (depth 112 m) is certainly from Courceyan 4 (B. M. Thornbury, pers. comm. 1981).

The exact age of the specimens from Feltrim Quarry is difficult to ascertain; palynological samples from the Cover Shales, in which they occur, have been barren and conodont extractions have not been completely conclusive. The latter indicate either Courceyan 4 or early Chadian (Marchant 1978, p. 53), but on the basis of regional correlation they are more likely to be earliest Chadian (T. R. Marchant, pers. comm. 1979).

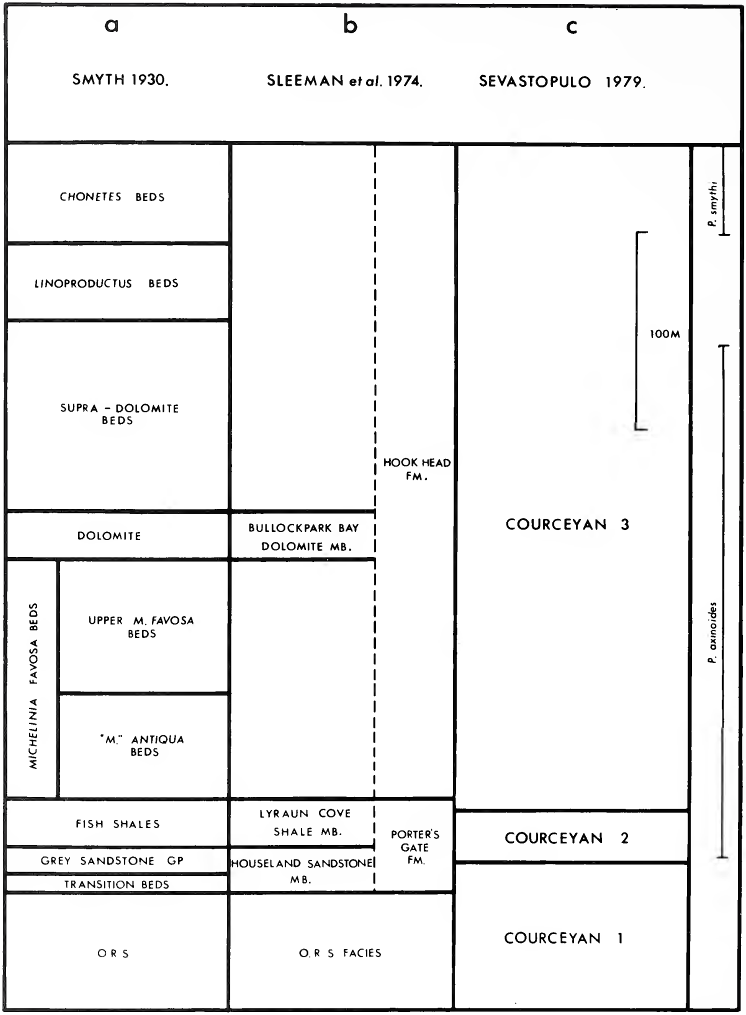
P. sp. nov. Conodonts from the Intra-Reef Shales of Feltrim Quarry, which have yielded the only known occurrence of this species, suggest that *P.* sp. nov. is of Courceyan 4 age (Marchant 1978, p. 53).

SYSTEMATIC PALAEONTOLOGY

Class ANTHOZOA Ehrenberg, 1831
Order TABULATA Milne-Edwards and Haime, 1850
Family PALAEACIDAE Roemer, 1883

[*nom. correct.* Miller, 1889 *ex* Palaeaciden Roemer, 1883.]

Family name. Moore and Jeffords (1945, p. 195) proposed Palaeacidae, but it was already available. Hill and Stumm (1956, p. 466) credited it to Počta (1902) and Jeffords (1955, p. 8) credited it to Miller (1892), but it was



TEXT-FIG. 1. Lithostratigraphical succession at Hook Head, County Wexford (columns *a*, *b*), with chronostratigraphical subdivisions (column *c*) and range of *Palaeacis axinoides* and *P. smythi*. GP = Group, MB = Member, FM = Formation.

first used in this form by Miller (1889, p. 153), and had already been used in the vernacular by Roemer (1883, p. 515). Under the present Rules of Nomenclature (Article 11(eii)) Roemer is credited with the authorship.

Subfamily PALAEACINAE Roemer, 1883

Genus PALAEACIS Haime *in* Milne-Edwards, 1857

[*nom. correct.* Milne-Edwards, 1860 *ex Paloeacis* Haime in Milne-Edwards, 1857.] [= *Sphenopoterium* Meek and Worthen, 1860; *Paleacis* Snider, 1915 (*nom. null.*); *Palaecis* Smith, 1930 (*nom. null.*).]

Diagnosis. Colonies small and wedge-shaped or conical; often adherent in young stages, but later free; few rounded, atabulate corallites radiate from base of colony. Walls thick, in two layers; internal wall of fibrous calcite, external wall of small calcite plates, both permeated by canals opening as pores. External surface of ridged coenenchyme; reproduction by lateral increase.

Type species. Palaeacis cuneiformis Haime *in* Milne-Edwards 1857, p. 9, pl. E1; fig. 2*a–d*; designated by monotypy; from Salem Limestone, Salem Formation, Meramecian (Middle Mississippian), Spergen Hill, Washington County, Indiana, North America.

Discussion. The genus, as diagnosed herein, excludes *Microcyathus* Hinde (1896), which differs by its aperforate internal wall, but is very closely allied. The relationship between these genera needs closer attention. *Ptychochartocyathus* Ludwig (1866) has also been identified with *Palaeacis*, but its type species, *P. laxus*, almost certainly belongs to *Microcyathus*.

Nomenclature. There has been controversy over the authorship of *Palaeacis*, many works attributing it to Milne-Edwards (e.g. Roemer 1883, p. 515; Gerth 1921, p. 120; Smyth 1929, p. 125), as its first mention was one year after Haime's death, in Milne-Edwards (1857). There was initially no indication that the name should not be attributed to Milne-Edwards, but later (1860) he revealed that Haime had described it before his death in a '*note inédite*'. According to the Rules of Nomenclature (Article 50) this is sufficient to credit the genus to Haime. There has also been disagreement over the spelling; the original citation in 1857 being '*Paloeacis*'. In 1860 this was altered, presumably by Milne-Edwards, to '*Palaeacis*', which appears twice in the index, and so must be considered as an intentional emendation. Although there is no verifiable evidence that Haime's original spelling was in error, it is reasonable to suppose that he derived the name from the Greek *palaios* (= ancient) and *akis* (= barb). The corallum of Haime's type species, *P. cuneiformis*, is barbed when viewed in profile. If, therefore, one regards Haime's spelling as an inadvertent error, Milne-Edwards's emendation becomes justified, and the usual spelling of *Palaeacis* can be retained.

Palaeacis axinoides Smyth, 1929

Plate 29, figs. 1–12, text-figs. 4*a*, *b*, 5

1929 *Palaeacis axinoides*, sp. nov.; Smyth (*pars*), p. 126, pl. 6, figs. 1–9; pl. 7, figs. 1–9; pl. 8, figs. 1–8; *non* pl. 6, figs. 10–12 [which are *P. smythi* Hudson].

Diagnosis. Wedge-shaped *Palaeacis* with up to twenty-four corallites. Normally adherent in young stages, with supporting bodies included in colony base.

Type specimens. Holotype, TCD T159, Pl. 29, figs. 1, 2; from Hook Head Formation, Courceyan Stage, Lower Carboniferous, 730 m ENE of lighthouse, Hook Head, County Wexford (Irish Nat. Grid Ref. X734973); original designation Smyth 1929, p. 126, pl. 6, fig. 1*a–c*.

Paratypes, BM R26151, BM R26152, NMI 98-1928; locality and horizon as for holotype; original designation Smyth 1929, p. 126.

Material. Over 400 specimens (TCD T159, F160–F167, F179–F190, 4648–4651, 4655–4658, 4660–4682, 4687–4696, 4702–4836, 4838–4841, 4843–4863, 4870–4922) from Hook Head, County Wexford. One specimen (TCD 19977) from Ballyvergin borehole, County Clare. [Hudson and Sevastopulo (1966, p. 296) listed two specimens from Ballyvergin, but the younger specimen is now missing from the collection.] One specimen from Scagh borehole, County Tipperary. One specimen (TCD 19981) from Knocktopher borehole, County Kilkenny. One specimen (TCD 19982) from Pallaskenry borehole, County Limerick.

Description. Corallum small and wedge-shaped with calices at the thicker end of the wedge. The lower peripheral margins are devoid of calices and diverge from the colony base at approximately 130°.

Number of corallites usually between two and fourteen, but as many as twenty-four have been observed; text-fig. 2 illustrates the frequency of specimens at each corallite stage. The two-corallite stage corallum attains a mean height of 6·8 mm, a mean width of 7·7 mm, and a mean thickness of 3·8 mm. These parameters increase in parallel during astogeny (text-fig. 3) and the largest colony recorded (23-corallite stage) had a height of 30·5 mm, a width of 33·7 mm, and a thickness of 16·2 mm.

External surface of the corallum has a characteristic ornament (Pl. 29, fig. 3) of irregular, sub-parallel, close-set ridges and grooves which run discontinuously down the sides of the corallum. They may be straight or sinuous and often bifurcate distally.

Corallites generally sub-circular, but may be polygonal, and reach a maximum diameter of 5–7 mm. Calices deep (up to 5 mm) with almost vertical inner walls marked by forty to fifty longitudinal septal ridges (Pl. 29, fig. 3). Concentric growth lines, normal to the septal ridges, may also occur (Pl. 29, fig. 3) so that the overall appearance is granular. The calice floor is flat, unornate, and tabulae do not occur.

Corallite wall usually 1–2 mm thick and consists of two layers (Pl. 29, figs. 6, 7). An internal layer forms the corallites' floors and walls (Pl. 29, fig. 6) and is composed of fibrous calcite. It is thick on the floors, but thins distally and in transverse section the septal ridges can be seen on its inner surface (Pl. 29, fig. 7). The external tissue forms an outer coating over the whole colony (Pl. 29, figs. 6, 7) and consequently corallite walls on the edge of the colony consist of two layers while those between corallites are composed only of internal tissue.

The external tissue is not fibrous, but is composed of successive calcite plates (200 μm wide) (text-fig. 4*a*) normal to the colony surface. The surface expression of each plate is a ridge, and of each plate boundary is a groove, forming the characteristic surface ornament. Their microstructure was described in detail by Smyth (1929, pp. 128, 129).

Corallite walls are penetrated by canals normal to the wall surface which pass through both layers of tissue (text-fig. 4*a*). In the external tissue they excavate the boundaries between adjacent plates and are 80–120 μm wide. They join with canals in the internal tissue which are wider (up to 200 μm) and often forked (Pl. 29. fig. 6). Canals also occur in the internal tissue between two corallites, and in the internal tissue of the corallite floor when they radiate downwards and outwards (Pl. 29, fig. 6).

EXPLANATION OF PLATE 29

Figs. 1–12. *Palaeacis axinoides* Smyth, 1929. 1, 2, TCD T159 (holotype), lateral views with undistorted base in mature corallum, ×2. 3, TCD F186, lateral view with external surface ornament of ridges and grooves and longitudinal septal ridges, concentric growth lines and pores in the calices, ×2. 4, TCD 4884, apical view with pores on floor and walls of calice, ×2. 5, TCD 4738a, lateral view with canals opening on to external surface as pores, ×2. 6, TCD F181d, longitudinal thin section with two-layered corallite wall showing forked canals in internal tissue and calcite plates in external tissue, ×2. 7, TCD F187b, transverse thin section with two-layered corallite wall and septal ridges on the internal layer, ×2. 8, TCD F180, longitudinal thin section showing absence of foreign inclusion in base of corallum, ×2. 9, 10, TCD F187d, TCD F179b, longitudinal thin sections with foreign inclusions in base of corallum, ×2. 11, 12, TCD F165, TCD F182, lateral views with brachiopod shell fragments protruding from colony base, ×3, ×2. All specimens from Hook Head Formation, Courceyan Stage, Lower Carboniferous, Hook Head, County Wexford.

Figs. 13–23. *Palaeacis smythi* Hudson, 1966. 13, TCD F177 (holotype), lateral view with undistorted base to corallum and slight notch between distal portions of corallites, ×4. 14, 15, TCD 19955, TCD F172, lateral views with corallites developed as well-separated branches, ×3, ×2. 16, TCD 4869, apical view with incipient third corallite, ×3. 17, 18, TCD F169, lateral and oblique apical views showing growth lines on external surface, regular base to corallum, and septal ridges in calice, ×3, ×4. 19, TCD F171, lateral view with growth lines on external surface, ×3. 20, TCD 4866j, apical view with pores on floor and walls of calice, ×4. 21, TCD 4698, apical view of ? single corallite stage, ×5. 22, 23, TCD 19979, TCD 19980, longitudinal thin sections with two-layered corallite wall and canals in both layers, ×2. 13, 15–23 from Hook Head Formation, Courceyan Stage, Lower Carboniferous, Hook Head, County Wexford; 14 from Cover Shales, ? Chadian Stage, Lower Carboniferous, Feltrim Quarry, County Dublin.

Figs. 24, 25. *Palaeacis* sp. nov. TCD 19511, lateral and apical views, ×4, ×5. From Intra-Reef Shales, Courceyan Stage, Lower Carboniferous, Feltrim Quarry, County Dublin.

PLATE 29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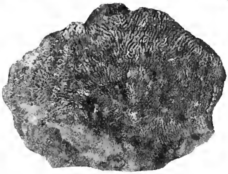
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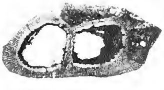
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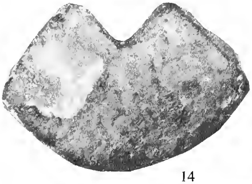
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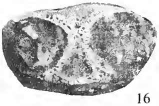
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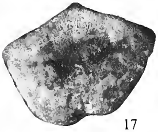
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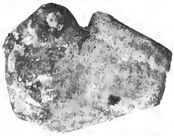
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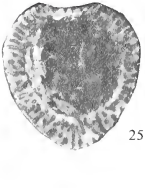
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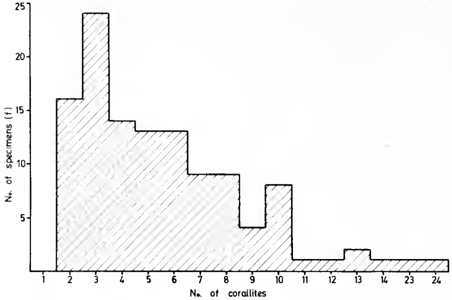
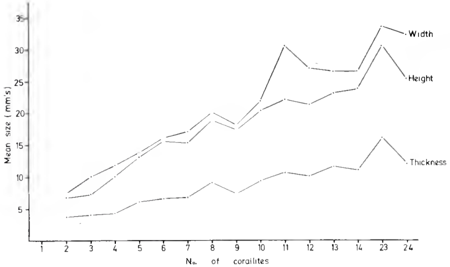
NUDDS, *Palaeacis*



TEXT-FIG. 2. Frequency of specimens at each stage of corallite development in *Palaeacis axinoides*.



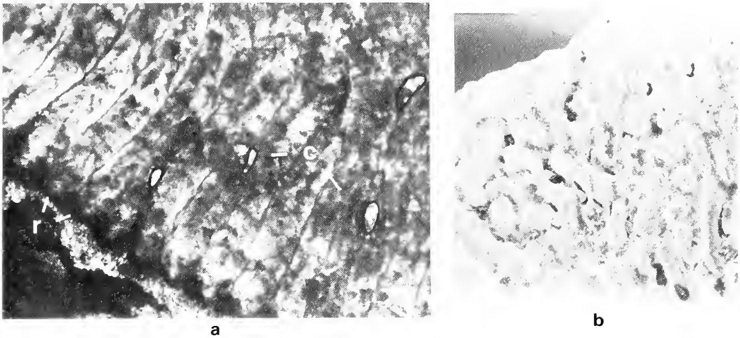
TEXT-FIG. 3. Growth of *Palaeacis axinoides* related to each stage of corallite development.

All canals eventually open on to the external surface (Pl. 29, fig. 5) or into the calices as pores (Pl. 29, fig. 4). Externally they occur in the grooves of external tissue (text-fig. 4*b*), on the calice walls they occur between the septal ridges (Pl. 29, fig. 3), and on the calice floors they are disposed in a radial pattern (Pl. 29, fig. 4).

In longitudinal section a foreign inclusion is nearly always revealed proximally (Pl. 29, figs. 9, 10) and in immature examples it may protrude from the colony base. Brachiopod, bivalve, crinoid, and gastropod fragments have all been observed (Pl. 29, figs. 11, 12). In other immature coralla the inclusion is completely concealed, but is still discernible owing to its awkward shape distorting the colony base. Many coralla in the two, three, and four corallite stages have an irregular base, but in most mature specimens the inclusion is invisible externally and the colony base is regular (Pl. 29, fig. 1). Any irregularities due to its presence have become gradually masked by progressive thickening of the surrounding external tissue.

Longitudinal sectioning has, however, occasionally revealed an absence of any inclusion in both immature and mature examples (Pl. 29, fig. 8). In such two-, three-, and four-corallite coralla the colony base is perfectly regular.

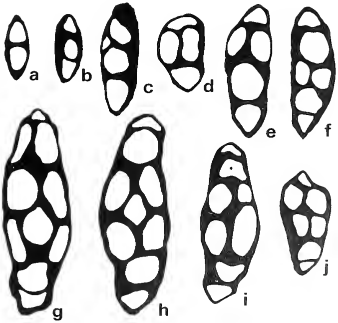
Astogeny. Development of the protocorallite. The foreign inclusion usually embedded in the colony base clearly formed a support during initial colony development. Settling planulae preferred the hard base that a shell fragment offered on which to commence protocorallite skeleton secretion. Growth lines in the external tissue parallel to the surface of the corallum suggest the tissue accreted by addition of layers to the external surface and,



TEXT-FIG. 4. *Palaeacis axinoides* Smyth, 1929. *a*, TCD F181d, photomicrograph showing external layer of corallite wall consisting of successive calcite plates, each of which has a surface expression as a ridge (r), and canals excavating the boundaries between plates (c), × 36; *b*, TCD 4660, SEM photograph showing pores on external surface (i.e. canal openings) occurring between the ridges of external tissue, × 20.

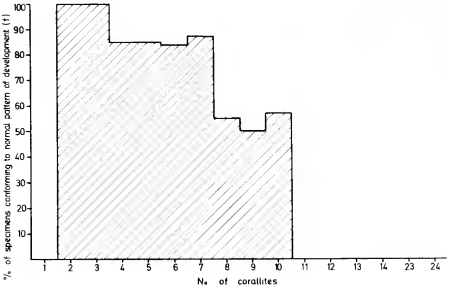
therefore, that the surface was enveloped in coenosarc. The coenosarc gradually extended over the supporting shell fragment (Pl. 29, fig. 12), eventually spread under its lower surface, and finally fused, trapping the supporting body inside the colony. At this moment the colony ceased its adherent mode of life and became free. Envelopment of the supporting body was usually complete by the two-corallite stage, but up to fourteen corallites may have formed before this occurred. Some colonies detached themselves from the support before enveloping it, leaving a scar on the external surface which reflects the shape of the shell fragment.

Corallite addition. No specimens of a one-corallite stage of *P. axinoides* have been found (see *Remarks* on *P.* sp. nov.), probably because the first bud appeared after such a short period of protocorallite growth. (The smallest well-developed two-corallite stage recorded is only 2·5 mm in height.) Further increase of corallites is illustrated in text-fig. 5; the first three corallites form in a single row (as in type species, *P. cuneiformis* (see Conkin, Bratcher and Conkin 1976)), from the four- to eight-corallite stage new buds were added in two rows, and from the ninth corallite onwards a third row was initiated. Symmetry was maintained in the colony by the positioning of each



TEXT-FIG. 5. Camera-lucida drawing showing astogeny of *Palaeacis axinoides* from the two-corallite stage to the ten-corallite stage, × 3·5. *a*, TCD 4796, *b*, TCD 4902c, *c*, TCD 4902a, *d*, TCD 4702, *e*, TCD 4836, *f*, TCD 4838, *g*, TCD F163, *h*, TCD F161, *i*, TCD T159, *j*, TCD 4887.

new bud. This pattern (text-fig. 6) occurs consistently up to the seven-corallite stage. In the eight- to ten-corallite stages approximately half the observed specimens conform, but above this number no pattern was discernible, owing to an insufficiency of samples.



TEXT-FIG. 6. Frequency of specimens conforming to normal pattern of corallite development in *Palaeacis axinoides*.

Palaeacis smythi Hudson *in* Hudson, Clarke and Sevastopulo, 1966

Plate 29, figs. 13-23

1929 *Palaeacis axinoides*, sp. nov.; Smyth (*pars*), p. 126, pl. 6, figs. 10-12; *non* pl. 6, figs. 1-9; pl. 7, figs. 1-9; pl. 8, figs. 1-8 [which are *P. axinoides* Smyth].

1966 *Palaeacis axinoides smythi* subsp. nov.; Hudson *in* Hudson, Clarke and Sevastopulo, p. 257.

Diagnosis. Wedge-shaped *Palaeacis* with only two corallites (rarely three) forming well-separated branches. Never adherent in young stages, no supporting bodies included in colony base.

Holotype. TCD F177, Pl.29, fig. 13; from Hook Head Formation, Courceyan Stage, Lower Carboniferous, 230 m south-east of Slade Castle, Hook Head, County Wexford (Irish Nat. Grid Ref. X747985); original designation Hudson *in* Hudson, Clarke and Sevastopulo 1966, p. 257; figured Smyth 1929, pl. 6, fig. 11.

Material. Fifty-eight specimens (TCD F168-F178, 4683-4686, 4697-4701, 4864-4869, 19979, 19980) from Hook Head, County Wexford. Twenty-one specimens (TCD 19955-19975) from Feltrim Quarry, County Dublin. One specimen (TCD 19983) from Newtown Castle, County Kilkenny. One specimen (TCD 19976) from Charlestown, County Kilkenny. One specimen (TCD 19978) from Moate borehole, County Westmeath.

Description. Similar in most features (surface ornament, wall structure, and canal system) to *P. axinoides*, but number of corallites restricted to two almost without exception. These diverge from the colony base at a mean angle of 120° in the Feltrim sample, and at 65° in the Hook Head sample.

From Hook Head (see Smyth 1929, p. 132) thirty-seven out of forty specimens possess two corallites and at Feltrim seventeen out of twenty-one are likewise. In the three exceptions from Hook Head one has a well-developed third corallite (figured Smyth 1929, pl. 6, fig. 12), one has an incipient bud between the first two corallites (Pl. 29, fig. 16), and the other is apparently a single corallite (Pl. 29, fig. 21). In the four exceptions from Feltrim one has a well-developed third corallite between the first two corallites, while in the others the third 'corallites' are small, secondary apertures opening on the sides of the two main branches.

The absence of a third corallite between the first two, coupled with their continued divergence, resulted in the eventual separation of the first two corallites and the development of two elongated branches, the margins of which are free. This feature is common in Feltrim specimens (Pl. 29, fig. 14), but rare at Hook Head (Pl. 29, fig. 15), where often only a slight notch developed (Pl. 29, fig. 13).

The corallum has a mean height of 8·0 mm at Hook Head and 9·0 mm at Feltrim, a mean width of 9·9 mm at Hook Head and 12·3 mm at Feltrim, and a mean thickness of 4·2 mm at Hook Head and 5·3 mm at Feltrim.

Corallites oval when in contact at the colony base, but after separation become circular and reach a mean diameter of 5·8 mm. Calices deep (up to 4 mm), the steep inner walls marked with concentric growth lines and about fifty longitudinal septal ridges (Pl. 29, fig. 18).

Unfortunately, the specimens from Hook Head and Feltrim have been silicified and their microstructure destroyed. However, the least altered coralla (Pl. 29, fig. 23) suggest an external tissue composed of calcite plates as in *P. axinoides* and a thick internal tissue (Pl. 29, figs. 22, 23). Canals in both layers of tissue more numerous than in *P. axinoides*. Almost every boundary between the plates of external tissue is excavated by a canal (80–120 μm wide) which passes into a wider canal (200 μm wide) in the internal tissue (Pl. 29, fig. 23).

Longitudinal sectioning of numerous coralla has revealed an absence of included supporting bodies. Consequently, the colony base is not distorted by accommodating awkward-shaped objects, and instead is perfectly regular. The contours of the protocorallite and its offset are clearly visible (Pl. 29, fig. 17), the latter disposed slightly above the former, and separated from it by a slight notch.

Astogeny. Records of a one-corallite stage in *Palaeacis* are rare (see *Remarks* on *P*. sp. nov.), but one specimen from Hook Head, a shallow cup 2·5 mm high and 3·5 mm in diameter, appears to consist of a single corallite (Pl. 29, fig. 21). The second corallite usually appears much sooner, sometimes when the protocorallite is only 0·5 mm high, and the early two-corallite stage is similar to that of *P. axinoides* except for its regular base (Pl. 29, fig. 13). The late two-corallite stage, with its corallites as separate branches (Pl. 29, fig. 14), is usually the most advanced astogenetic stage reached. Rarely a third corallite develops in the space created by the divergence of the first two (Pl. 29, fig. 16).

Discussion. Specimens of this species were described by Smyth (1929, p. 132) from two horizons in the *Chonetes* Beds at the top of the Hook Head succession in County Wexford (text-fig. 1*a*), differing from typical *P. axinoides* in several respects:

1. Most possess only two corallites and none possesses more than three.
2. Corallites grow as separate independent branches.
3. Most are larger than typical two-corallite specimens of *P. axinoides* (height, width, thickness).
4. No evidence that they were adherent in young stages; supporting bodies are not found at the colony base, which is regular and undistorted.

Smyth (1929) doubted that they belonged to a separate species and argued that they were stunted forms of *P. axinoides* responding to an unfavourable environment; other species in these beds (e.g. *Vaughania vetus* Smyth, 1927) were also dwarfed. Either genetic control or phenotypic variation could explain the differences listed above. If a colony is restricted to two corallites (either genetically or ecologically), and if those corallites continue to grow, they will also continue to diverge and will eventually separate as independent branches. They will also be larger (height, width, and thickness) than typical two-corallite members of *P. axinoides*.

Phenotypic variation cannot explain the absence of an included supporting body. Suitable supports were certainly available, as *V. vetus* is found in the same beds attached to brachiopod and bivalve shells. Smyth considered that the support had been obscured by silification, but in these beds it is not intense and in any case the regular colony base provides external evidence of its absence. *P. axinoides* does sometimes lack such a support, but there seems no reason why stunting should only affect the few non-adherent colonies. One might also expect an ecological stunting to have more effect on corallite size than on colony size (i.e. one would not expect the almost total restriction to two corallites). It seems more likely that these two-corallite forms are a distinct species, genetically restricted to two corallites by a mutation which affected a sample of non-adherent *P. axinoides*. Their distinct stratigraphical occurrence supports this theory. Hudson *in* Hudson, Clarke and Sevastopulo (1966, p. 257) found a similar two-corallite fauna at Feltrim Quarry, County Dublin, likened them to those from Hook Head, and, believing corallite number to be worthy at least of sub-specific separation, described them as *P. axinoides smythi*, which is here elevated to specific level.

P. smythi is similar to the American *P. bifidus* from the Lower Carboniferous of Missouri (Weller 1909, p. 277), which is also restricted to two corallites and has a comparable morphology. It is slightly larger in size, but specimens figured by Weller (1909, pl. 10, figs. 8–11) are very close to some from

Feltrim Quarry. *P. conica* (Easton 1944, p. 56), from the Lower Carboniferous of Missouri, also has two corallites, but the corallum is conical and not wedge-shaped (see *P.* sp. nov.).

In Ireland this species is most similar to *P. axinoides*. Mature examples are easily distinguishable as *P. axinoides* has more than two corallites. Immature specimens of *P. smythi*, before corallite separation, are, however, very similar to immature two-corallite *P. axinoides*. Distinction is still usually possible as *P. axinoides* normally has an included supporting body and consequently an irregular base; *P. smythi* has no such inclusion and a regular base. Occasionally *P. axinoides* does not possess a supporting body, in which case the two-corallite stage is indistinguishable from immature *P. smythi*. Separation is then only possible by examination of a population; *P. smythi* is characterized by an almost total domination of two-corallite stages, whereas *P. axinoides* exhibits a frequency distribution of corallite stages as shown in text-fig. 2.

Palaeacis sp. nov.

Plate 29, figs. 24, 25; text-fig. 7

1966 *Palaeacis* sp. nov.; Hudson *in* Hudson, Clarke and Sevastopulo, p. 256.

Diagnosis. Conical *Palaeacis* with a single corallite. ?Not adherent in young stages, no supporting bodies included in colony base.

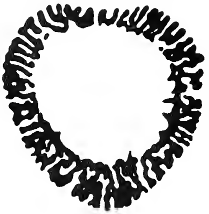
Material. One specimen (TCD 19511) from Feltrim Quarry, County Dublin.

Description. Corallum consists of a single conical corallite, 6·8 mm high, the sides diverging from the apex at about 40° (Pl. 29, fig. 24). Two transverse constrictions on the outer surface, approximately 2 mm and 4 mm from the base, may represent external growth lines. The base tapers to a fine point, which is broken in the only available specimen, but the corallum is almost complete and there is no evidence of any scar of attachment to a supporting body.

The external surface ornament of ridges and grooves is identical to other species of *Palaeacis*, but the single specimen has been polished distally, so details of the calice are not known. In transverse section, however, the corallite is sub-circular with a maximum diameter of 5·9 mm (Pl. 29, fig. 25). There is no axial structure, but projecting into the calice from the wall are a number of random extensions (right-hand side of text-fig. 7) comparable to the septal ridges of *P. axinoides* and *P. smythi*.

The wall is up to 1·2 mm thick, and is regularly traversed by numerous canals (120 μm wide) normal to the wall surface (text-fig. 7), which open interiorly and exteriorly as pores. Externally they always occur in the grooves of external tissue (text-fig. 7).

The preservation is such that it is impossible to elucidate wall microstructure, but septal ridges in the calices suggest a similarity with the internal tissue of *P. axinoides* and *P. smythi*, while the regular canals, their magnitude and consistent position opposite external grooves, recall the external tissue of these species. In this specimen the canal walls would correspond to the plates of external tissue described on p. 216 and would be of the order of 200 μm in width, comparable to those in *P. axinoides*. In other words, the corallite wall in *P.* sp. nov. is probably double-layered as in other species of *Palaeacis*.



TEXT-FIG. 7. Camera-lucida drawing of transverse section of *Palaeacis* sp. nov. showing numerous canals in corallite wall and ? septal ridges extending into calice (right side), × 8.

Discussion. There is too little material for adequate sectioning, and there is accordingly no direct evidence of tabulae and supporting bodies, or the wall structure. It is safe to assume that tabulae do not exist; there is no trace of them in the one transverse section and they are unknown in *Palaeacis*. It is also unlikely that a supporting body is included in the colony base; this tapers to a fine point while a supporting body would distort it as in *P. axinoides*.

Specimens of *Palaeacis* with one corallite are rare: Conkin, Bratcher and Conkin (1976, p. 13) alleged that Smyth (1929, p. 130) recorded a one-corallite stage of *P. axinoides*, but he was actually describing a postulated astogeny deduced from growth lines on mature specimens. Etheridge and Nicholson (1878, p. 222) mentioned a one-corallite stage of '*P.*' *cyclostoma*, and Hinde (1896, p. 441, pl. 23, fig. 7) figured a one-corallite stage of '*P.*' *humilis*, but these are both now placed in *Microcyathus*. The only unquestionable records are those of Williams (1943, p. 59) and Conkin, Bratcher and Conkin (1976, p. 13), who reported one-corallite stages in *P. enormis* and *P. cuneiformis* respectively, and the description in this paper of a one-corallite stage of *P. smythi*. In all three cases the specimens were interpreted as the first astogenetic stage of a colonial species, but with *P.* sp. nov. there are three possible explanations. (1) It could be a one-corallite stage of the colonial *P. smythi*, the only other species present at Feltrim. This is untenable because the one-corallite stage of *P. smythi* is a shallow, rounded cup (Pl. 29, fig. 21), not a slender, pointed cone, and never attains a height of 6 mm before budding. (2) It could be the one-corallite astogenetic stage of another colonial species yet unrecorded from Feltrim. *P. conica* (Easton 1944, p. 56), from the Kinderhookian of the Mississippi Valley, has a comparable conical corallum and only differs from the Feltrim specimen in possessing a small secondary corallite at the distal end of the cone. It is possible that the Feltrim specimen is an example of *P. conica* that has not yet budded. *P. conica*, known from only two specimens, is 12 mm in height. The fact that no other American species are known from Ireland, and vice versa, suggests, however, that the two are unlikely to be conspecific and *P.* sp. nov. is more probably a separate species which has evolved a conical colony by homeomorphy. (3) The final explanation is that this is a solitary species of *Palaeacis*. As such it would be unique amongst the tabulate corals, which are generally considered an exclusively colonial group. Conversely, the existence of solitary *Palaeacis* might suggest that the genus is not a tabulate coral.

Whether it is solitary, or whether it is a colonial species awaiting its first bud, is impossible to determine until more material is available. However, its gross morphology is so unlike any astogenetic stage of either *P. axinoides* or *P. smythi* that it is here considered a distinct species.

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REFERENCES

CHUDINOVA, I. I. 1976. The first find of *Palaeacis* (Tabulata) in the Carboniferous of the Verkhoyansk region. *Paleont. Zh.* **10** (3), 30-35, pl. 1. [In Russian.]

CLAYTON, G., COLTHURST, J. R. J., HIGGS, K., JONES, G. LL. and KEEGAN, J. B. 1977. Tournaisian miospores and conodonts from County Kilkenny. *Bull. geol. Surv. Ireland*, **2**, 99-106.

—— HIGGS, K., KEEGAN, J. B. and SEVASTOPULO, G. D. 1978. Correlation of the palynological zonation of the Dinantian of the British Isles. *Palinologia*, **1**, 137-147, pl. 1.

—— JOHNSTON, I. S., SEVASTOPULO, G. D. and SMITH, D. G. 1980. Micropalaeontology of a Courceyan (Carboniferous) borehole section from Ballyvergin, County Clare, Ireland. *J. Earth Sci. R. Dubl. Soc.* **3**, 81-100.

CONKIN, J. E., BRATCHER, T. M. and CONKIN, B. M. 1976. *Palaeacis cuneiformis* Haime, 1857, in Milne-Edwards, 1860, emended: its morphology, ontogeny, and stratigraphic significance. *University of Louisville Studies in Paleontology and Stratigraphy*, **5**, 27 pp., 5 pls.

CONKIN, J. E., BRATCHER, T. M. and CONKIN, B. M. 1978. *Palaeacis obtusa* (Meek and Worthen), 1860, emended: its morphology, ontogeny, and stratigraphic significance. Ibid. **7,** 26 pp., 5 pls.

EASTON, W. H. 1944. Corals from the Chouteau and related formations of the Mississippi Valley region. *Rep. Invest. Ill. St. geol. Surv.* **97,** 93 pp., 17 pls.

EHRENBERG, C. G. 1831. *Symbolae physicae; seu icones et descriptiones corporum naturalium novorum . . . Pars Zoologica, 4.* Berlin. 10 pls. with descriptive letterpress.

ETHERIDGE, R. Jnr. 1873. Appendix 3. Notes on certain genera and species . . ., pp. 93–105. *In* GEIKE, A. Explanation of Sheet 23. Lanarkshire: Central Districts. *Mem. geol. Surv. U.K.* Edinburgh. 107 pp.

—— and NICHOLSON, H. A. 1878. On the genus *Palaeacis*, and the species occurring in British Carboniferous rocks. *Ann. Mag. nat. Hist.* **1** (5), 206–227, pl. 12.

GEORGE, T. N. and OSWALD, D. H. 1957. The Carboniferous rocks of the Donegal Syncline. *Q. Jl geol. Soc. Lond.* **113,** 137–183, pls. 14–16.

GERTH, H. 1921. Die Anthozoën der Dyas von Timor. *In* WANNER, J. Paläontologie von Timor, **9** (16), 67–147, pls. 145–150. Stuttgart.

GIRTY, G. H. 1910. New genera and species of Carboniferous fossils from the Fayetteville Shale of Arkansas. *Ann. N.Y. Acad. Sci.* **20,** 189–238.

GROESSENS, E. 1977. Distribution de conodontes dans le Dinantien de la Belgique. *Int. Symp. Belgian Micropaleontol. Limits, Namur 1974,* **17,** 1–193.

HIGGS, K. 1975. Upper Devonian and Lower Carboniferous miospore assemblages from Hook Head, County Wexford, Ireland. *Micropaleontology,* **21,** 393–419, pls. 1–7.

HILL, D. 1934. The Lower Carboniferous corals of Australia. *Proc. R. Soc. Qd.* **45,** 63–115, pls. 7–11.

—— and STUMM, E. C. 1956. Tabulata, pp. 444–477. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part F. Coelenterata.* Boulder, Colorado and Lawrence, Kansas. xx + 498 pp.

HINDE, G. J. 1896. Descriptions of new fossils from the Carboniferous Limestone . . . *Q. Jl geol. Soc. Lond.* **52,** 438–451, pls. 22, 23.

HUDSON, R. G. S., CLARKE, M. J. and SEVASTOPULO, G. D. 1966. A detailed account of the fauna and age of a Waulsortian knoll reef limestone and associated shales, Feltrim, Co. Dublin, Ireland. *Scient. Proc. R. Dubl. Soc.* (A), **2,** 251–272, pl. 23.

—— and SEVASTOPULO, G. D. 1966. A borehole section through the Lower Tournaisian and Upper Old Red Sandstone, Ballyvergin, Co. Clare. Ibid. (A), **2,** 287–296.

JEFFORDS, R. M. 1955. Mississippian corals from New Mexico and a related Pennsylvanian species. *Paleont. Contr. Univ. Kans., Coelenterata,* art. 3, 1–12, 2 pls.

JOHNSTON, I. S. and HIGGINS, A. C. 1981. Conodont faunas from the Lower Carboniferous rocks at Hook Head, County Wexford. *J. Earth Sci. R. Dubl. Soc.* **4,** 83–96.

KONINCK, L. de. 1872. Nouvelles recherches sur les animaux fossiles. . . . *Mém. Acad. r. Sci. Lett. Belg.* **39,** iv + 178 pp., 15 pls.

KUNTH, A. 1869. Beiträge zur Kenntniss fossiler Korallen. *Z. dt. geol. Ges.* **21,** 183–220, pls. 2, 3.

LUDWIG, R. 1866. Corallen aus Paläolithischen Formationen. Parts 2, 3. *Palaeontographica,* **14,** 173–244, pls. 31–72.

MARCHANT, T. R. 1978. The stratigraphy and micropalaeontology of the Lower Carboniferous (Courceyan–Arundian) of the Dublin Basin, Ireland. Unpublished Ph.D. thesis, University of Dublin.

MEEK, F. B. and WORTHEN, A. H. 1860. Descriptions of new Carboniferous fossils from Illinois and other western states. *Proc. Acad. nat. Sci. Philad.* **20,** 447–472.

MILLER, S. A. 1889. *North American geology and palaeontology. . . .* Cincinnati. 664 pp.

—— 1892. Palaeontology. *Rep. Indiana Dep. Geol. nat. Resour.* **17,** 611–705, 20 pls.

MILNE-EDWARDS, H. 1857. *Histoire naturelle des Coralliaires ou polypes proprement dits.* Atlas. Paris. 11 pp. 31 pls.

—— 1860. Ibid. Paris. Vol. 3, 560 pp.

—— and HAIME, J. 1950. A monograph of the British fossil corals. Part 1. *Palaeontogr. Soc.* (*Monogr.*), i–lxxxv, 1–71, pls. 1–11.

MOORE, R. C. and JEFFORDS, R. M. 1945. Description of Lower Pennsylvanian corals from Texas and adjacent states. *Univ. Tex. Publs.* **4401,** 77–208, pl. 14.

PERCEVAL, S. G. 1876. On the discovery of *Palaeacis cuneata*, Meek & Worthen, in Carboniferous Limestone near Henbury, Bristol. *Geol. Mag.* N.S., dec. 2, **3,** 267–268.

PHILLIPS, J. 1836. *Illustrations of the geology of Yorkshire . . . Part 2.* London. xx + 253 pp., 25 pls.

POČTA, P. 1902. Anthozoaires et Alcyonaires. *In* BARRANDE, J. *Systême silurien du centre de la Bohême.* Prague. Vol. 8, part 2. viii + 347 pp., pls. 20–118.

ROEMER, F. 1883. *Lethaea geognostica . . . I. Theil. Lethaea palaeozoica. I. Band, Part 2,* 113–544. Stuttgart.

SEEBACH, K. von. 1866. Die Zoantharia perforata der palaeozoischen Periode. *Z. dt. geol. Ges.* **18,** 304–310, pl. 4.

SEVASTOPULO, G. D. 1979. The stratigraphical setting of base-metal deposits in Ireland. *In* JONES, M. J. (ed). *Prospecting in areas of glaciated terrain*, 8–15. Institution of Mining and Metallurgy, London.

SLEEMAN, A. G., JOHNSTON, I. S., NAYLOR, D. and SEVASTOPULO, G. D. 1974. The stratigraphy of the Carboniferous rocks of Hook Head, Co. Wexford. *Proc. R. Ir. Acad.* (B), **74,** 227–243.

SMITH, S. 1930. The Calostylidae, Roemer: a family of rugose corals with perforate septa. *Ann. Mag. nat. Hist.* **5** (10), 257–278, pls. 10–12.

SMYTH, L. B. 1927. On the index fossil of the *Cleistopora* Zone. *Scient. Proc. R. Dubl. Soc.* N.S., **18,** 423–431, pls. 20–22.

——1929. On the structure of *Palaeacis*. Ibid. **19,** 125–138, pls. 6–8.

——1930. The Carboniferous rocks of Hook Head, County Wexford. *Proc. R. Ir. Acad.* (B) **39,** 523–566, pls. 15–20.

SNIDER, L. C. 1915. Palaeontology of the Chester Group in Oklahoma. *Bull. Okla. geol. Surv.* **24,** 67–122, pls. 3–7.

TERMIER, G. and TERMIER, H. 1950. Paléontologie Marocaine. Vol. 2. Invertébrés de l'ère primaire. Fasc. 1. Foraminifères, Spongiaires et Coelentérés. *Notes Mém. Serv. Mines Carte géol. Maroc*, **73,** 218 pp., 51 pls.

WELLER, S. 1909. Kinderhook faunal studies—5, The fauna of the Fern Glen Formation. *Bull. geol. Soc. Am.* **20,** 265–332, pls. 10–15.

WILLIAMS, J. S. 1943. Stratigraphy and fauna of the Louisiana Limestone of Missouri. *Prof. Pap. U.S. geol. Surv.* **203,** 133 pp., 9 pls.

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A REAPPRAISAL OF THE EUROPEAN EOCENE PRIMATE *PERICONODON*

by IAN TATTERSALL *and* JEFFREY H. SCHWARTZ

ABSTRACT. The Eocene primate *Periconodon* has recently been widely regarded as belonging to the family Adapidae, and several authors have synonymized it with *Anchomomys*, another adapid. Re-examination of the type material of *Periconodon* has revealed that the genus is distinct, and that its affinities lie not with Adapidae but with the otherwise exclusively North American family Omomyidae. *Periconodon* contains only the type species, *P. helveticus*; recently named new species of *Periconodon* are wrongly assigned.

THE primate genus *Periconodon* was created in 1916 by Stehlin, to accommodate two maxillary fragments from the Swiss middle Eocene (Auversian) locality of Egerkingen (Huppersand). These specimens had originally been described some years earlier by Rütimeyer, who had allocated one of them to ?*Pelycodus* (Rütimeyer 1888), and who with more confidence had based on the other (text-fig. 1) a new species of *Pelycodus*, *P. helveticus* (Rütimeyer 1891). Stehlin compared *Periconodon* quite widely with other Eocene primates, European and North American, and concluded that the closest comparison was with certain North American forms generally regarded today as omomyids. He was more strongly struck, however, by the close resemblances he perceived between the upper molars of *Periconodon* and the squirrel monkey *Saimiri* (his '*Chrysothrix*') *sciureus*, although he felt that the gap in time precluded any close relationship. In 1945 Simpson affirmed his acceptance of the tarsioid affinities of *Periconodon*, but placed the form *incertae sedis* in his family Anaptomorphidae (which included the subfamily Omomyinae, more or less as defined by Wortman in 1904, and limited to North American genera). Subsequently Simons (1962) assigned *Periconodon helveticus* to the tarsiiform family Omomyidae, to which Omomyinae had been raised by Gazin in 1958.

An alternative suggestion as to the affinities of *Periconodon*, and one that rapidly gathered general acceptance, was put forward by Russell, Louis and Savage (1967), who concluded that *Periconodon* might better be classified in the family Adapidae. In particular, they suggested a relatively close affinity between *Periconodon* and the adapid *Anchomomys* (although they did not specify a species of *Anchomomys*, a genus that seems to us as currently classified to represent a non-homogeneous assemblage). In 1974 Szalay followed Russell, Louis and Savage in stressing the resemblances between *Anchomomys* and *Periconodon*, and three years later Gingerich (1977) took the step of synonymizing *Periconodon helveticus* with *Anchomomys pygmaeus*, an action that resulted in the new combination *Periconodon pygmaeus*. Szalay subsequently concurred with this synonymy (Szalay and Delson 1979), and reaffirmed his belief in the adapid affinities of *Periconodon*.

Gingerich (1977) proposed two new species of *Periconodon*. One of these, *P. lemoinei*, he based on an assortment of isolated teeth from the French lower Eocene site of Grauves, plus a fragmentary lower jaw from Castigaleu, Spain, that had been assigned by Crusafont (1967) to his new genus *Agerina* (now *Agerinia*); the other, *P. huerzeleri*, he based on a right dentary from the middle Eocene (Lutetian) site of Buchsweiler (Bouxwiller) in Alsace, and on unspecified other material from Buchsweiler and elsewhere. Gingerich suggested that his *P. lemoinei* was descended from a form he named *Protoadapis louisi*, and that *P. huerzeleri* and *P. pygmaeus* represented later, successive, stages in a linear sequence leading to *Anchomomys*; between *lemoinei* and *huerzeleri* he interposed '*Periconodon*' *roselli*, as a result of having synonymized Crusafont's species *Agerinia roselli* with *Periconodon*. Szalay (Szalay and Delson 1979) objected to this set of conclusions, pointing to the lack of morphological justification provided by Gingerich; provisionally, he assigned the *P. lemoinei*

[Palaeontology, Vol. 26, Part 1, 1983, pp. 227-230]

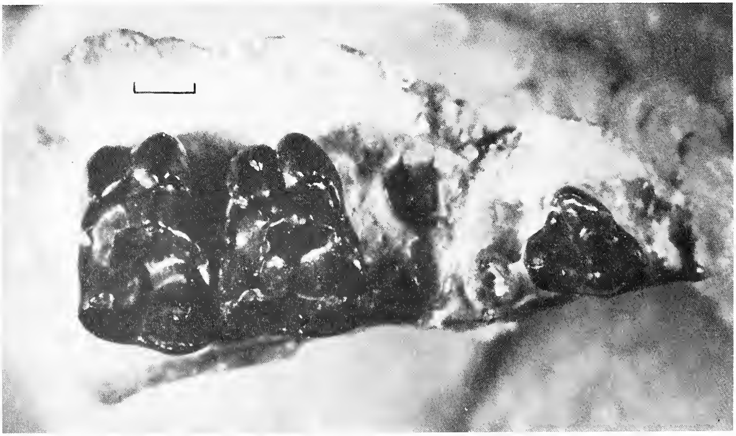
specimens to *A. roselli*, and claimed that *P. huerzeleri* merely represented the lower dentition of *P. pygmaeus*.

DESCRIPTION AND DISCUSSION

Whatever their disagreements, recent authors have thus unequivocally assigned *P. helveticus* to the family Adapidae, and have noted particular resemblances to *Anchomomys*. Recently, however, we have had the opportunity to examine the type specimen and other material of *P. helveticus* in the collections of the Naturhistorisches Museum, Basel (BNM), and it is clear to us that recent assessments of the form's affinities are inaccurate. Since statements about the relationships of *Periconodon* have been made liberally since the time of Stehlin without more than passing reference to the morphologies involved, we describe the pertinent material below.

The holotype of *P. helveticus*, BNM Ef 366 from the Huppersand locality of Egerkingen (text-fig. 1), consists of a partial left maxilla containing the penultimate premolar, M^{1-2}, three roots for the last premolar, two alveoli for M^3, and a partial alveolus anterior to the preserved premolar. The remaining premolar appears to be three-rooted; it is a simple tooth, essentially single-cusped, and is premolariform although high-crowned. M^{1-2} are markedly transverse; there is a very long lingual slope to the protocone, resulting in a very broad but truncated trigon. The buccal cusps are moderately compressed, and the pre- and postprotocristae are sharp. The preprotocrista in M^{1-2} swings anteriorly around the paracone and terminates in a small parastyle; in M^1 this crest bears a small paraconule that is barely represented on M^2. Both molars show distinct buccal cingulae. M^1 is slightly smaller than M^2, from which it also differs in having a small style on the lingual face of the hypocone. M^3 may, on the evidence of the alveoli, have been subequal in size to M^2.

In sum, the upper molar morphology of *P. helveticus* is totally un-adapid. In those characters of the upper dentition in which *P. helveticus* departs most markedly from the adapids, however, it closely approaches the omomyids with which it was associated by Simons (1962) and, by implication, earlier authors. The strong transverseness of the upper molars, the broadly parabolic protocristae, the development of the hypocone, and particularly the long lingual slope of the strong protocone, all



TEXT-FIG. 1. BNM Ef 366, type of *Periconodon helveticus*: occlusal view. Scale represents 1 mm.

point to the omomyid affinities of *Periconodon*, which most closely resembles *Washakius* among North American primates.

Just as its identification as an adapid is inappropriate, the synonymy of *P. helveticus* with *Anchomomys pygmaeus* favoured by Gingerich (1977) and Szalay (Szalay and Delson 1979) is unwarranted. The type specimen of *A. pygmaeus* is BNM Ef 367, an upper first molar from Egerkingen. The species was first described by Rütimeyer (1890) as *Caenopithecus pygmaeus*, and was transferred to *Anchomomys* by Stehlin (1916), who also allocated to it BNM Ef 372, another upper molar from Egerkingen. Other material subsequently referred to *A. pygmaeus* by Szalay (1974) does not belong in the species, as Gingerich (1977) also recognized; we will discuss it elsewhere. The type M^1 lacks a buccal cingulum but shows traces of buccal enamel pillars on the rather buccolingually compressed paracone and metacone. A large paraconule is present, and a diminutive metaconule; there is a small but distinct parastyle but barely a hint of a metastyle. A precingulum extends from the parastyle and terminates at the base of the protocone in a small style. The hypocone is more like a shelf than a cusp, and is confluent with a postcingulum. The protocristae are broad and the trigon basin is truncated but deep. The referred M^2 Ef 372 is very similar to the tooth just described. Together, these two teeth are totally distinctive, and the relationships of the species they represent are unclear to us. Certainly no special affinity of *A. pygmaeus* to *Periconodon* is indicated.

The type specimen of Gingerich's new species *P. huerzeleri* is a right dentary from Bouxwiller, BNM Bchs 495, that preserves the last premolar and the three molars. Direct comparison of this specimen with the type of *P. helveticus* is impossible, since the latter is represented by the upper dentition. However, it is clear that while the latter aligns with Omomyidae, '*P.*' *huerzeleri* does not. None of the molars of Bchs 495 bears a well-defined paraconid, while this cusp is characteristically distinct on the lower molars of omomyids, especially M_1. The last premolar of Bchs 495 is highly compressed laterally, and is relatively long; it bears a very pronounced, centrally positioned hypoconid, and a smaller paraconid anteriorly. A strong buccal cingulid connects these two cusps, which are dwarfed by the protoconid. In omomyids, on the other hand, the last lower premolar, although dominated by the protoconid, bears a broad, tear-shaped talonid that terminates posteriorly in a wide, transverse 'heel'. Paraconid development is variable. Since Bchs 495 thus fails to show any convincing evidence of omomyid affinities, there is no obvious reason for allocating it to a new species of *Periconodon*. In fact, among known primates Bchs 495 is most reminiscent of certain cheirogaleids, most notably *Mirza* and *Phaner*, particularly, in the morphology of the last premolar, the latter.

The holotype of Gingerich's other new species of *Periconodon*, *P. lemoinei*, is an isolated lower right molar (Louis coll. Gr-106) from the French early Eocene site of Grauves. This specimen is heavily worn. The trigonid is not greatly compressed, and bears a broad paracristid that terminates at the base of the metaconid, from which it is separated by a distinct groove. The cristid obliqua seems to have arced across to meet the metaconid, thus forming a deep hypoflexid notch. A rather arcuate hypocristid encloses the talonid basin, and a well-developed buccal cingulid is present, especially around the trigonid and posterior to the hypoconulid. Like BNM Bchs 495, Gr-106 is totally non-omomyid in aspect and thus provides no grounds for its allocation to *Periconodon*. In its trigonid construction, and particularly in its downwardly sweeping, shelf-like paracristid that fails to become confluent with the base of the metaconid, this tooth is quite characteristic of *Protoadapis*, the genus to which we prefer to assign it.

Conclusion

We conclude that the affinities of *Periconodon* lie not with the lemuriform primate family Adapidae, but with the tarsiiform family Omomyidae. This latter family is otherwise known only from North America; and this confirmation of the existence of a European representative enhances the growing realization that the Eocene primate faunas of Europe and North America show a greater unity than is generally believed. *Periconodon* is, moreover, a clearly distinct genus, showing no affinities with any species that has ever been referred to the genus *Anchomomys*. As currently known this genus is monotypic, containing only the type species *P. helveticus*; two new species recently erected within *Periconodon* have been misattributed.

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REFERENCES

CRUSAFONT-PAIRO, M. 1967. Sur quelques prosimiens de l'Éocène de la zone préaxiale pyrénaïque et un essai provisoire de reclassification. *Coll. Int. Cent. Nat. Sci.* **163,** 611–632.

GAZIN, C. L. 1958. A review of the middle and upper Eocene primates of North America. *Smithsonian Misc. Coll.* **136,** 1–112.

GINGERICH, P. D. 1977. New species of Eocene primates and the phylogeny of European Adapidae. *Folia Primat.* **28,** 60–80.

RUSSELL, D. E., LOUIS, P. and SAVAGE, D. E. 1967. Primates of the French early Eocene. *Univ. of California Publ. Geol. Sci.* **73,** 1–46.

RÜTIMEYER, L. 1888. Beziehungen zwischen Säugethierstammen Alter und Neuer Welt. *Abh. Schweiz. Paläont. Gesell.* **15,** 1–63.

——1891. Die eocane Säugethier-Welt von Egerkingen. Ibid. **18,** 1–53.

SIMONS, E. L. 1962. A new Eocene primate genus, *Cantius*, and a revision of some allied European lemuroids. *Bull. Brit. Mus.* (*Nat. Hist.*), *Geol.* **7,** 1–30.

STEHLIN, H. G. 1916. Die Säugetiere des schweizerischen Eocaens. *Abh. Schweiz. Paläont. Gesell.* **41,** 1299–1552.

SZALAY, F. S. 1974. New genera of European Eocene adapid primates. *Folia Primat.* **22,** 116–133.

——and DELSON, E. 1979. *Evolutionary history of the primates*. New York and London: Academic Press.

WORTMAN, J. 1904. Studies of Eocene Mammalia in the Marsh Collections, Peabody Musuem, Part 2: Primates. *Amer. Jour. Sci.* **17,** 23–33, 133–140, 203–214.

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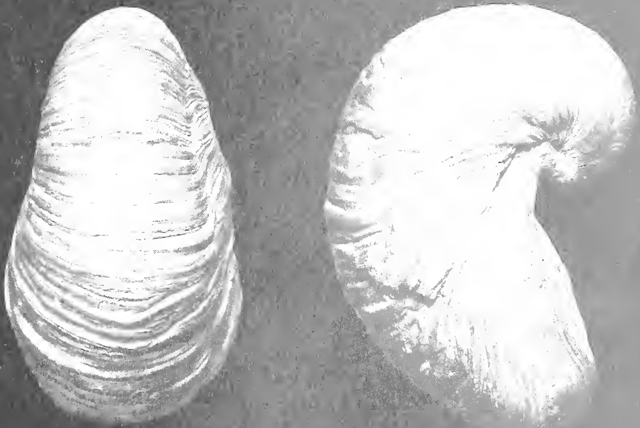

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Cover: The Lower Liassic (Jurassic) oyster *Gryphaea arcuata incurva* J. Sowerby, 1815, from Gloucestershire, England; known popularly as 'The Devil's Toenail'. Specimens in the National Museum of Wales.

THE EXPERIMENTAL FORMATION OF PLANT COMPRESSION FOSSILS

by G. M. REX *and* W. G. CHALONER

ABSTRACT. Despite the common occurrence of plant compression fossils, little experimental work has been done on the processes leading to their formation and their exposure by fracture. Models of the plant (in foam rubber) and the matrix (sawdust) systems have been subjected to deformation in an apparatus constructed so that the vertical plane can be kept under observation. The process of collapse and compression observed in vertical sections of plant fossils are more closely reproduced when the compression force acts through a number of free-moving pistons applied to the matrix than when a single larger piston is employed. The processes involved in the formation of compression fossils of *Calamites*, *Lepidodendron*, *Stigmaria*, and *Sawdonia* are explored and discussed. It is shown that the topography of a plant compression is governed not only by the structures revealed on the surface exposed, but by collapse of underlying plant tissue within the matrix. It is also demonstrated in lycopod leafy shoots that the fracture plane exposing the fossil is largely controlled by the angle between the bedding planes and the plant material.

ONE of the commonest forms of fossilization by which plants have been preserved is in the condition known as 'compression fossils'. Such fossils were formed when plant organs, buried in sediment, underwent partial degradation so as to produce a much flattened version of the original structure, with its tissue represented by a layer of coalified plant material.

This paper presents an account of a simple experimental investigation of some of the processes involved in the formation of plant compression fossils. Plants showing this type of preservation are generally less informative than those preserved by permineralization (showing three-dimensional cellular structure). However, compression fossils are undoubtedly far more abundant than permineralizations, and many fossil plants are known only in this state of preservation. It is therefore important that the processes of formation of such fossils and their subsequent exposure by fracture should be understood.

We attempted in the first instance to see if we could reproduce the form of compression fossils, seen in nature, by experimentation. By doing this we hoped to determine something of the deformation that plants underwent during compression, especially by investigating whether deformation was just in the vertical dimension, as many workers have believed (Walton 1936; Schopf 1975), or whether horizontal deformation also took place. We also wished to see if we could learn more about the physical processes involved during the formation of compression fossils; for example, how collapse distorts the shape of an organ and the associated matrix and how appendages such as spines and leaf cushions reacted to the accumulation and compaction of sediment and the ensuing deformation. We believe that by making a physical model of the plant-plus-matrix system which accurately reproduces the observed form of the fossil, we could learn something about the compression process as it occurs in nature. This understanding would give us a basis for reconstructing the original form of plants known to us only in the state of compression fossils. Although there are obvious shortcomings in modelling in a 'dry' system, we believe that our model may represent an improvement on the hypothetical consideration of the compression process, suggested by some authors (Boulter 1968; Rigby 1978).

A compression-type apparatus was designed and experiments conducted using artificial materials to represent plant and matrix, to try to reproduce the kind of preservation observed in fossils of *Sawdonia*, *Calamites*, *Stigmaria*, and *Lepidodendron*. These genera were chosen as representing rather well-known plants which illustrate a range of problems relating to the processes involved in their compression.

[Palaeontology, Vol. 26, Part 2, 1983, pp. 231–252, pls. 30–33.]

THE FOSSILIZATION PROCESS

Degradation and collapse

Plant compression fossils formed when plant material was deposited in the sedimentary environment, and was subsequently buried. During burial the cell contents and eventually the cell walls underwent microbial breakdown; in some cases this biodegradation may well have begun before burial. Whether in any given case this process (collapse of the plant organ) occurred ahead of the compression (produced by the weight of the overlying sediment) or whether it occurred as a direct result of the compression forcing the plant to collapse is difficult to determine. It is clear, though, that the compression process and the collapse/decay process are closely linked and may well have occurred synchronously. The residual plant material was then diagenetically altered to coaly matter, and a compression fossil formed. The terminology of the diagenetic process and its products are well reviewed in Schopf (1975). Very little is known about the details of these several processes.

We have elected to study Palaeozoic, mainly Carboniferous, material, in which the alteration (diagenesis) of the plant material has generally proceeded to the state of a bituminous coal. In younger sediments of Tertiary age, for example, the coalification process may only have reached the state of lignite ('brown-coal'). We believe despite the limited choice of our material, we are seeing phenomena resulting from universal physical processes which will apply with minor modifications to plant fossils from a wide age range.

The size scale effect

The degree of deformation affecting a plant organ is to some extent a function of the scale of the whole plant structure concerned. Plant stems which have suffered burial and have been compressed typically show a change in the shape of their cross-section from circular to elliptical. Close examination of the topography of the stem surface after deformation shows that, on a microscopic scale, distortion was much less pronounced. For example, Chaloner and Collinson (1975) demonstrated that in compression fossils of *Sigillaria* the ribs had been reduced to a flat ribbon-like form whereas the stomatal pits showed no comparable distortion. It would appear that compression is acting in this case on the macrostructure of the plant, but smaller scale topography is somehow sheltered from the deformation.

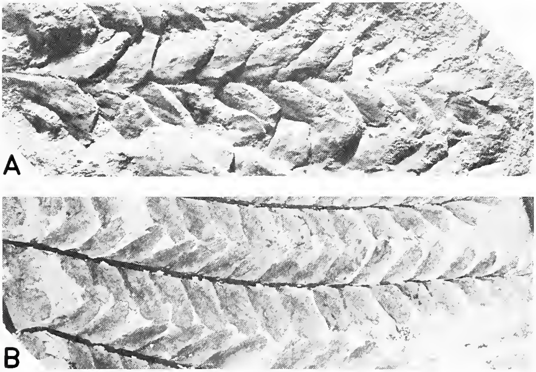
Spicer (1977) showed a possible mechanism that may explain this size scale phenomenon. He demonstrated that an iron-rich encrusting layer can build up on leaf surfaces only a few weeks after entry into the depositional environment. Spicer postulates that such an encrustation may be the basis of impression fossils replicating epidermal features in much finer detail than the sediment grain size would seem to allow. Comparing Recent leaves with fossil leaves from the Dakota sandstone, he showed by X-ray analysis that the fossil leaves had a very high iron-peak compared to silicon, indicating that the leaf impression surface was characterized by a concentration mainly of iron-rich material. This 'iron-coating' may limit biological degradation and may also serve as a structural protection for the microtopography of the plant surface during subsequent compression. This has the effect of preserving, apparently more or less undistorted, small features of the plant surface, e.g. stomatal pits, while the cross-sectional shape of the whole stem is drastically modified by collapse and compression.

Sediment grain size

During the deposition of sediments compaction occurs as a result of water movement and the pore-volume is consequently reduced. Coarse-grained sediments, e.g. sands, will hold very little water and maximum compaction will occur early in diagenesis. Porous sediments which are very fine-grained or composed of colloidal constituents retain large amounts of water. The initial water content of most argillaceous muds is 50–80%; compaction of this type of mud will be accompanied by extensive dewatering. Animal or plant organs incorporated within sands or muds will suffer diagenetic deformation (compression) as a result of compaction of their own tissue and of the sediment. The degree to which the plant or animal is deformed is a function of the amount and type of sediment that surrounds and infiltrates the structure of the dead organism. For example, sandy pith cavity infills of *Calamites* will be much less distorted than an argillaceous infill. This is because the sand grains tend to support each other, halting compaction of the infill (but not of the plant tissue) at an early stage. The clay minerals of an argillite on the other hand align themselves and move together producing a platyness, losing a large amount of water which was trapped between the clay particles in the process. It is therefore the compressibility of the matrix in which the organism is incorporated that dictates the final form of the compression fossil. The thickness of the coaly matter produced will, in contrast, show very little variation in either case, since it is the original amount of organic matter contained by the organism or plant that dictates the thickness of the residual coal layer.

These general statements require qualifying where early cementation of the matrix gives it a rigidity unrelated to its particle size. This is the process described by Schopf (1975) as authigenic preservation, typically involving 'early precipitation of authigenic minerals in sediment pore space'. It is represented by the plants preserved in the Mazon Creek nodules, and the comparable clay-ironstone nodules from other parts of the world. As Schopf remarks 'the distinction between . . . (such preservation) . . . and coalified compression is not absolute probably because of variation in degree and time of cementation'.

The effect of compressibility of the matrix on the final form of the fossil is illustrated in a direct way by the leafy shoot of *Archaeopteris* from the Devonian of Ireland shown in text-fig. 1B. The shoot ('frond' of earlier workers) has been compressed in an argillaceous matrix resulting in the formation of a very flat compression fossil. In text-fig. 1A a shoot of the same species was buried in a less compressible, sandy matrix (within the same rock unit of the 'Kiltorcan Beds'). Here, the fossil formed shows a closer approximation to the original form of the leafy shoot, in which the leaves ('pinnules' of earlier workers) are seen to be borne all around the stem ('rachis'). It was the very flat, two-dimensional state of the leafy shoots, compressed in fine-grained matrices, which encouraged earlier authors to interpret the *Archaeopteris* leafy shoot as a pinnate, fern-like frond. Only



TEXT-FIG. 1. A. *Archaeopteris hibernica* (Forbes) Dawson, preserved in a coarse-grained matrix giving the compression fossil greater relief, showing the true arrangement of leaves around the axis. ×0·7. B. *A. hibernica* preserved in a fine-grained matrix giving a 'flat compression', suggestive of a pinnate leaf. ×0·7. Both specimens are from Kiltorcan Old Quarry, Kilkenny, Republic of Ireland, Upper Devonian.

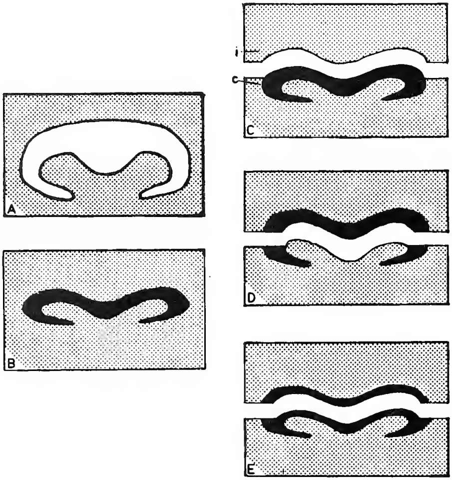
subsequent work on permineralized material, and the degaging of compressions demonstrated the original three-dimensional character of this fossil (Beck 1971).

A considerable amount of work has been undertaken by invertebrate palaeontologists to examine and recognize the effects of early diagenesis on invertebrate shells (Moore 1979) and on arthropods (Conway Morris 1979). The way in which ammonite shells react to compression is evidently very different to that of higher plant tissue, since the shell has a rigidity and toughness not diminished by biological degradation. Arthropods behave rather more similarly to plants than do ammonoid shells, for here the tough chitinous exoskeleton in the former has something of the physical properties of a thick plant cuticle enclosing readily degradable soft tissue. The role of such chitin layers in governing fracture planes is dealt with below.

THE PATHWAY OF FRACTURE PLANES

An important factor affecting the form of a plant compression fossil is the fracturing of the matrix which resulted in its exposure. The pathway of the fracture is governed by the characteristics of the matrix, the fossil-matrix interface, and the shape and orientation of the actual plant fossil.

Coaly matter is usually retained on one or other face of the matrix exposed by fracture (text-fig. 2). The surface bearing the coaly matter is in this case commonly called a 'compression', while the fracture surface showing no organic matter is referred to as an 'impression' fossil (showing a mould of the fossil's surface topography, text-fig. 2c). Sometimes a fracture plane passes unevenly through the minute 'coal seam' constituting the plant material giving two 'incomplete compressions'



TEXT-FIG. 2. A. Vertical section of a leaf buried in matrix. B. Leaf after compression; the plant tissues have collapsed and been altered to coaly matter. C. Fracturing of the matrix produces an impression fossil (i) and a compression fossil (c). D, E. Different pathways of fracture produce two different versions of an 'incomplete compression'.

(text-fig. 2, D and E). The pathway of the fracture surface dictates the extent to which the fossil is exposed.

The manner in which a fracture plane exposes a fossil has been discussed by Conway Morris (1979) with reference to arthropods from the Burgess Shale. He has found that these invertebrates do not occupy a single bedding plane but cross two or more levels of microbedding. The appendages of the arthropods are separated by thin layers of sediment. Whittington (1975) showed that slight variations in the plane of splitting determined which part of the arthropod was exposed. This plane of splitting, according to Whittington, is governed by competition as a pathway for fracture between various parts of the arthropod body and is dictated by: (*a*) the surface area of the structure; (*b*) its thickness; and (*c*) its angle to the bedding. Conway Morris (1979) deomonstrates this pathway of the fracture plane with reference to *Canadia spinosa* in determining which parts of the animal are exposed and which remain buried in the matrix. This role of fracture planes can be similarly demonstrated in plant compression fossils, for example in the leafy shoots of lepidodendrids. The angle between the leaf and the stem, as seen at the side of the fossil stem helps to explain the pathway of fracture seen over the central part of such a fossil. For example, *Lepidodendron wortheni* bears leaves which make an angle of about 60° with the stem. When this species is exposed by fracturing, the fossil seen on the fracture surface is of a stem, bearing leaf cushions, with leaves seen at both sides lying 'in profile' in the matrix. This has understandably led some workers (e.g. Crookall 1964) to identify 'leaf scars' on the cushions of *L. wortheni* even when leaves have been described attached at the sides of the stem. Close examination of these 'scars' shows them to be irregular and structureless, and these fracture features have been designated 'false scars' (Chaloner and Boureau 1967), in contradistinction to true abscission scars formed in life.

It appears that such a break across the coalified leaf, lying in the matrix, occurs when the angle between the bedding plane and the coalified plant organ gets too steep for the fracture plane to run on along the leaf surface (text-fig. 3, A–C), and the leaves are removed in the counterpart. Where the angle between leaf and stem is more acute (e.g. as in *L. acutum* or *L. simile*) the fracture above the stem surface runs some or all the way along the leaf, revealing partial or complete leaf surfaces (e.g. *Bothrodendron minutifolium*) overlying the stem (text-fig. 3, G–I). An intermediate condition occurs in *L. simile* where leaves of sigmoidal profile leave the stem surface at a moderate angle. Here the fracture plane runs a short distance along the leaf surface, so showing short, truncated leaf segments above the stem on the compression fossil (text-fig. 3, D–F).

METHODS OF INVESTIGATING COMPRESSION FOSSILS

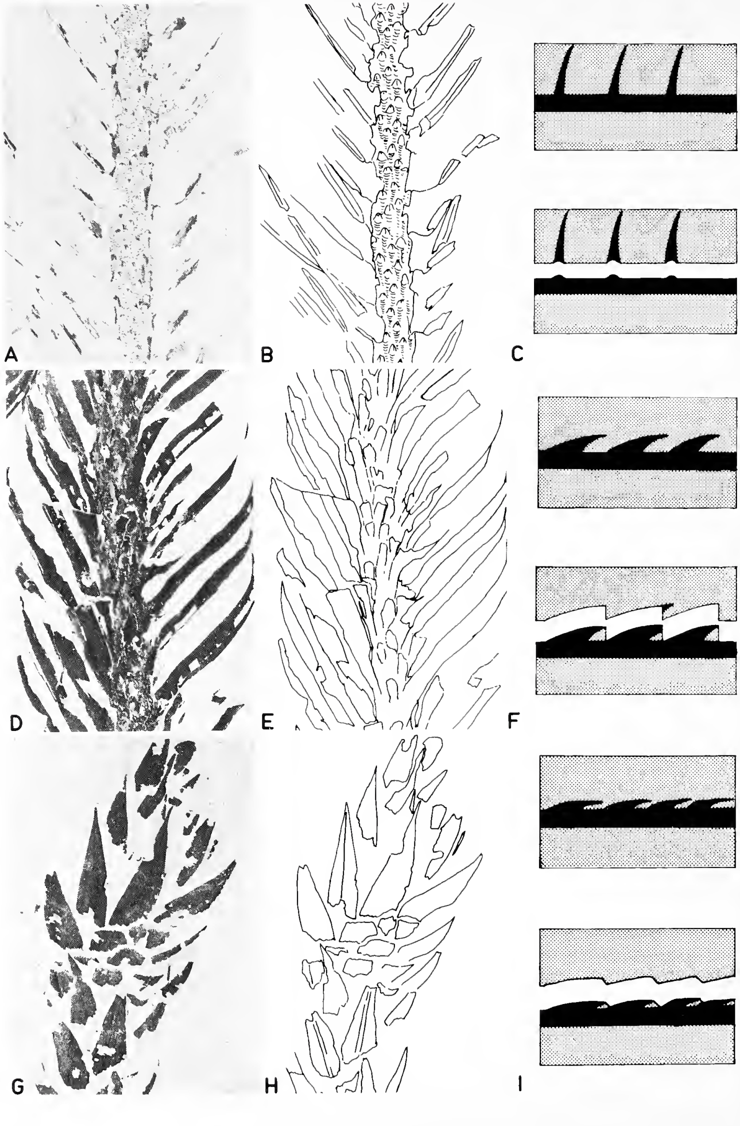
Since the early years of the last century many palaeobotanists have regarded plant compression fossils as essentially two-dimensional objects, rather comparable to 'pressed plants' (herbarium specimens). Where angiosperm leaves or large multipinnate fronds are concerned, this is a reasonable approximation. The earlier view that such fossils were in effect entirely two-dimensional objects is well exemplified by Johnson's (1913) quoted remark that splitting open the Kiltorcan shales to reveal plant fossils was 'like turning over the leaves of a picture-book'.

This 'herbarium view' of compression fossils tended to discourage serious consideration of the vertical dimension in such fossils and the complexity of factors governing their form. Walton (1936) was probably the first palaeobotanist to give serious consideration to the vertical dimension in compression fossils. Significantly it was he who developed one of the most fruitful ways of studying such fossils beyond direct observations of the exposed fracture surface (Walton 1923).

Five principal methods have been developed by palaeobotanists for looking at the 'third dimension' of compression fossils. We enumerate these here briefly to emphasize that while they involve different procedures, they have in common that they contribute to our knowledge of the vertical dimension of the compressed plant material.

The transfer technique

This procedure, developed by Walton (1923), consists of sticking the exposed (fracture) surface of plant material to a transparent surface (plastic film or balsam on glass) and dissolving the rock matrix with appropriate acid


A
B
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(e.g. hydrofluoric acid). The coaly film is then available, free of matrix, to be examined on either surface, and the topography of the surface previously hidden in the matrix, revealed.

Vertical sectioning

This is a standard procedure used for examining permineralized plant material, but has been used very little in the study of compression fossils. A few authors have sectioned such specimens; Selling (1944), for example, studied a Calamitean cone compression in this way and Boulter (1968) sectioned lycopod sporophylls, both using information from the sections to interpret the three-dimensional form of the collapsed plant organ.

Degagement

Leclercq (1960) pioneered the development of this technique, which involves removing the matrix 'grain by grain' to expose the plant fossil in depth, below the initial fracture plane. It has been highly successful in revealing the three-dimensional character of branch systems lacking large laminar appendages, particularly those preserved in non-indurated coarse matrices, e.g. *Rhacophyton*—Leclercq (1951), *Calamophyton*—Leclercq and Andrews (1960), *Archaeopteris*—Beck (1971).

Solution of matrix

If the plant tissue in sufficiently coherent (undegraded), dissolution of the matrix with HF may release entire branch systems in a three-dimensional state. This technique has been used with notable success by Doran (1980) in his preparations of Canadian *Psilophyton*.

Direct observation of the fractured surfaces (part and counterpart)

Many workers have used information gathered from the examination of the plant compression fossil as it has been exposed, by fracturing of the matrix, to reveal the two faces (part and counterpart) of the fossil. The data obtained has been used to make reconstructions of how the extinct plant fossil may have looked in life. For example, Plumstead (1952) used this method in postulating the structure of *Glossopteris* fructifications and Rigby (1978) has recently used this method in producing a rather different interpretation of comparable structures. The divergence of opinion arising with such reconstructions (see, for example, discussion in Plumstead 1952; Rigby 1978) emphasizes the incompleteness of our knowledge of the configuration of plant organs resulting from the compression process.

EXPERIMENTS IN THE PROCESS OF FOSSILIZATION

PREVIOUS WORK

Transport processes

The process by which plant material becomes incorporated in sediment is obviously very relevant to the study of compression fossils. Ferguson (1971) was one of the first people to investigate this, and conducted a series of experiments to determine how thick and thin leaves reacted to water transport. He constructed an apparatus consisting of water and sand filled cylinders, in which leaf fragments suffered the equivalent of 80 km transport along a river system. At the end of that period neither the thick nor thin leaves showed any signs of degradation.

Spicer (1980, 1981) has also considered the manner by which plant organs become incorporated in sediment. He has examined modern sedimentary environments, e.g. fluviolacustrine delta in an artificial lake, and shown

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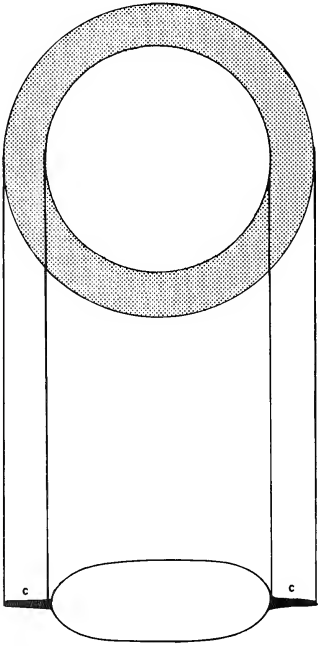
TEXT-FIG. 3. (*opposite*) A. Leafy shoot of *Lepidodendron wortheni* Lesquereux. × 0·6. B. Tracing of the specimen showing detail of the leaf orientation. C. Diagrammatic vertical section through *L. wortheni*. The fracture plane that exposes the fossil passes along the stem surface, leaving the steeply rising leaves in the counterpart. D. *Lepidodendron simile* Kidston. × 3. E. Tracing of the specimen showing detail of the leaf orientation. F. Diagrammatic vertical section through *L. simile*. The fracture plane runs a short distance along the leaves, then reverts to the bedding planes. G. *Bothrodendron minutifolium* (Boulay). × 3·5. H. Tracing of the specimen showing detail of the leaf orientation. I. Diagrammatic vertical section through *B. minutifolium*. The fracture plane runs along the almost horizontal leaf surfaces above the stem, so that the entire leaf outline is exposed. (A: Institute of Geological Sciences, Kidston Collection, No. 1013, D: No. 4890, G: No. 1472. All are from the Coal Measures of Yorkshire.)

where plant organs, mainly leaves, are deposited along the sedimentary system. The leaves form distinct leaf beds, one on the lake bottom and one on the foreset slope of the delta. The major mechanisms by which plant material is deposited appear to be selective transport of plant organs and biological and mechanical degradation.

Processes in the sediment

The manner in which plant material behaves once it is buried in sediment has been investigated experimentally by very few workers. Walton (1936) was the first palaeobotanist to consider the mechanisms by which plant material was compressed in sediment. He did not describe any experimental investigation of the mechanism, although it is believed that he did carry out experiments (T. M. Harris pers. comm. 1981). Instead he published a theoretical account of the processes involved. Walton postulated that after a plant fragment had undergone burial in mud the horizontal components acting on the plant were zero, the only remaining force being vertical. As a result of this, water was displaced upwards and the plant fragment suffered considerable reduction in the vertical dimension with no horizontal deformation occurring. As an example Walton considered a hollow cylinder of fairly compressible tissue embedded in a less compressible matrix which also infilled the cylinder; this is the type of fossil represented by a *Calamites* pith cast. Walton postulated that after compression the horizontal diameter of the fossil would be the same as that of the original axis. The collapsed plant tissue formed a 'compression border' at the sides (text-fig. 4), its width being a measure of the thickness of the woody cylinder.

The first account of actual experimental work is given by Harris (1974) who considers compression mechanisms as they apply to spherical pollen grains. This work arose in the course of an investigation of the colpus-like folds of distorted *Williamsoniella* pollen grains. Harris constructed hollow balls of various artificial materials which were then compressed between flat surfaces. The results showed that such spheres do expand horizontally.



TEXT-FIG. 4. The result of compression of a cylinder of highly compressible material infilled with sediment. The compressible material forms compression borders (c) bounding the infill. (After Walton 1936.)

Harris also carried out a preliminary investigation of spores buried in matrix, again using artificial materials, e.g. wax and plastic balls in sand. In this case no measureable horizontal extension occurred, largely as Walton had predicted. After examining many dispersed spores within sediments, Harris concluded that the spores showed no evidence of spreading laterally into the enclosing matrix.

This was the first experimental work attempted since Walton set out his hypothesis in 1936. It is clear that spore exines retain a resilience and elasticity after their contents have been degraded which may not be matched in larger plant structures. In this respect, the behaviour of his spore models may differ from the collapse of plant tissue undergoing biodegradation; but Harris's work has shown that experiments with simple, physical models of the plant-matrix system can help to elucidate the structure of the fossil as it is observed in the rock.

Whether distortion during compression is only in the vertical plane and that the diameter of the fossil is the same as that of the original plant, was investigated by Niklas (1978), in an attempt to test Walton's assumptions. Niklas calculated that total flattening of a cylinder would produce a maximum diameter increase of 57%. A series of experiments designed to monitor the deformation of a cylinder during compression, using artificial materials, were conducted; he also conducted further experiments using natural materials such as sand, clay, and mud with fresh plant axes embedded in them. Unfortunately, Niklas does not describe the actual procedure adopted for any of these experiments, but several conclusions are given. These include:

1. That horizontal deformation (expansion) of a cylindrical body may occur during compression.
2. That the theoretical maximum diameter increase is never reached.
3. That solid cylinders of tissue show a maximum 10% diameter increase.

This work was the first really to consider compression of stems experimentally, but the detailed mechanisms of collapse and compression of the plant organs does not emerge from the results published so far.

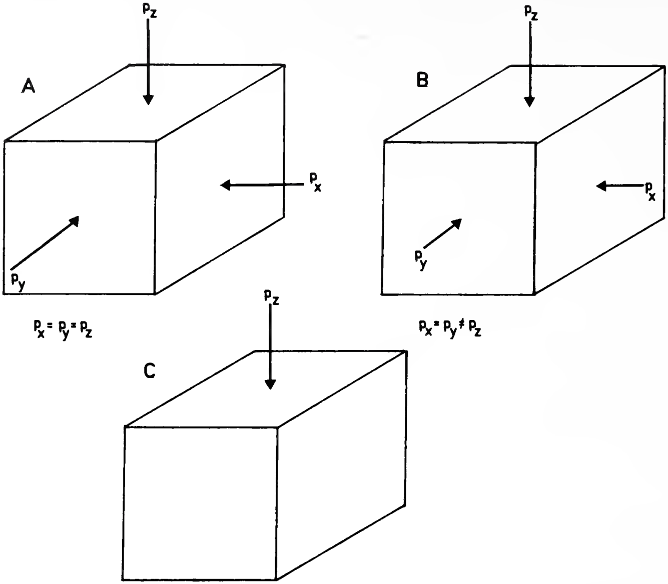
THE PRESENT WORK

General considerations

In order to investigate compression processes experimentally, we have constructed an apparatus in which the vertical dimension can be observed during the experiment. Rieke and Chilingarian (1974) considered the type of mechanism required to experiment with compaction processes, i.e. the best means of reproducing conditions existing in naturally compacting sediment. They consider that during the initial stages of sedimentation the pressure was hydrostatic (three principal stresses are equal) (text-fig. 5); as sedimentation proceeds, the pressure becomes biaxial (two out of the three principal stresses are equal, namely those in the horizintal plane). As the overburden increases and the matrix becomes more rigid, the pressure, in effect, becomes uniaxial; that is, the compression force is parallel to the vertical axis. Using this principal, an apparatus was constructed in which the pressure was uniaxial, thereby creating conditions comparable to those which occur after burial of plant material with an overburden.

The apparatus consisted of a piston system which acted on the contents of a loading box 19·0 × 19·0 × 1·5 cm in which the individual 'fossils' were placed and sealed in by a vertical perspex cover. The piston system was operated by a large screw mechanism (Pl. 30).

In this first investigation into the behaviour of plant and matrix on compression we wished to use the simplest system possible. One of the difficulties in studying the compaction of natural sediments is to reproduce the effect of upward movement of water through the sediment. In order to do this a water-tight apparatus is required in which there is a strict control over the movement of water out of the system. Another problem to consider in this type of study is the impossibility of reproducing the load of hundreds of metres of sediment exactly as it occurs in sedimentary basins. We therefore decided to use an apparatus in which simple artificial models could be compressed using a totally dry system, thereby removing the problems described above. We considered it was important to begin an investigation of this type to see if such experimental modelling could help us to interpret what we observe in plant compression fossils. Foam rubber was chosen to represent plant tissue since it is easily prepared and is very compressible (by 85% of its original volume under our maximum load). Finely sieved sawdust was used as matrix since it was particulate, could be packed freely around the fossil like settling sediment, but was less compressible than foam rubber (compresses by 47% of its original volume under our maximum load). It also becomes tightly compacted, i.e. increases in rigidity with compression, like natural fine-grained sediments. Air in the matrix interstices in effect



TEXT-FIG. 5. Different loading stresses on sediments in laboratory experiments. A. Hydrostatic loading, the three principal stresses are equal $p_x = p_y = p_z$. B. Triaxial loading in which only the two horizontal principal stresses are equal, $p_x = p_y \neq p_z$. This situation develops as the matrix consolidates. C. Uniaxial loading, only one principal stress acting in the vertical axis; this is the condition in a consolidated matrix under heavy load. (After Reike and Chilingarian 1974.)

took the place of the water in a natural sedimentary system, and was, of course, displaced freely during compression.

The design of the piston system was changed during the course of experimentation. Originally we used a single piston but this did not produce the results seen in compression fossils. Using this type of system resulted in sediment at the margins of the cylinder becoming totally compacted and so holding up the descending piston, preventing further deformation of the 'plant' material (Pl. 31, 1–2).

In order to get a form closer to known compression fossils the piston system was changed to a parallel series of ten independent pistons each 1·9 cm wide. Each piston was spring-loaded, still being

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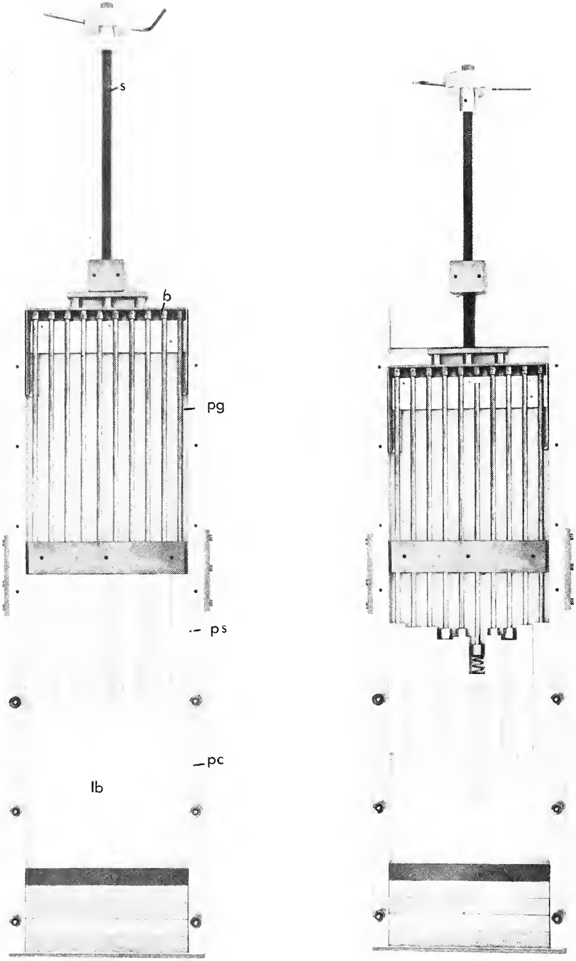
EXPLANATION OF PLATE 30

The compression apparatus used in the experimental work. × 0·3. This consists of a large screw mechanism (s) which acts on a bar (b) to which ten plungers (pg) are attached. On compression the plungers push into ten independent spring-loaded pistons (ps). Each piston will move independently when acting on the matrix in the loading box (lb) in which the plant and matrix are placed, and sealed by a perspex cover (pc). In the right-hand photograph the central piston has been dropped to reveal the expanded end of the plunger and the spring, which is recessed into the upper part of all the pistons.



REX and CHALONER, compression apparatus

operated by the single common screw mechanism (Pl. 30). This type of system produced a very different effect, since when the sediment at the sides of the stem became totally compacted the central pistons were still capable of movement. This allowed further deformation of the stem and it underwent compression, producing an asymmetrical shape. The upper surface, facing the compressional force, had 'collapsed' into the lower surface, which had retained some of its original curvature; this gave the compression an orientation with regard to the direction of pressure, as is seen to occur in nature (Pl. 31, 3–4). The results produced by this 'multipiston' system were much nearer to the structures observed in sections of compression fossils than those produced by the single piston, and we subsequently used the apparatus in this form for the experiments described below.

During the course of experimentation it became obvious that the diameter of the cylinder used in the experiments was important. The smaller the compressed plant structure in relation to the size of the whole matrix body (our compression box) the more the matrix at the margins supported the compression load and 'protected' the plant tissue from distortion (Plate 31, 5–8).

Experimental results

A series of experiments was designed to attempt to reproduce experimentally known compression fossils using artificial materials. We were particularly interested to see:

1. Whether the external features of the plant could appear on an internal cast, e.g. leaf cushions in Lepidodendrids appearing on an 'endocortical cast'.
2. Whether the internal features of the plant could be translated on to the outer surface of the fossil, e.g. 'ribs' on the inner face of the woody cylinder in *Calamites*, appearing as topographic features on the outer surface of a stem compression.
3. The way in which spines behaved on compression of a spiny axis, e.g. *Sawdonia*.
4. Whether the compression border predicted and observed by Walton in *Calamites* could be reproduced.
5. How the collapse of an internal structure, e.g. the woody cylinder in *Stigmaria*, produces features on the outer surface of the fossil.

External features appearing on an internal cast. When species of *Lepidodendron* are found as compression fossils, only a piece of the outer layer of the stem (broadly, the outer cortex) is usually found, bearing leaf cushions, rather than an entire stem. This may be due to 'sloughing off' of the outer (primary) stem surfaces during the life of the tree, as suggested by Chaloner and Collinson (1975) for the '*Syringodendron*' state of *Sigillaria*, or to post-mortem break up of the hollow cortical cylinder.

On careful examination of some *Lepidodendron* specimens, the 'leaf cushions' appear to be poorly

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EXPLANATION OF PLATE 31

Fig. 1. The single piston system before compression, acting on a solid cylinder of foam rubber in a sawdust matrix.

Fig. 2. After compression, the cylinder shows only slight collapse effect; compression has been halted by the total compaction of the sediment at the margins of the cylinder. (Note here and in the following, the four spots outlining the plant axis on the perspex cover at the start of each experiment.)

Fig. 3. The multipiston system, before compression, acting on a solid cylinder of foam rubber in a sawdust matrix.

Fig. 4. The same after compression; the matrix marginal to the cylinder has compacted, but the central pistons have continued independent movement, causing further deformation of the cylinder.

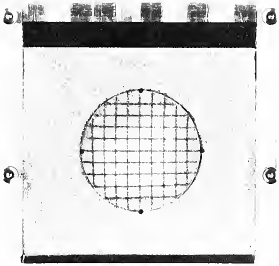
Fig. 5. Foam rubber cylinder reaching across the full width of the loading box, before compression.

Fig. 6. The same after compression; the resulting form of the foam rubber shows that the curvature of the lower surface has been retained to some extent while the upper surface has collapsed into the lower.

Fig. 7. Small solid foam rubber cylinder in loading box before compression.

Fig. 8. The same after compression; distortion of the cylinder is much less than in 6, as the completely compressed matrix at either side of the cylinder protects it from further deformation.

(All, × 0·5.)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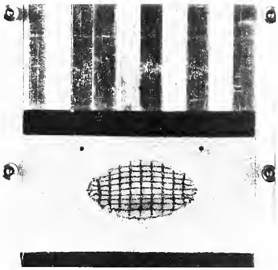
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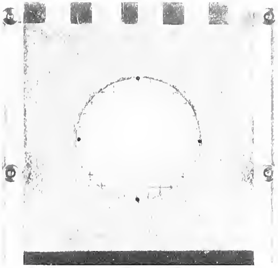
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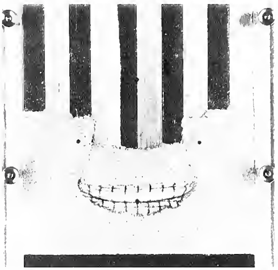
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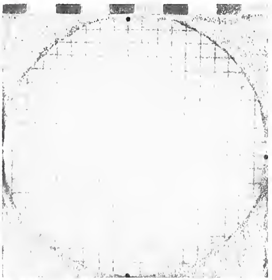
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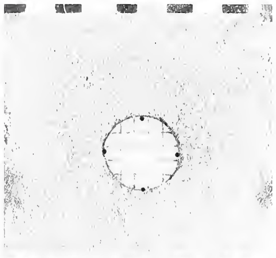
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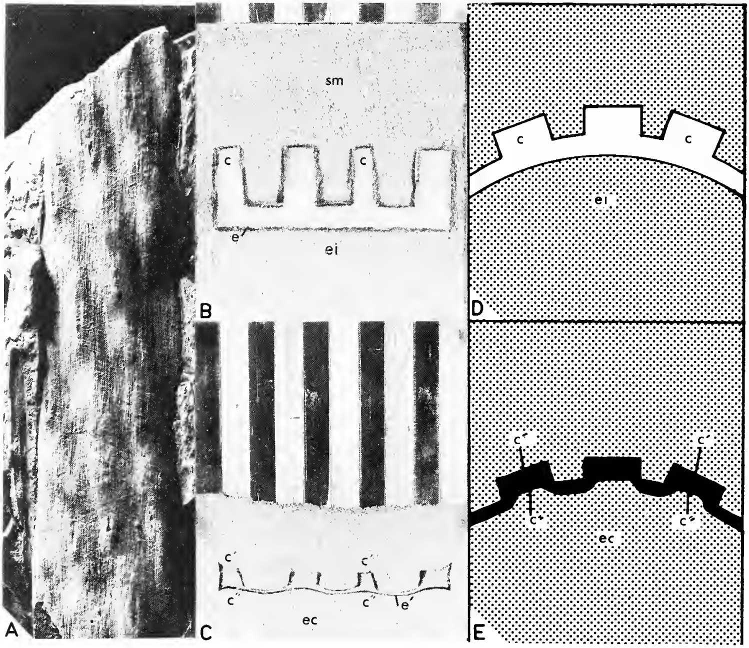
REX and CHALONER, the deformation of cylinders of varying dimensions



TEXT-FIG. 6. A. Endocortical cast of a lepidodendrid showing the spiral arrangement of leaf cushions indistinctly. × 1·7. From Radstock, Somerset. B. Experiment constructed to explain this specimen. This consists of a strip of foam rubber sculptured into 'leaf cushions' (c). Endocortical infill (ei), surrounding matrix (sm), inner surface of 'cortex' (e). C. On compression the inner surface (e′) of the 'cortex' has collapsed into the cushions (c′) taking up their form (c″). D. Explanatory diagram showing leaf cushions and infill before compression. E. On compression the cortical tissue is altered to coaly matter and the endocortical cast (ec) takes up a subdued version of the form of the outer cushions (c″). The surface of the endocortical cast (e′) is the same as that shown in the fossil in A.

defined structures, lacking leaf scars and cellular detail but showing the spiral arrangement of the leaf cushions common to the Lepidodendrids (text-fig. 6A). It is suggested that this effect is produced by the pattern of the cushions appearing on the endocortical cast, when this has collapsed into the leaf cushions on compression. In order to produce this effect experimentally, a strip of foam rubber was sculptured into leaf cushions as they might be seen in section and then compressed in a matrix of fine sawdust (text-fig. 6B). On compression (text-fig. 6C) the topography of the cushions on the outer surface of the strip was lowered considerably. The much more interesting effect was that the grooves (infilled with matrix) between the cushions impressed their topography as ridges on to the inner surface of the strip. Correspondingly, the inner surface of the leaf cushions formed depressions. Hence, where there had been no relief on the inner surface of the strip (bounding the endocortical cast) before deformation, on compression the pattern of the cushions was translated on to the endocortical cast. The surface labelled e′ on our experiment corresponds to the exposed surface of the fossil shown in text-fig. 6A. The fact that such cushions on the endocortical cast are postive features may misleadingly encourage the observer into believing he is seeing a poorly preserved original surface topography.

The extent to which external topography is communicated to a cortical infill (endocortical cast) is evidently a function of cortical thickness, and compressibility of matrix. Generally it seems that a lycopod with rather thin development of cortex preserved in a coarse matrix will show positive 'external' topography (cushions) on the endocortical cast more readily than one of thicker cortical development and finer grained matrix.

Internal features appearing on an external surface. The reverse situation of the above is where the internal features of the plant are translated on to the outer surface during the compression. For example, the internal topography of the pith cavity wall appearing on the outer surface. This is seen in some *Calamites* specimens where internal ribs appear on the outer surface of a stem compression, where in effect the coaly residue of the stem tissue is 'draped' over the pith cast. Such a specimen is not technically a pith cast, but rather a pith cast lying within a stem compression, but this term has been used loosely for material of this kind.

An experiment was devised to reproduce this effect; foam rubber was sculptured into ribs and embedded in a sawdust matrix. On compression, the ribs were transmitted from the internal surface of the layer on to the external surface (Pl. 32, 1–3), a process obviously closely analagous to that described above for a lycopod leaf cushion.

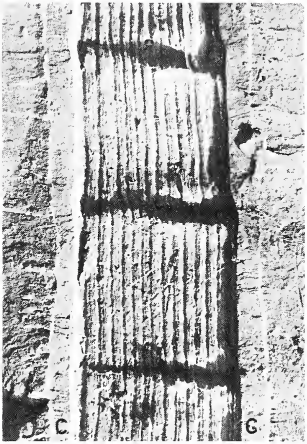
The behaviour of spines during compression. When examining compression fossils one of the most interesting aspects is the behaviour of appendages such as spines on plant axes. Chaloner *et al.* (1978) examining *Sawdonia* specimens from borehole cores in Oxfordshire suggest the processes that may have affected the axis during compression, but did not investigate this experimentally.

If we consider what happens to a spiny axis when it touches and lodges on a river or lake bottom, we may picture the spines facing the sediment acting as supports, holding the stem slightly above the sediment surface. In this situation it is unlikely that sediment will get into the gaps between the spines and the sediment surface below the stem until burial has occurred, while sediment will continue to settle gradually on the upper (exposed) surface of the axis as it is buried.

We designed an experiment to copy this process as closely as possible. As compression proceeded the lower spines gradually 'sank' into the sediment and the hollow axis (left hollow in our model since *Sawdonia* had a relatively small stele, and its fossils show no sedimentary infill) gradually closed up. During closure, the upper surface gradually 'collapsed' into the lower producing an asymmetric, C-shaped section. The spines borne laterally on the stem were reduced considerably in thickness but retained their original length. Those spines facing the compression on the upper surface shortened considerably and showed some distortion (Pl. 32, 4–6). The lower spines shortened but not to the same extent. It appears that most of the deformation is taken up by 'collapse' of the stem and the subsequent deformation of the spines on the upper surface. The spines on the lower surface seem to have been more 'protected' from the compression than was suggested to be the case by Chaloner *et al.* (1978).

Formation of compression borders. Walton (1936) suggested that on either side of a matrix infill ('pith cast') a flattened coaly margin would form; he also suggested a similar process occurred with a leaf having an incurled margin (text-fig. 2). In both cases the greater compressibility of plant tissue adjoining the less compressible matrix infill produced a 'compression border', the width of which represents the thickness of the original plant structure (woody cylinder, leaf thickness). Modelling of this in our apparatus produced a result similar to Walton's predictions (Pl. 32, 7–9) and is shown in some *Calamites* specimens (text-fig. 7). This compression border, as indicated earlier, is produced only when multiple pistons are used rather than the 'single piston' earlier version of the apparatus.

The effect of collapse of an internal structure on the outer surface of the fossil. Examination of compression fossils of *Stigmaria* show interesting features beyond those considered above. In fossils



TEXT-FIG. 7. *Archaeolcalamites radiatus* (Brongn.) Stur. This shows an impression of internal ribs and the formation of compression borders (c) produced by the collapse and compression of secondary xylem bounding the infill. The fossil is therefore a pith cast, within an impression. The high compressibility of the oil shale matrix produced a fossil of very low relief. Oil shale, Calciferous sandstone series, Lower Carboniferous, Scotland. ×2.

of this type, a very thin coaly layer, bearing impressions of points of attachment of rootlets (commonly called 'rootlet scars') bounds a matrix-filled cylinder (an endocortical cast). Examination of a vertical section of the infill often shows the presence of the highly compressed woody cylinder bounded at its margins, as would be expected, by small compression borders (Pl. 33, fig. 3).

The stele (woody cylinder) is often seen to be displaced in such *Stigmaria* compressions, commonly lying either against the upper or lower inner surface of the cortical cylinder. The stele evidently became separated from the cortex during growth by a 'middle cortex cavity'. The stele was free to either float or sink within the cortex, or to lodge in the mid point of the infill. *Stigmaria* often shows the presence of a groove running along one of the outer surfaces. This was thought by Pant (1956) to be related to the late collapse of the xylem cylinder, after infill of the cavity. The groove was considered by Walton (quoted in Pant, loc. cit.) to occur only on the upper surface of the stigmarian axis, since orientated specimens (e.g. Williamson's specimen of *Stigmaria ficoides* from Clayton, Lancs., held at the Manchester Museum) sometimes show the groove to be on this surface. This is

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EXPLANATION OF PLATE 32

Fig. 1. Experiment to investigate the behaviour of internal ribs (r) on a woody cylinder during compression. Intial state.

Fig. 2. On compression the outer surface collapses onto the ribs (r′) and the surrounding outer matrix (sm) takes up the form of the internal ribs (r″). This is very similar to, but the reverse of, what is described in text-fig. 6.

Fig. 3. Close up of the above to show detail.

Fig. 4. Experiment to investigate the behaviour of spines during compression. Initial state.

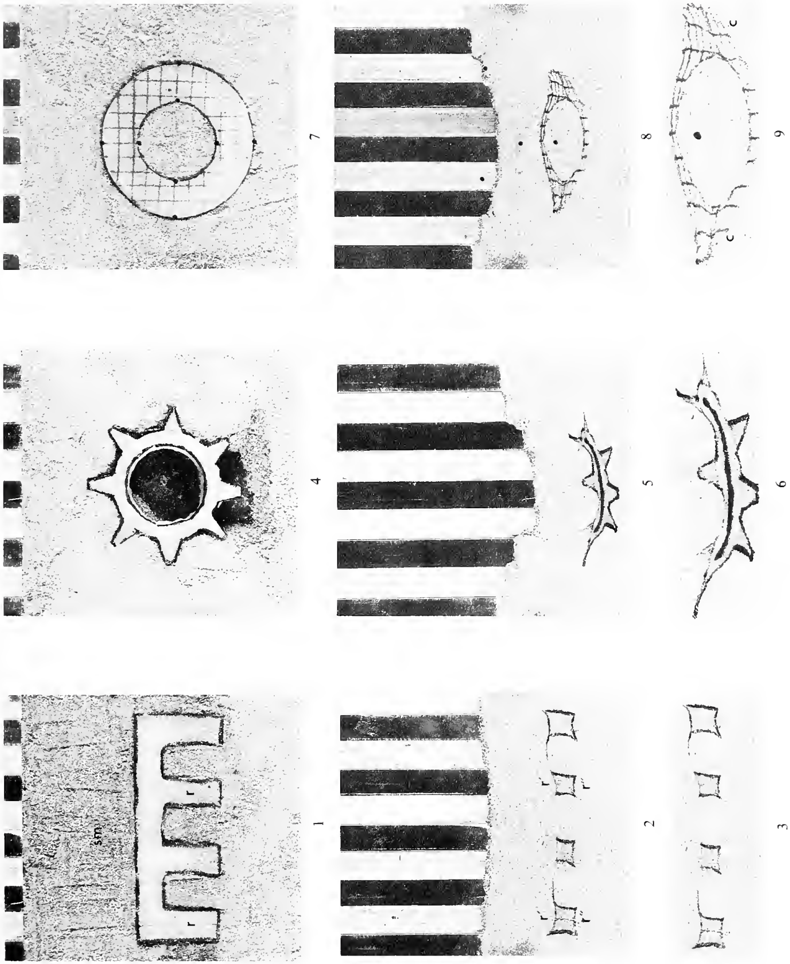
Fig. 5. On compression the marginal spines are flattened. The spines directed upwards are shortened to a greater extent than those on the lower surface.

Fig. 6. Close up of the above to show detail.

Fig. 7. Experiment to investigate formation of a *Calamites*-type fossil. Initial state.

Fig. 8. Under load, compression borders (c) form at the margins of the infill. These have the horizontal dimension (diameter) of the original cylinder.

Fig. 9. Close up of the above to show detail.



REX and CHALONER, experiments showing the compression of different plant structures evidently not always the case since material we have collected *in situ* from Swillington Quarry (Yorkshire) (Scott 1978) shows that a groove may be present on the lower surface in some circumstances.

In fossil stigmarians of this type there are evidently three fracture planes along which plant material may be exposed (text-fig. 8). One is the (compressed) outer surface (A) the other, the outer surface of the woody cylinder (B). A specimen exposed by fractures may accordingly show outer surface with rootlet attachment at the margin and internally the exposed woody cylinder (C). Pant (1956) showed that specimens known as *Gymnostrobus* were in fact the isolated woody cylinders of *Stigmaria*, exposed by a fracture plane running along the inner surface of the stele infill (pith cast) and through the woody cylinder at either side, and not cones, as they had originally been thought to be by Lesquereux (1879–80) and Bureau (1914).

Small spirally arranged lenticular structures are seen on the surface of the exposed stele. Frankenburg and Eggert (1969) have identified in petrifactions of *Stigmaria* what they call 'lateral appendage gaps' on the inner surface of the stele. These are the points from which the traces to the rootlets arose and in any transverse section are seen as small gaps which cause division of the woody cylinder into blocks. During infill of the axis these gaps filled with sediment producing the lenticular structures observed on the compression of the woody cylinder.

Experiments were constructed to see if we could reproduce this stigmarian-type fossil with its stelar groove. The model used consisted of a very thin outer cylinder of foam rubber with a thicker inner cylinder, all infilled with matrix. First, the stele was placed in a central position and compressed, the stele formed compression borders and a 'stelar groove' appeared in the upper surface of the cylinder (Pl. 33, 1–3). In a separate experiment the stele was placed at the outset towards the top of the cylinder. On compression the stele formed compression borders and became slightly asymmetric, while a furrow of the same width as the stele diameter (Pl. 33, 4–6) began to appear on the upper surface.

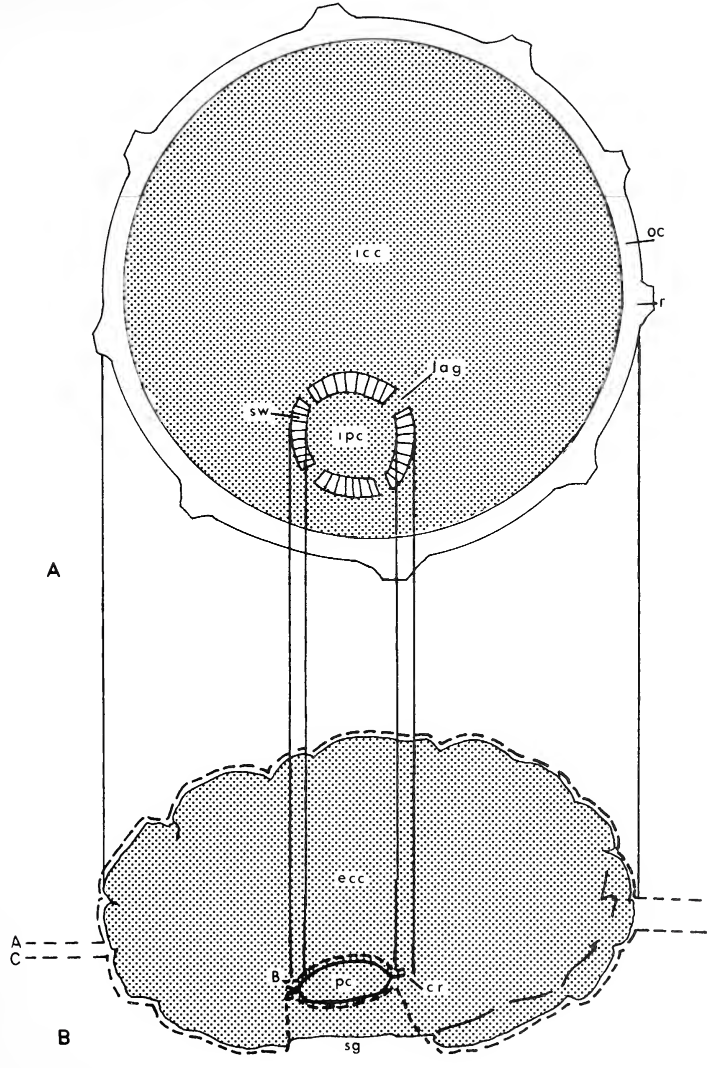
When in a further experiment the stele was placed at the bottom of the cylinder, a slight uneveness formed on the lower surface, but not a distinct groove (Pl. 33, 7–9).

It would appear that the furrow is in fact related to the presence of the stele near the upper or lower surface of the cylinder; it provides a local area of further compressibility after the sedimentary infill has compacted causing this feature of a stelar groove to be produced. It would appear that the closer the stele is to either surface of the axis, the greater the effect on the external topography of the outer surface.

CONCLUSIONS

The outcome of this preliminary excursion into the formation of compression fossils has been to show that the deformation observed in such specimens can be reproduced in a simple mechanical model. As we learn more of this interaction of collapsing plant tissue and the enclosing matrix, it should become possible to extrapolate back to the original three-dimensional form from the many compression fossils where we have no information from permineralized specimens. This is important for our understanding of the many genera of plants based only on compression or impression states of preservation.

TEXT-FIG. 8 (*opposite*). A. Diagrammatic section through an infilled Stigmarian axis. *oc:* outer cortex; *r*: rootlets: *icc*: infill of cortical cavity; *lag*: lateral appendage gap; *sw*: secondary xylem; *ipc*: infill of pith cavity. B. Compression fossil of a *Stigmaria*, showing a vertical section, drawn from a specimen found at Swillington Quarry, Yorkshire. Westphalian B. The three possible fracture planes that may expose the fossil are: (A) the fracture plane passing over the outer surface of the axis; (C) the fracture plane which exposes the outer surface of the axis and then 'jumps' into the infill to expose the outer surface of the stele compression (sc); (B) the fracture plane which exposes the compression of the stele only, occurring as isolated cylinders, and is the '*Gymnostrobus* state' of *Stigmaria* (see this page). *sg*: stelar groove; *cr*: compression rim; *ecc*: endocortical cast; *pc*: pith cast. × 1.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One particularly important aspect of the behaviour of compressed plant material is that topography on one surface of the plant organ may be 'printed through it' during compression to appear on the opposite face. This means that a positive topography of, for example, leaf cushions on a matrix surface must not be construed as proof that outer surface is being seen; on the contrary, it is likely to be matrix which has collapsed into the site of cushions from the endocortical cavity (e.g. *Lepidodendron*). Equally, stelar features may show, in various ways, as the outer surface of a compression (e.g. *Stigmaria*).

A further complicating factor in our interpretation of compression fossils is that the configuration of the plant material itself influences the fracture surface which reveals the fossil. The way in which leafy shoots of lycopods are exposed by fracture demonstrates that the rock cleavage may be diverted from the bedding planes by the extent and angle of inclination of the coaly layers constituting the substance of the fossil. Plant compression fossils are in these various aspects very different from a 'pressed plant' lying on a fracture surface. Further experimentation using plant tissue in actual water-lain sedimentary environments is most desirable in order to substantiate (and no doubt modify) the conclusions offered here.

Acknowledgements. We thank Mr. S. White of the Science Workshop, Bedford College, for constructing the apparatus and Mr A. Davis for help with the photography. G. M. Rex gratefully acknowledges receipt of a NERC studentship, during the course of which this work was carried out.

REFERENCES

BECK, C. 1971. On the anatomy and morphology of the lateral branch systems of *Archaeopteris*. *Am. J. Bot.* **58,** 758–784.

BOULTER, M. C. 1968. A species of compressed lycopod sporophyll from the Upper Coal Measures of Somerset. *Palaeontology*, **11,** 445–457.

BUREAU, M. E. 1914. *Bassin de la Basse Loire. Études des gîtes minéraux de la France* (atlas, 1913). Paris.

CHALONER, W. G. and BOUREAU, J. E. 1967. *In* BOUREAU, E. (ed.). 'Lycophyta' in *Traité de paléobotanique*, vol. 2. Masson: Paris. 435–802.

—— and COLLINSON, M. E. 1975. Application of SEM to a Sigillarian Impression fossil. *Rev. Palaeobot. Palynol.* **20,** 85–101.

—— HILL, A. and ROGERSON, E. C. W. 1978. Early Devonian plants from a Southern England borehole. *Palaeontology*, **21,** 693–707.

EXPLANATION OF PLATE 33

Fig. 1. Experiment to reproduce the Stigmarian type fossil in which the stele is central, bounded by a thin outer cortex. × 0·5.

Fig. 2. Result on compression of above; a 'stelar groove' is formed in the outer surface of the compression above the stele. The stele shows compression rims. × 0·5.

Fig. 3. Vertical section through a fossil *Stigmaria* showing central position of stele (arrow). × 0·75. This and the other *Stigmaria* specimens on this plate were collected *in situ* at Swillington Quarry, near Leeds, Yorkshire (Westphalian B), so that their orientation in the matrix is known.

Fig. 4. Experiment to reproduce the Stigmarian type of fossil in which the stele is displaced towards the upper surface. × 0·5.

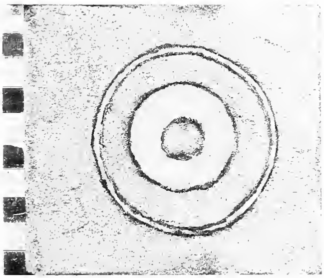
Fig. 5. On compression the stele becomes asymmetric and compression rims form. A stelar groove forms in the upper surface of the compression. × 0·5.

Fig. 6. Vertical section through a fossil *Stigmaria* showing initial upward displacement of the stele (arrow), and the stelar groove lying above it. × 0·5.

Fig. 7. Experiment to reproduce the Stigmarian type of fossil in which the stele is displaced towards the lower surface. × 0·5.

Fig. 8. On compression the stele forms compression rims and a slight concavity on the lower surface of the outer cylinder is produced.

Fig. 9. Vertical section through a *Stigmaria* in which the stele (arrow) is displaced towards the bottom of the cylinder and a stelar groove has been formed in the outer surface of the cylinder. × 0·75.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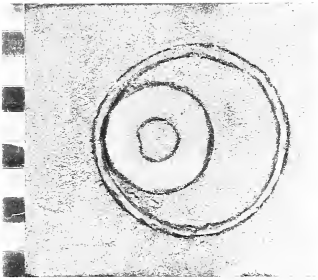
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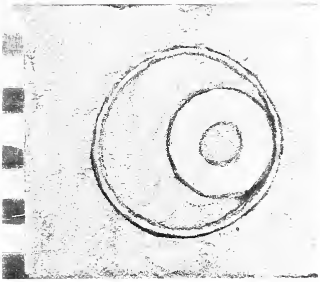
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REX and CHALONER, compression experiments reproducing known vertical sections of *Stigmaria*

CONWAY MORRIS, S. 1979. Middle Cambrian Polychaetes from the Burgess Shale of British Columbia. *Phil. Trans. R. Soc.* (B) **285,** 227–274.

CROOKALL, R. 1964. Fossil plants of the Carboniferous rocks of Great Britain. *Mem. Geol. Surv. G.B., Palaeontol.* **4,** 217–354.

DORAN, B. J. 1980. A new species of *Psilophyton* from the Lower Devonian of Northern New Brunswick, Canada. *Can J. Bot.* **58,** 2241–2262.

FERGUSON, D. A. 1971. *The Miocene flora of Kreuzau, Western Germany. 1, The leaf remains.* Amsterdam and London, North London Pub. Co.

FRANKENBURG, J. M. and EGGERT, D. A. 1969. Petrified *Stigmaria* from North America: Part 1. *Stigmaria ficoides*, the underground portions of Lepidodendraceae. *Palaeontographica* (B) **128,** 1–47.

HARRIS, T. M. 1974. *Williamsoniella lignicri*: its pollen and the compression of spherical pollen grains. *Palaeontology*, **17,** 125–149.

JOHNSON, T. 1913. On *Bothrodendron* (*Cyclostigma*) *kiltorkense*, Haughton sp. *Sci. Proc. Roy. Dublin Soc.*, NS **13,** 500–528.

LECLERCQ, S. 1951. Étude morphologique et anatomique d'une Fougère du Dévonien Superieur, le *Rhacophyton zygopteroides* nov. sp. *Annls. Soc. geol. Belg. Mem.* 4^B, **9,** 62.

—— 1960. Refendage d'une roche fossilifère et dégagement de ses fossiles sous binoculaire. *Senckenberg. leth.* **41,** 483–487.

—— and ANDREWS, H. 1960. *Calamophyton bicephalum*, a new species from the Middle Devonian of Belgium. *Ann. Mo. bot. Gdn.* **47,** 1–23.

LESQUEREUX, L. 1880. *Description of the coal flora of the Carboniferous formation in Pennsylvania and throughout the United States*, **2,** 355–694, (atlas, 1879). Harrisburg, Pa.

MOORE, R. C. (ed.) 1979. *Treatise on Invertebrate Paleontology*. Part A. *Introduction*, 53–57. Geological Society of America.

NIKLAS, K. J. 1978. Morphometric relationships and rates of evolution among Paleozoic Vascular Plants. *Evol. Biol.* **11,** 509–543.

PANT, D. D. 1956. On two compressed Palaeozoic axes: *Stigmaria ficoides* in the *Gymnostrobus* condition and *Vertebraria indica*. *Ann. Bot.* NS **20,** (79), 419–429.

PLUMSTEAD, E. P. 1952. Description of two new genera and six new species of fructifications borne on *Glossopteris* leaves. *Trans. geol. Soc. S. Afr.* **55,** 281–328.

RIEKE, H. H. and CHILINGARIAN, G. V. 1974. *Developments in sedimentology, 16. Compaction of Argillaceous sediments.* Elsevier, Amsterdam.

RIGBY, J. F. 1978. Permian Glossopterid and other Cycadopsid fructifications from Queensland. *Geol Soc. Queensland Palaeontological Pap.* **41,** 3–21.

SCHOPF, J. M. 1975. Modes of fossil preservation. *Rev. Palaeobot. Palynol.* **20,** 27–53.

SCOTT, A. C. 1978. Sedimentological and ecological control of Westphalian B plant assemblages from west Yorkshire. *Procs. Yorks. geol. Soc.* **41,** 401–508.

SELLING, O. H. 1944. Studies on Calamitean cone compressions by means of serial sections. *Svensk. bot Tidskr.* **38,** 295–333.

SPICER, R. A. 1977. The pre-depositional formation of some leaf impressions. *Palaeontology*, **20,** 908–912.

—— 1980. The importance of depositional sorting to the biostratigraphy of plant megafossils. *In* DILCHER, D. L. and TAYLOR, T. N. (eds.). *Biostratigraphy of fossil plants.* Copyright 1980 by Dowden, Hutchinson & Ross Inc.

—— 1981. The sorting and deposition of allochthonous plant material in a modern environment at Silwood Lake, Silwood Park, Berks., England. *Geol. Survey Prof. Paper* (USGS), 1143.

WALTON, J. 1923. On a new method of investigating fossil plant impressions or incrustations. *Ann. Bot.* **27,** 379–390.

—— 1936. On the factors which influence the external form of fossil plants: with descriptions of the foliage of some species of the Palaeozoic Equisitalean genus *Annularia* Sternberg. *Phil. Trans. R. Soc.* **226,** 219–237.

WHITTINGTON, H. B. 1975. The enigmatic animal *Opabina regalis*, Middle Cambrian, Burgess Shale, British Columbia. *Phil Trans. R. Soc.* (B) **271,** 1–43.

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SALTERELLA (EARLY CAMBRIAN; AGMATA) FROM THE SCOTTISH HIGHLANDS

by ELLIS L. YOCHELSON

ABSTRACT. *Serpulites maccullochi* Murchison, the earliest described species to be assigned to *Salterella*, is redescribed. Specimens are illustrated from thin sections from the Salterella Grit exposed on Loch Eriboll. Additional specimens are illustrated from the overlying Ghrudaidh Formation, there and at several other localities. Specimens from the Salterella Grit of *Salterella maccullochi* are identical to *Volborthella tenuis* from Estonia and that species is placed in the synonymy of *Salterella maccullochi*. The species is a senior synonym of *S. rugosa* Billings, *S. expansa* Poulsen, and probably *S. mexicana* Lochman.

A SMALL conical fossil, now known as *Salterella*, has been reported from the Scottish Highlands for almost a century and a half, yet it has been little studied. In an area where fossils are sparse, neglect of this form is curious. It is an indicator of the late Early Cambrian (*Bonnia–Olenellus* zone), and the limited vertical distribution of *Salterella* in eastern North America is strongly suggestive that it ranged only through an extremely short time interval during the Early Cambrian.

AUTHORSHIP, ORTHOGRAPHY, AND TYPE LOCALITY OF *SERPULITES MACCULLOCHI*

Tubes of a minute organism were found nearly a century and a half ago by geologists working in the Scottish Highlands and were interpreted as minute cephalopods. The geologic section at Skiag Bridge, near Inchnadamph, and discovery of this same fossil near there were mentioned in early accounts of the geology. Nevertheless, from the standpoint of nomenclature, the only significant literature is that which first mentions a specific name. Murchison (1859*a*, p. 222) was the first to do so; he wrote: 'The minute Annelide before spoken of as abounding in the quartz rocks of the N.W. Highlands is here figured. Although the tube is thicker in proportion than in any known species of Serpulites, it is here provisionally referred to that genus, and is named Serpulites MacCullochii, after the distinguished geologist who first noticed it.'

The figure caption of an accompanying woodcuct gives to the left of figure 'Small, thick shelly tubes of Annelides (Serpulites? MacCullochii)'. To the right is recorded 'Collected from the Lower Quartz-rock of Durness, Sutherland, by Mr. C. Peach'.

Later in the same year, Murchison (1859*b*, p. 366) wrote: 'The minute cylindrical bodies which Macculloch supposed to be Orthoceratites have completely satisfied Mr. Salter that they belong to the class of sea-worms. I have therefore named them, in the new edition of "Siluria" (1859*a*, p. 222) *Serpulites Maccullochii*, in honour of the first discoverer of the oldest perceptible organic remains of the Highland Rocks.' The legend to plate 13, figure 31, is '*Serpulites*? *MacCullochii*, Murchison. In a mass of sandstone. These thick, short, free annelide-tubes are very common in the quartzose sandstones of Durness.' This illustration is of a different size and shape than the one used in *Siluria*; the fossils on it are somewhat larger. Within the article, a section on 'Fossils of the Durness Limestone' is attributed to J. W. Salter, but the quote given above is not included in that section, nor is the fossil in question mentioned.

Billings (1861, p. 954), after naming the genus *Salterella* and the species *S. rugosa*, wrote: 'This species must be closely allied to *Serpulites Macullochi* (Salter), but upon an average they are smaller than those figured by Salter in Jour. Geol. Soc. Vol. XV, Pl. 13, fig. 31.'

[Palaeontology, Vol. 26, Part 2, 1983, pp. 253–260, pls. 34–35.]

A few years later in the fourth edition of *Siluria*, Murchison (1867, p. 166) wrote: 'Although the tube of this Salterella (Billings) is thicker in proportion than in any known Serpulites, it was provisionally referred in my last edition to that genus, and named, at my request, Serpulites Maccullochii by Mr. Salter, after the distinguished geologist who first noticed it.' The same lithographic plate used in the third edition of *Siluria* is reproduced, and the material in the caption is identical, except the illustration is referred to as 'Salterella Maccullochi, Salter'.

With so many interesting variants in the name of a Scottish geologist, one is hard pressed to pick the best. Fortunately, it is possible to invoke the principle of first usage. Rules on punctuation and endings as currently treated by the International Code of Zoological Nomenclature indicate that the species name ought to be rendered today as *Serpulites maccullochi*.

The authorship is clear-cut, for the specific name must be attributed to Murchison as the first person to propose it in such a way as to fulfil the requirements of availability. That the scientific underpinnings of *S. maccullochi* Murchison were supplied by Salter, I have no doubt. He was a great figure in British paleontology, and Murchison recognized his contributions. Nevertheless, Murchison is unquestionably the author of this specific name. My private suspicion is that Salter may have done a fair amount of ghost writing for Murchison, but, for nomenclatural purposes, that is irrelevant.

In the current geologic literature of the north-west Highlands of Scotland, 'Fucoid Beds' still appears, and this name for a stratigraphic unit can be readily traced back to Murchison's work. The overlying quartz rock became known as the Serpulite Grit, and, in turn, as the Salterella Grit. This grit is overlain by a carbonate unit, the Ghrudaidh Formation, the lowest part of the Durness Group (Cowie *et al.* 1972); the contact between the two is gradational with thin beds of limestone and of siltstone alternating for about a meter. The information accompanying the original woodcut indicates that the *Salterella maccullochi* was originally described from the unit now known as the Salterella Grit. At Inchnadamph, *Salterella* occurs within the Ghrudaidh, but that locality is not the type locality although MacCullough and Peach collected there.

West of Durness, between Balnakiel Bay and the Kyle of Durness, the beds underlying the carbonates of the Durness Group barely crop out along the shore; the area is an exposed headland and is difficult of access except in very good weather (J. W. Cowie, oral comm., 1978). This area is probably where Peach collected the *Salterella* illustrated by Murchison (1859*b*). The same sequence crops out on An-t-Sron ('The nose') on the east side of Loch Eriboll, about 10 km to the east along the strike. In his discussions Murchison (1859*b*) differentiated Loch Eriboll from Durness and thus it is out of consideration as the type locality.

None of my material is from Durness as defined in a strict sense, but the Loch Eriboll section is so similar to the Durness one that I am confident that systematic conclusions based on fossils from there may be drawn with confidence and applied to the type. Throughout north-west Scotland, the Lower Cambrian section is thin, and *Salterella* is probably limited to an interval of 15–20 ms in the upper part of the Salterella Grit and the lower part of the Ghrudaidh Formation combined (Cowie 1974, pp. 130–137). None of the holdings of *Salterella* in the British Museum of Natural History or the Institute of Geological Sciences refer to the shore at Durness. The type lot illustrated by Murchison (1859*b*) cannot be identified with certainty and may have been lost.

Although it has nothing to do with the matters directly at hand, a footnote by Murchison (1867, p. 166) touches on the history and biology of *Salterella*:

'Speaking of these obscure little fossils, in a lecture on the Geology and Scenery of the North of Scotland (1866), Professor J. Nicol says (p. 31), "In the quartzite period organic life undoubtedly existed. Twoscore years ago Dr. Macculloch pointed out curious conical hollows, ending in long pipe-like bodies. These he described as Worm-holes, the prototypes of those seen on the shore, where the Lobworm sinks into the sand left dry by the retiring tide" (Geol. trans. vol. ii, p. 461). We have seen other, smaller holes identical in form with the holes which some small Crustacea on the Kyle of Durness are now digging in the sand washed out of these very rocks. The same sand is now lying in the same place, and beings of like organization are still burrowing it out for food or shelter. Yet the mind almost refuses to grasp the myriad ages that have intervened. The poor worm or insect in its daily occupation was building itself a monument "aere perennius"—a tomb more enduring than king or kaiser. The moral needs not be drawn.'

SALTERELLA FROM THE SALTERELLA GRIT

The small fossil *Serpulites maccullochi* Murchison is described as follows: of simple conical shape, the walls diverging at an angle near 20°; apex simple and with same angle of divergence as sides. Cone laminated, with a variety of small grains arranged in layers, the laminae diverging from a narrow central tube, which extends through all laminae, at an angle of about 45°. The various features mentioned above are illustrated in Pl. 34, figs. 1 and 2, and Pl. 35, fig. 2.

This descriptive information is derived from the illustrated thin sections and others, all of which were cut from a fine-grained quartzite. Many specimens have been distorted and most are worn. So far as I can determine, all specimens from the outcrop at An-t-Stron fall within a single species. Because of accumulation of small grains which collectively are far larger and much darker than the arenaceous matrix, the specimens of *Salterella* are prominent in thin section. On the outcrop they are abundant but only in quite thin scattered layers; their distribution supports the observation that most, if not all, specimens are transported. All the material illustrated from the Salterella Grit is from an interval of less than 10 cm and not all of that thickness contained fossils.

In addition to the material I collected, I have examined weathered specimens from An-t-Sron in the collections of the British Museum of Natural History and Institute of Geological Sciences, London. Some material housed in Edinburgh was also sectioned in connection with this study; collection GSE 5396 located only as 'Loch Broom, Ullapool' in what is lithically the same as the Salterella Grit, also contains this species.

As will be developed, it is my view that the specimens in the Salterella Grit are quite incomplete in that there is nothing preserved to retain the laminae. Although it is within the realm of possibility that an organic sheath was present, I prefer the view that a calcium carbonate shell was present but that all specimens have lost it as a result of solution or transport, or both.

SALTERELLA FROM THE GHRUDAIDH FORMATION

In contrast to the specimens in the Salterella Grit, those in the overlying Ghrudaidh at An-t-Sron are not nearly so readily differentiated from the matrix. Although specimens are abundant, finding good ones is difficult. Many of the specimens are secondarily deformed, and some show evidence of partial recrystallization and solution. Representative individuals are shown in Pl. 34, fig. 5 and Pl. 35, fig. 3. In part, because of recrystallization of the laminae, the central tube is seldom seen but was observed in several thin sections.

Material from the type locality of the formation near Ghrudaidh Farm is a bit less deformed. The farmhouse is long abandoned, but its ruins are still preserved about 4 km south of the village of Durness. Along the shore of the Kyle of Durness at the spot indicated by 517 on the map of Peach and Horne, a carbonate unit was collected. A specimen is illustrated in Pl. 35, fig. 4.

Finally, some specimens 0·4 km south of Skiag Bridge, or 3·1 km north of the hotel at Inchnadamph, are illustrated in Pl. 34, figs. 2 and 3, and Pl. 35, fig. 1. These specimens are also moderately well preserved. Collectively these show that a species of *Salterella* occurs in this formation which has straight tapering sides, expanding at an angle of about 20°. Internal laminae are composed primarily of grains of calcium carbonate, but a few impurities do occur in some specimens. In addition, as noted at An-t-Sron in the Ghrudaidh, some specimens show no outer wall and are broken at the aperture and apex; the central specimen on Pl. 35, fig. 1, is representative of what one is likely to find in the average thin section.

Overall, finding a well-preserved specimen in the Ghrudaidh is difficult. Many are corroded on the edges, some are partially broken at the aperture, and still others are coated with algae. Nevertheless, one gains the impression that only a single, narrowly conical, species is present.

In addition to the straight-sided *Salterella*, another rare fossil has been seen in thin section. It might be a curved species of *Salterella*, it might be a badly deformed example of the poorly known *S. pulchella*, or it might be completely unrelated. The material is not adequate to describe at this time, or even to illustrate.

JUNIOR SYNONYMS OF *SALTERELLA MACCULLOCHI*

I have indicated in this paper that *S. maccullochi* occurs in a carbonate unit as well as in a fine siltstone. If, as suggested, the organims filled the tube with whatever particles were available (Yochelson 1977), principal specific features must be drawn from the external shape, not from the material filling the inner laminae. It is also evident that the kind of material does have secondary effects. Thus, those cones filled with calcium carbonate may deform whereas those filled with more discrete grains will break, in the same way that sandstones and carbonates react differently to the same geological forces.

If one allows for variation in the infilling, one has no alternative but to place several names in synonymy. Comparison of type material convinces me that *S. rugosa* Billings, the type species of the genus, is a junior synonym of *S. maccullochi. Salterella expansa* Poulson was earlier placed in the synonymy of that name (Yochelson and Peel 1980). If one allows for a lamination which is composed almost exclusively of calcium carbonate, it follows that *S. mexicana* Lochman (1952) is a synonym of *S. maccullochi.* The geographic gap between this form described from Sonora and *S. rugosa* from Labrador is lessened by the inclusion of undescribed specimens from southern Pennsylvania (Yochelson *et al.* 1968) and what was then called *Salterella* new species from south-western Virginia (Byrd *et al.* 1973). Additional documentation may be needed to confirm the identity of the excellent specimens from Mexico and the substantially poorer ones from northern Scotland.

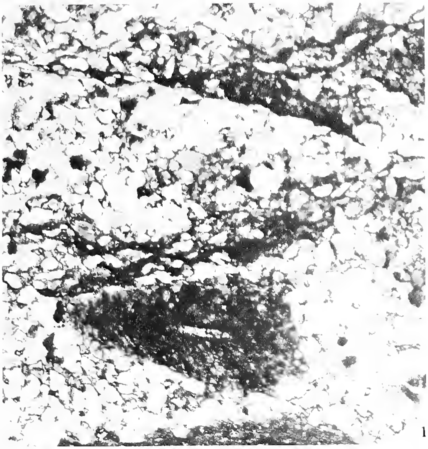
SALTERELLA AND *VOLBORTHELLA*

I have contended (Yochelson *et al.* 1970; Yochelson, 1977) that *Volborthella* from the Baltic region and *Salterella* may be the same organism, only affected differently by diagenesis. The material from northern Scotland seems to confirm this argument.

The Salterella Grit contains specimens that European specialists would identify as characteristic *Volborthella*. One individual, shown in Pl. 34, fig. 1, is identical in every aspect that I am aware of to *V. tenuis* Schmidt. Within the same rock occur more elongate specimens of *Salterella*, lacking only the outer calcareous shell (Pl. 35, fig. 2).

EXPLANATION OF PLATE 34

Figs. 1–5. Thin sections of *Salterella maccullochi* (Murchison) from the areas of Durness and Inchnadamph, Scotland. 1, two individuals in longitudinal section under polarized light, the one below having all the other characteristics of *Volborthella tenuis* Schmidt, and the one above, a V-shaped piece of calcite, which appears dark in the illustration, partly penetrated by grains from the matrix, having the shape and size of the apical area of a *Salterella*; from the Salterella Grit at An-t-Sron, × 25. USNM 311433. 2, specimens in various orientation and degree of wear, but showing the inner laminated area and thicker material filling the apertural cavity; from the Salterella Grit at An-t-Sron, × 15. USNM 311431. 3, cross-section of a specimen: the outer wall is sparry calcite, the area of inner laminations appears dark, and the lower part of the apertural cavity or the uppermost part of the connected central tube is sparry calcite; from the Ghrudaidh Formation at the top of a small road-cut just south of Skiag Bridge, Inchnadamph, × 15. USNM 311436. 4, longitudinal section of a small specimen; from the Ghrudaidh Formation at the top of a small road-cut just south of Skiag Bridge, Inchnadamph, × 15. USNM 311437. 5, below, a better-preserved specimen with the outer wall obvious; and above, a slightly distorted specimen with only the inner laminae preserved. The figure is rotated about 45° to the bedding so as to fit the illustration into the available space; from the Ghrudaidh Formation at An-t-Sron, × 15. USNM 311434.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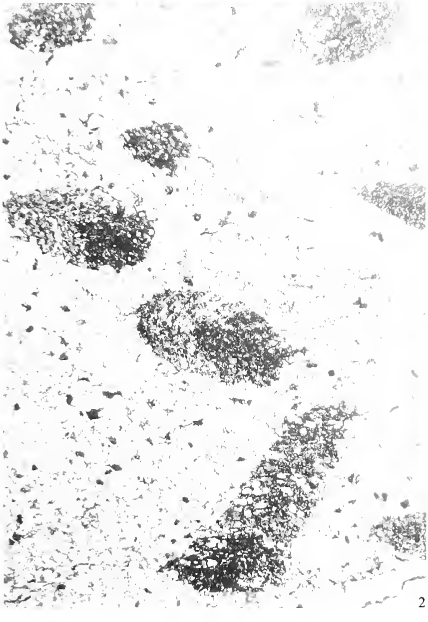
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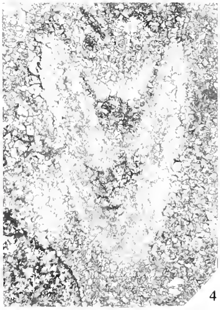
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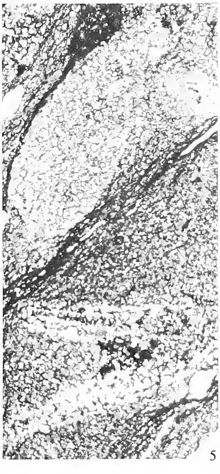
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YOCHELSON, *Salterella*

Although the Salterella Grit is a quartz siltstone, rare pieces of calcite occur. These are smaller than the *Volborthella* specimens. The pieces are essentially triangular, the sides diverging at an angle of 15°–20°. If one is willing to allow for some pressure solution of the sides and intrusion of individual quartz grains, these pieces can be interpreted as the apical portions of the *Salterella* shell, too small to show the characteristic infilling of detrital particles. It is impossible to rule out these occurrences as being calcite cement in the siltstone, but their rarity in the general matrix, their occurrence in the same laminae as those containing *Volborthella*, their orientation parallel to the *Volborthella*, and their consistency of shape regardless of the size or shape of surrounding quartz grains is to me strong evidence that these pieces of calcite are of organic origin. Because the type locality for *V. tenuis* Schmidt is in the non-indurated Blue Clay (Lükati Formation) of Estonia, I see little prospect of ever finding calcium carbonate remnants of shell in that matrix. It seems a lucky chance which has left some calcium carbonate in the Salterella Grit. It is an even luckier chance that left a *Salterella* fragment adjacent to as typical a *Volborthella* as one could hope to find (Pl. 34, fig. 1).

In addition to these two occurring together in the Salterella Grit, as further illustrated herein, *Volborthella* and *Salterella* occur intermixed in the overlying Ghrudaidh Formation. Because the Ghrudaidh is a carbonate unit, specimens filled the cone with carbonate detritus. However, a few individuals of *Salterella* do show the presence of sparse non-carbonate detritus in a calcium carbonate conical shell (Pl. 35, fig. 3). Worn specimens of 'pure *Volborthella*' occur in the same thin sections from Durness as *Salterella* (Pl. 35, fig. 5). To me this is the final piece of evidence needed to equate the two generic names. At several localities on Svalbard (Lauritzen and Yochelson 1982) these two preservational forms also occur together.

In order that there be no ambiguity in my position, on the basis of the evidence presented here, I formally place *V. tenuis* Schmidt in the synonymy of *S. maccullochi* (Murchison); the generic name *Salterella* has priority. I do not believe that any systematist can find a significant difference between topotypes of *V. tenuis* and of *S. maccullochi*. After looking at a number of collections, I have no reason to believe that more than one species of *Volborthella* exists, in spite of the fact that several varieties or subspecies have been named from the type area in Estonia. Further, I suggest that the various occurrences in eastern Europe are all of *S. maccullochi*.

STRATIGRAPHIC IMPLICATIONS

The occurrence of *Salterella* in the Scottish Highlands is within the zone of *Olenellus*; though trilobites are rare in the region, they do occur in the key stratigraphic sections (Cowie and McNamara 1978). In the outcrops in North America where *Salterella* can be dated by other fossils (Yochelson 1981), as well as in the Scottish Highlands, the genus is in beds of younger Early Cambrian age.

The range of *Volborthella* (A. Yu Rozanov, oral comm., 1974) is supposed to be throughout the Atdabanian and into the lower part of the Lenian, coincident with the *Holmia* zone; in his view, it

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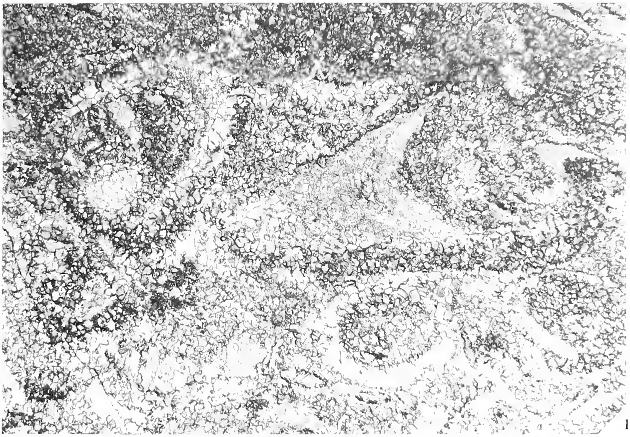
EXPLANATION OF PLATE 35

Figs. 1–5. Thin sections of *Salterella maccullochi* (Murchison) from the areas of Durness and Inchnadamph, Scotland. 1, abundant specimens in varying orientations and varying degrees of wear; from the Ghrudaidh Formation at top of a small road-cut, just south of Skiag Bridge, Inchnadamph, Scotland. USNM 311436. 2, a worn specimen in longitudinal section, showing many laminae; from the Salterella Grit at An-t-Sron, × 15. USNM 311429. 3, to the right, a longitudinal and a transverse section showing the outer wall and, to the left, several partly deformed individuals lying just above a small scour; these specimens of '*Volborthella*' are composed mostly of calcium carbonate, but a few dark grains are included in the partly recrystallized laminae; from the Ghrudaidh Formation at An-t-Sron, × 15. USNM 311433. 4, longitudinal section of an unusually well-preserved specimen, turned at right angles to the bedding; from the type locality of the Ghrudaidh Formation at Ghrudaidh Farm south of Durness. The light areas prominent on the right side are sparry calcite, × 15. USNM 311435.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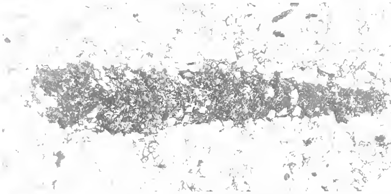
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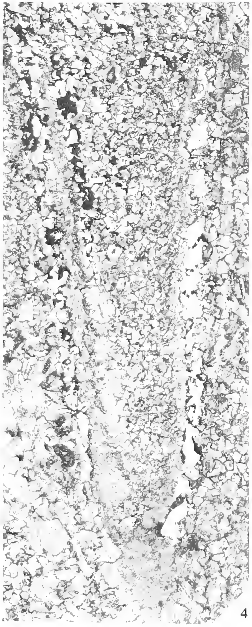
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YOCHELSON, *Salterella*

extends upward to overlap slightly the range of *Salterella*, which presumably occurs throughout the Lenian and Elankian, being most abundant near the boundary between these two stages.

As documented herein, there is no difference of biologic significance between the genera, and, I stand firm that there is no difference between *S. maccullochi* and *V. tenuis*. If my interpretation is correct, there is no reason to think the occurrences of '*Volborthella*' in the Baltic area are of any different age than those in the Salterella Grit. Thus, I would place the Norden '*Volborthella*' within the *Bonnia–Olenellus* zone, although they are conventionally dated as older.

Acknowledgements. I thank Dr. and Mrs. John Cowie, Bristol University, for providing lodging at Durness, Scotland, during April 1978. Without the guidance of Dr. Cowie in the field, probably no *Salterella* would have been found. Dr. Michael Bassett provided transportation to Durness and was an able field companion. Dr. A. W. A. Rushton, Institute of Geological Sciences (IGS), London, allowed me to examine fossils under his care, and Dr. R. B. Wilson, IGS, Edinburgh, lent additional collections in his charge. Dr. J. Pierce, Museum of Natural History, Washington, DC, USA, provided insight on sedimentary petrology. Thin sections and photomicrographs were prepared by Mr. Keith Moore, US Geological Survey.

REFERENCES

BILLINGS, E. 1861. On some new or little known species of Lower Silurian fossils from the Potsdam group (Primordial zone). *In* HITCHCOCK, E. (ed). *Report on the geology of Vermont; descriptive, theoretical, economical, and scenographical*, 942–955. [This material is repeated with some minor changes in *Paleozoic Fossils*, **1.** Geological Survey of Canada, 1865. Descriptions of *Salterella* on pp. 17–18 of that work are unchanged from pp. 954–955 of the 1861 reference.]

BYRD, W. J., WEINBERG, E. L. and YOCHELSON, E. L. 1973. *Salterella* in the Lower Cambrian Shady Dolomite of southwestern Virginia. *Am. Jl. Sci.* **273** (A), 252–260.

COWIE J. W. 1974. The Cambrian of Spitsbergen and Scotland. *In* HOLLAND, C. H. (ed.). Cambrian of the British Isles, Norden, and Spitsbergen. 123–183. *Lower Palaeozoic Rock of the World*, **2,** John Wiley & Sons, London, New York, Sydney, Toronto.

——and MCNAMARA, K. J. 1978. *Olenellus* (Trilobita) from the Lower Cambrian of North-West Scotland. *Palaeontology*, **21,** 615–634.

——RUSHTON, A. W. A. and STUBBLEFIELD, C. J. 1972. Cambrian. *Geol. Soc. London Spec. Rept.* **2,** 1–42.

LAURITZEN, Ø. and YOCHELSON, E. L. 1982. *Salterella rugosa* (Early Cambrian: Agmata) on Nordanstlandet and Spitsbergen, Svalbard. *Polar Research*, **1,** 1–10.

LOCHMAN, C. 1952. Trilobites. *In* COOPER, G. A. *et al.* Cambrian stratigraphy and paleontology near Caborca, Northwestern Sonora, Mexico. 60–161. *Smithsonian Misc. Coll.* **119** (1), 1–184.

MURCHISON, R. I. 1859*a Siluria, the history of the oldest fossiliferous rocks and their foundations; with a brief sketch of the distribution of gold over the earth*, 3rd edn., John Murray, London, 592 pp.

——1859*b*. On the succession of the older rocks in the northernmost counties of Scotland, with some observations on the Orkney and Shetland Islands. *Proc. Quart. Jl. Geol. Soc. London*, **15,** 352–418.

——1867. *Siluria*, 4th edn., John Murray, London. 566 pp.

YOCHELSON, E. L. 1977. Agmata, a proposed extinct phylum of early Cambrian age. *Jl. Paleont.* **51,** 437–454.

——1981. A survey of *Salterella* (Phylum Agmata). *U.S. Geol. Survey Open-file Report*, **81-743,** 244–248.

——and PEEL, J. S. 1980. Early Cambrian *Salterella* from north-west Greenland. *Gronlands Geol. Unders. Rap.* **101,** 29–36.

——TAYLOR, M. E. and CLOSS, E. 1968. The Lower Cambrian genus *Salterella* at Thomasville, Pennsylvania. *Geol. Soc. America, Northeastern Sect., 3rd Ann. Meeting, Washington, D. C., Program*, p. 64 (abstract).

——PIERCE, J. W. and TAYLOR, M. E. 1970. *Salterella* from the Lower Cambrian of central Nevada. *U.S. Geol. Survey Prof. Paper*, **643-H,** H1–H7.

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Note added in proof: *Salterella mexicana* Lochman has been placed in synonymy of *S. maccullochi* by J. S. Peel and E. L. Yochelson, 1982. A review of *Salterella* (Phylum Agmata) from the Lower Cambrian in Greenland and Mexico. *Gronlands Geols. Unders. Rap.* **108,** 31–39.

SILICIFIED GYMNOCODIACEAN ALGAE FROM THE PERMIAN OF NANJING, CHINA

by XINAN MU *and* ROBERT RIDING

ABSTRACT. Silicification of gymnocodiacean algae in the Lower Permian at Kongshan Hill, Nanjing, China, has preferentially replaced the calcareous wall of the thallus. The original skeletal microstructure is not preserved, but acid-extraction of the silicified fossils provides information on the cortical structure and surface features of the segments and allows the gross morphology of the plants to be reconstructed. *Nanjinophycus* gen. nov., is recognized, and includes *N. ovatus* sp. nov. and *N. endoi* (Nguyen). Comparisons with Recent algae indicate that these belong to either the Rhodophyta or Chlorophyta, and the presence of sporangia-like surficial pits on the segments further support a rhodophyte-affinity. They are provisionally placed in the family Gymnocodiaceae.

南京二叠纪硅化裸海松藻类化石

穆西南　罗伯特·瑞定

摘　要

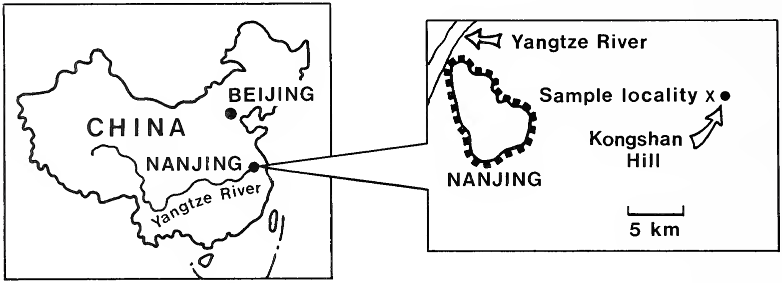
南京孔山下二叠统一些裸海松藻类的钙质壁受到选择性硅化。虽然原始骨骼的显微构造未保存下来，但用酸浸解后获得的标本却揭示了节片的皮层构造和表面特征，从而能够重塑植物体的宏观形态。本文建立了一新属 — 南京藻属 *Nanjinophycus* gen. nov., 它包括两个种： *N. endoi* (Nguyen) 和*N. ovatus* sp. nov. 通过与现生藻类进行比较， 表明它们可能属于红藻门， 或者可能属于绿藻门。然而其节片表面所具有的孢子囊状孔穴构造证实了它们的红藻属性。暂时将之归于红藻门裸海松藻科。

STUDIES of benthic marine calcareous algae are traditionally based on thin-sections. This method has some limitations, because it is difficult to fully understand the three-dimensional morphology of the fossils in this way. Ideally thin-section examination of wall structure should be combined with study of solid specimens which can be extracted from the rock and studied in three dimensions.

In 1977 a silicified fossil horizon was found in the Lower Permian Chihsia Formation at Kongshan near Nanjing, China. This bed is rich in skeletal fossils including algae which were originally calcareous. Owing to the selective silicification, the silicified calcareous algae stand out on the weathered limestone surface. After dissolving samples, well-preserved complete segments of calcareous algae were obtained. Based on this material, together with specimens in thin-section, a new genus, *Nanjinophycus*, is recognized, represented by two species: *N. ovatus* sp. nov. and *N. endoi* (Nguyen).

[Palaeontology, Vol. 26, Part 2, 1983, pp. 261–276, pls. 36–37.]

After comparing these fossils with Recent algae, we consider that it is most likely that they are red algae, and we provisionally place them in the Gymnocodiaceae. These range from Permian to Tertiary. They are common in Cretaceous, and especially in Permian, shallow marine limestones of the Tethyan area and of Central and North America. It was first thought that *Gymnocodium* was a green alga (hence its name) (Pia 1920). Subsequently Pia (1937) transferred it to the red algae and Elliott established the family Gymnocodiaceae in 1955.



TEXT-FIG. 1. Location of Kongshan Hill, near Nanjing.

LOCALITY AND STRATIGRAPHY

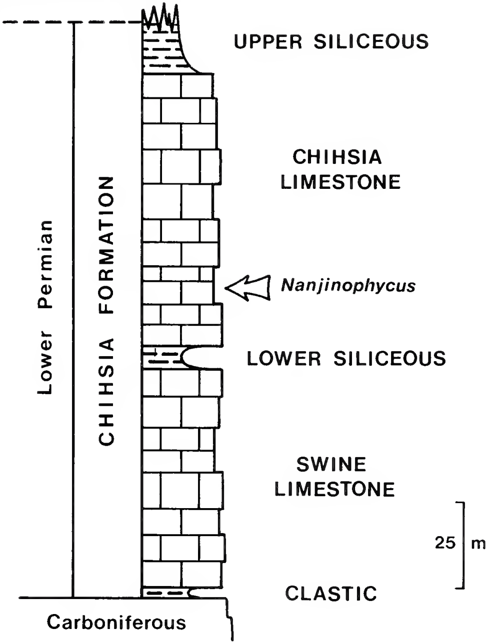
A good section of the Chihsia Formation is exposed at Kongshan Hill, 20 km east of Nanjing, in eastern China (text-fig. 1). The Chihsia Formation consists of limestone with chert nodules, and siliceous shale, and is subdivided into five members in descending order (text-fig. 2):

1. Upper Siliceous Member, black thick-bedded siliceous limestone and shale (17·4 m^{+}).
2. Chihsia Limestone Member, black to grey, medium to thick-bedded limestone with abundant chert concretions (80·9 m).
3. Lower Siliceous Member, black argillaceous chert (8·4 m).
4. Swine Limestone Member, black to grey, thick-bedded limestone with occasional chert nodules (66·7 m).
5. Clastic Member, black to grey shales with thin intercalations of greenish-grey limestone (2·3 m).

The Chihsia Formation in the Kongshan area disconformably overlies the Chuanshan Formation of late Carboniferous age. Its top is not exposed, but in the Chihsiashan area to the north-west it is overlain conformably by the Lower Permian Kuhfen Formation of Guadaloupian age.

The Chihsia Formation is rich in calcareous algae and invertebrate fossils, including fusulinids: *Misellina claudae* (Deprat), *Nankinella orbicularia* Lee, *Parafusulina multiseptata* (Schellwien); corals: *Wentzellophyllum volzi* (Yabe et Hayasaka), *Polythecalis yangtzeensis* Huang, *Hayasakaya elegantula* (Yabe et Hayasaka); brachiopods: *Linoproductus core* (Orbigny), *Orthotichia chekiangensis* Chao; ostracodes: *Bairdia chasae* Kellett, *Amphissites* Hou. Stratigraphically the Chihsia Formation corresponds to the Artinskian/Leonardian stage. Details of this succession are given in a field guide published by Nanjing Institute of Geology and Palaeontology (1979).

The material described here comes from the middle of the Chihsia Formation, 93 m above the base. Fossils directly associated with calcareous algae in this silicified bed include fusuline and smaller foraminifers, bivalves, ostracodes, echinoderms, and siliceous sponge spicules. The algae include *Nanjinophycus ovatus* (nov.), *N. endoi* (Nguyen), *Succodium* sp., *Sinoporella* sp., *Pseudovermiporella* sp., and *Tubiphytes*. sp. Figured specimens are deposited in the palaeobotany collections (PB) of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing.



TEXT-FIG. 2. Subdivisions of the Chihsia Formation and the position of the horizon containing *Nanjinophycus*.

SYSTEMATIC PALAEONTOLOGY

Division RHODOPHYTA
?Family GYMNOCODIACEAE Elliott
Nanjinophycus gen. nov.

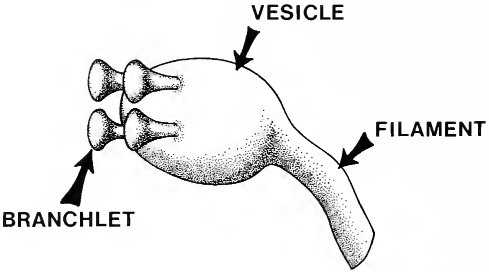
1970 *Succodium* Konishi; Nguyen, pp. 32–33, pl. I, figs. 6–8, 10–12; pl. IV, figs. 5–6.

Type Species. *Nanjinophycus ovatus* sp. nov.

Derivation of name. Nanjin from Nanjing, the new rendering of Nanking, capital of Jiangsu Province, China. Phycus from Greek phykos seaweed.

Generic diagnosis. Thallus erect; branched or, unbranched (?); segmented. Segments cylindrical, club-shaped, ovoid, or spherical. The central part of the segment is composed of longitudinally arranged medullary filaments which branch to produce divergent cortical filaments curving towards the exterior surface. The distal parts of the cortical filaments expand to form ovoid or nearly spherical vesicles, connected to the surface by at least two, probably four, terminal branchlets (text-fig. 3). The short branchlets expand exteriorly and have circular cross-sections. Thus, the cortex is divided into a thick inner part with curved filaments and vesicles, and a thin outer part with terminal branchlets. The vesicles are mutually juxtaposed and in plan view form a polygonal network.

Cavities, believed to be concerned with reproduction (sporangia or gametangia), occur within the cortex, opening directly on to the surface to form broad hollows (here termed 'sporangia' to conform with general usage in other papers on similar fossil algae). Calcification largely confined to the cortex, but the medulla is also occasionally calcified, perhaps secondarily.



TEXT-FIG. 3. Reconstruction of the distal part of cortical filament in *Nanjinophycus ovatus* showing ovoid vesicle and four terminal branchlets.

Remarks. Nguyen (1970, p. 32) described specimens, from loose pebbles of Permian limestone at Campha Harbour in northern Viet Nam, which she regarded as belonging to *Succodium*. She recognized, however, that they 'present some previously unknown characteristics in the outermost cortical layer. In these specimens, each utricle swelled up into ball-like expansions, then forked in developing two ultimate and minute cup-shaped vesicles.' She assumed that this production of branchlets from the utricles 'has not been well-preserved in the original specimens' (Nguyen 1970, p. 32).

We believe that the material figured by Konishi (1954) is sufficiently well preserved to demonstrate that the vesicles of *Succodium* do not branch (see Discussion below). In addition, specimens of *Succodium* which occur in the material from Kongshan described here, confirm this interpretation. Consequently, we here place *S. endoi*, described by Nguyen, in *Nanjinophycus*.

EXPLANATION OF PLATE 36

Figs 1–6. *Nanjinophycus ovatus* gen. et sp. nov., Lower Permian Chihsia Limestone, Kongshan Hill, Nanjing. Scanning electron photomicrographs. 1, complete segment showing ovoid shape and surface pits interpreted as reproductive organs (PB 68036, holotype), × 20. 2, as 1, top view of specimen showing terminal opening (PB 68036, holotype) × 17. 3, broken specimen showing peripheral row of holes formed by the cortical vesicles (PB 68037, paratype), × 18. 4, as 1, showing partial spalling of the outer part of the cortex revealing the vesicles just below the surface. Spalling occurs where the cortex is weakened at the plane of greatest width of the vesicles (PB 68036, holotype), × 45. 5, side view of vesicles showing their ovoid shape. Vesicle on right shows the cortical filament entering at its base. Terminal branchlets are not visible (PB 68038, paratype), × 185. 6, side view of outer part of cortex showing lower parts of vesicles, connected below with cortical filaments (middle of figure) and upper parts of vesicles with terminal branchlets (top of figure, not in focus). At extreme top right a terminal branchlet (arrowed) is seen clearly extending upwards from a vesicle. Spalling of the surface of the skeleton has occurred, as in fig. 4 (PB 68039, paratype, × 185.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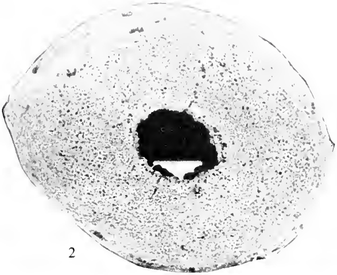
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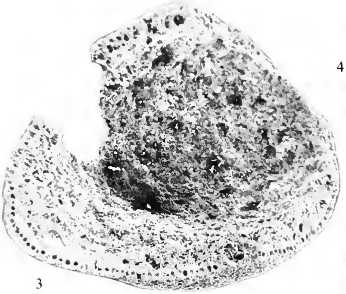
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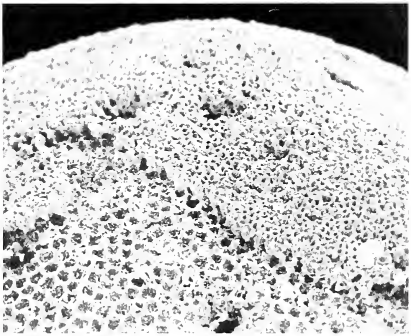
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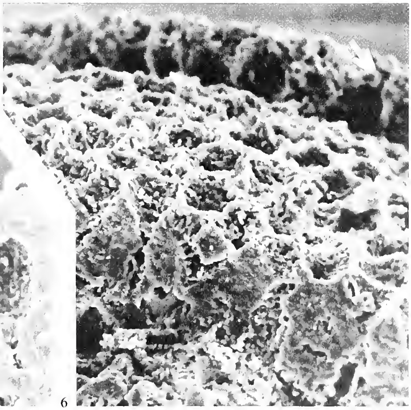
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MU and RIDING *Nanjinophycus ovatus*

Nanjinophycus ovatus sp. nov.

Plate 36, figs. 1–6

Types. Holotype, PB 68036; paratypes, PB 68037, PB 68038, PB 68039. All solid (unsectioned) specimens on SEM stubs.

Material. Eight complete segments and one segment in thin section.

Diagnosis. Nanjinophycus with large ovoid, pear-shaped or spherical segments.

Description. Segments up to 5·6 mm long and 4·0 mm or more in diameter. Circular openings 0·49–0·87 mm in diameter occur at both ends of the segments. Outer cortex up to 0·058 mm thick, inner cortex thickness not determined. Vesicles spherical or ovoid, in the latter case narrowing exteriorly up to 0·080 mm in diameter. Terminations of branchlets at the surface of the segment are 0·010–0·029 mm in diameter (Table 1).

TABLE 1. Dimensions of *Nanjinophycus ovatus* from Kongshan Hill, Nanjing. L, segment length; D, segment external diameter; Pc1, vesicle diameter; Pc2, diameter of external opening of terminal branchlet; Sp, 'sporangium' diameter.

Specimen	L (mm)	D (mm)	Pc1 (μm)	Pc2 (μm)	Sp (μm)
PB 68036 (holotype)	4·6	3·7	40–80	10–20	150–180
PB 68037 (paratype)	3·5	2·7	35–47	12–23	210
PB 68038 (paratype)	> 5·6	4·0	55–66		
1	4·9	3·5	35–58	18–23	
2	2·2	2·2	41	23	
3	> 2·1	2·2	35–58	23	
4	2·8	2·8	41–58	23	
5	4·1	3·1	41–58		
6	∼2·5		47–58	17–29	

Remarks. N. ovatus is distinguished from *N. endoi* by having larger, rounded segments. Because the fossil has so far only been studied from isolated segments we do not know the nature or occurrence of branching.

Occurrence. Lower Permian, Chihsia Formation, Jiangsu Province, China.

Nanjinophycus endoi (Nguyen)

Plate 37 figs. 1–6

1970 *Succodium endoi* Nguyen, pp. 32–33, pl. I, figs. 6–8, 10–12; pl. IV, figs. 5–6.

Material. Many complete segments and fragments of segments with numerous specimens in thin section.

EXPLANATION OF PLATE 37

Figs. 1–6. *Nanjinophycus endoi* (Nguyen), Lower Permian Chihsia Limestone, Kongshan Hill, Nanjing. 1–5 are scanning electron photomicrographs, 6 is thin section photomicrograph. 1, complete segment showing cylindrical form and surface pits interpreted to be reproductive organs (PB 68040), × 17. 2, as 1, oblique view of surface, specimen is broken revealing vesicles in outer part of cortex (PB 68040), × 41. 3, detail of 2, showing layer of vesicles just below surface, smooth surface in lower part of photograph is glue (PB 68040), × 160. 4, complete segment showing terminal opening, the fine pores on the surface are the openings of the terminal branchlets arising from vesicles below the surface (PB 68041), × 42. 5, complete segment, partially broken at end revealing internal structure. Four pits, interpreted as reproductive organs, are visible on the surface (PB 68042), × 20. 6, oblique section of segment showing outer cortical zone with vesicles and inner medulla with traces of filaments preserved by bituminous material (PB 68043), × 60.


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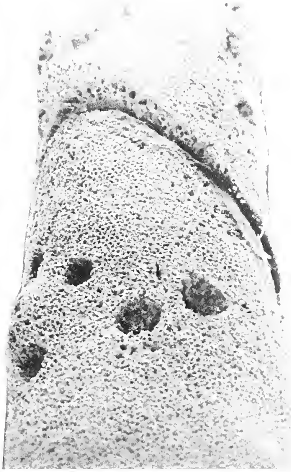
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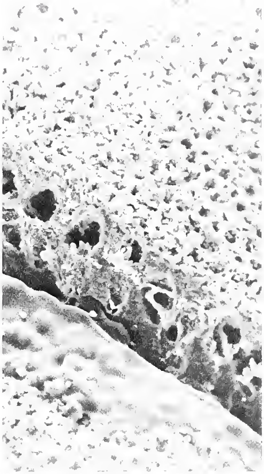
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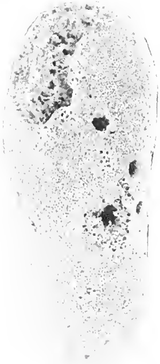
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6

MU and RIDING, *Nanjinophycus endoi*

Diagnosis. Small *Nanjinophycus* with cylindrical or club-shaped segments.

Description. Thallus dichotomously branched. Cylindrical segments commonly constricted in the middle, with the diameter of the upper part larger than that of the lower part; ends rounded. Segments 1·17 to 4·68 mm long and 0·22–1·74 mm in diameter. Circular openings, 0·35–0·52 mm in diameter, occur at the upper and lower ends. Cortex up to 0·46 mm thick, outer cortex up to 0·077 mm. Vesicles elliptical or ovoid, narrowing exteriorly, usually 0·035–0·058 mm in diameter. Terminations of branchlets at the surface of the segment are up to 0·011–0·029 mm in diameter. The opening of the sporangia on the surface is 0·120–0·2 mm in diameter (Table 2).

TABLE 2. Dimensions of *Nanjinophycus endoi* from Kongshan Hill, Nanjing. Abbreviations as for Table 1; Pm, diameter of medullary filament.

Specimen	L (mm)	D (mm)	Pm (μm)	Pc1 (μm)	Pc2 (μm)	Sp (μm)
1	4·7	1·5	39–45	13–29	10–20	130–210
2	3·6	1·5	35–41	12–23	12–23	140–200
3	2·0	0·9	39–44	11	18–23	
4	1·6	1·0	37–47	17–23	23	
5	1·9	0·9	35–58	17–20	23	
6	2·4	1·0	41–58	23	18–23	81–120
7		1·6	43–57	11–29		
8	3·3	1·7	47–70	17–29	17–29	

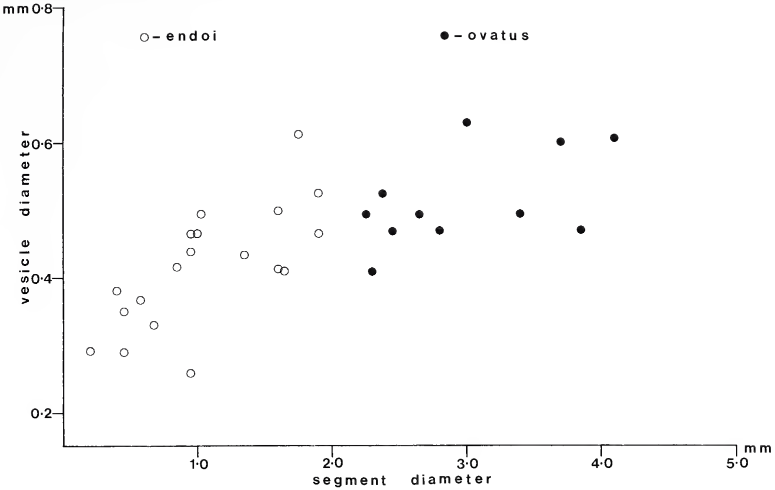
Remarks. This species differs from *ovatus* in having an elongate segment and being generally smaller in size. The material described by Nguyen (1970) is comparable with that from Kongshan in the shape of the segments and morphology of the vesicles. It is also similar in vesicle size, but in segment size it occurs within the lower range of that for the Kongshan material: Nguyen (1970, p. 33) reports a segment length of 1·03 mm and segment diameters of 0·26–0·67 mm, which compare with dimensions of 1·17–4·68 (length) and 0·22–1·90 mm (diameter) for this species from Kongshan (text-fig. 4). Consequently, the vesicle size of the Campha Harbour specimens is large relative to segment size, when compared with the Kongshan material. Another difference is the absence of conceptacle-like structures in the Campha Harbour material. This may be apparent rather than real because Nguyen examined the material in thin section and we have only observed conceptacles in solid silicified specimens etched from the matrix. Therefore, some differences exist between the material from these two localities but we consider them to be insufficient to separate the specimens on taxonomic grounds.

Occurrence. Lower Permian, Chihsia Formation, Jiangsu Province, China. Loose pebbles possibly from ?Permian, ?Campha Harbour Formation, Campha Harbour, northern Viet Nam (Nguyen 1970, pp. 2 and 33).

DISCUSSION

The shape of the segments and the internal structure of *Nanjinophycus* are similar to those of *Succodium* Konishi, the cortex of which is also subdivided into inner and outer parts. There are two main differences between these genera:

(*a*) The vesicles of *Succodium* (called gametangia by Konishi 1954) are not branched, but taper into thin filaments distally; this tapered part making the outer cortex. This is clearly shown in Konishi's (1954, fig. 1) reconstruction of *S. multipilularum* and is supported by our examination of *Succodium* from Konshan and also by Korde's (1965, figs. 51 and 52) description of the genus. In *Nanjinophycus* the vesicles divide distally into several terminal branchlets (text-fig. 3). The exact number of terminal branchlets present in *Nanjinophycus* is uncertain. In thin section at least two branchlets can be seen (Pl. 37, fig. 6), but SEM examination of the surface of the cortex (Pl. 36, fig. 4; Pl. 37, fig. 3) shows several branchlet



TEXT-FIG. 4. Vesicle and segment dimensions of *Nanjinophycus endoi* (open circles) and *Nanjinophycus ovatus* (black circles) from Kongshan Hill, Nanjing. Position of circle indicates mean value of vesicle size.

openings relative to each underlying vesicle. By comparing vesicle size with branchlet openings we estimate that there are probably four branchlets in both *N. ovatus* and *N. endoi* (text-fig. 3), although the number could range from two to five.

(*b*) In *Succodium* no conceptacle-like structures have been reported in the type species, but Korde found a new species, *S. difficile*, with large ovoid structures deep within the cortex (Korde 1965, pl. 55, fig. 3*a*, *b*). She regarded these as sporangia although the photographs do not represent conclusive evidence for this. In *Nanjinophycus* from Kongshan sporangia-like structures are conspicuous on the surface of some segments (Pl. 36, fig. 1; Pl. 37, fig. 1). We do not regard the apparent absence of sporangia in the Campha Harbour specimens as a serious obstacle to placing them in *Nanjinophycus*. The principal feature in thin section which distinguishes the genus is the shape of the vesicle and presence of branchlets. 'Sporangia' are, however, significant for assessing the systematic position of the alga.

The structure of the cortex of *Nanjinophycus* is similar to that of the phylloid alga *Eugonophyllum* Konishi and Wray which is subdivided into inner and outer cortex. In *Eugonophyllum* the inner part of the cortex is composed of ovoid utricles which give rise to branchlets in the outer part. There are also sporangia-like structures in *Eugonophyllum*. The principal differences between these two genera are that *Eugonophyllum* has a leaf-like thallus while *Nanjinophycus* is cylindrical and segmented, and the sporangia-like structures in *Eugonophyllum* usually form protuberances on the surface (Konishi and Wray 1961, pl. 75, figs. 6, 8–13, 16, 17) whereas they do not in *Nanjinophycus*. *Nanjinophycus* is also similar to *Gymnocodium* Pia and *Permocalculus* Elliott in thallus shape and internal structure, but the cortex of *Gymnocodium* and *Permocalculus* lacks vesicles.

Nanjinophycus is one of a number of genera (*Gymnocodium*, *Permocalculus*, *Succodium*, *Eugonophyllum*), common in parts of the Carboniferous and Permian, which show several similarities in their organization (text-fig. 5). Of these, *Nanjinophycus*, *Gymnocodium*, *Permocalculus*, and *Succodium* form a coherent group which shares a branched, segmented structure and which, with the exception of *Succodium*, definitely have reproductive organs. They are distinguished principally on the structure of the cortical filaments: those of *Succodium* having a vesicle but being unbranched, those of *Gymnocodium* and *Permocalculus* having no vesicle but dividing into two or more branchlets, while *Nanjinophycus* is characterized by a distinctive vesicle giving rise to several terminal branchlets.

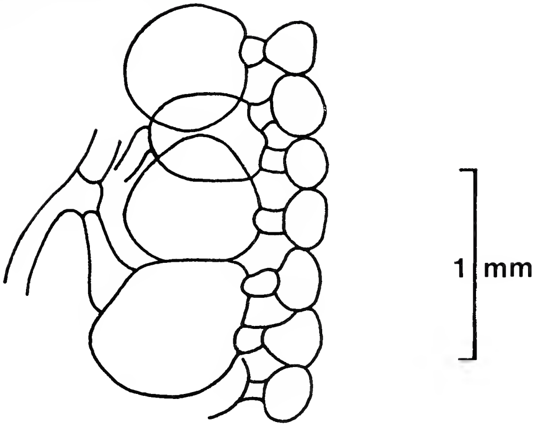
	SEGMENT/THALLUS	REPRODUCTIVE ORGANS	CORTEX (in thin section)
Nanjinophycus	ovoid cylindrical or spherical segments	internal, opening on surface	
Gymnocodium			
Permocalculus			
Succodium		?	
Eugonophyllum	phylloid thallus	make protuberances on surface	

TEXT-FIG. 5. Morphological features of *Nanjinophycus* and comparable Upper Palaeozoic genera.

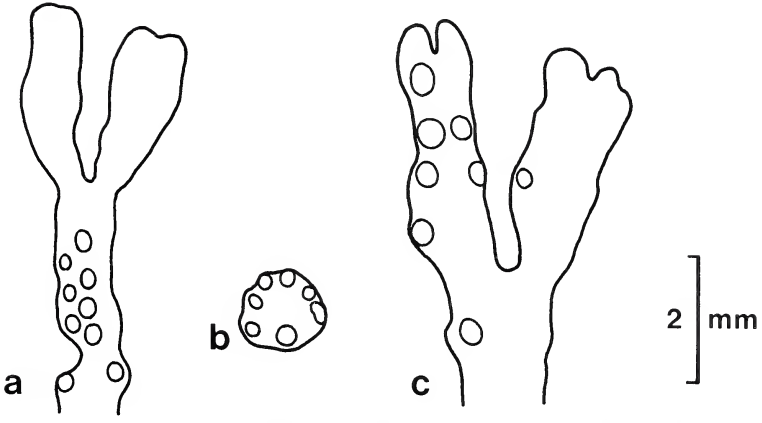
If the existence of reproductive organs reported by Korde (1965) in *Succodium* can be substantiated, then we would agree with her that this too belongs with the Gymnocodiaceae, which would then comprise *Gymnocodium*, *Nanjinophycus*, *Permocalculus*, and *Succodium*. The existence of reproductive organs is an important factor in such an assignment because otherwise the vegetative morphology alone of these genera is also consistent with them being codiaceans (Riding 1977, p. 207). The differences between *Nanjinophycus* and these other genera (presence of vesicle plus branchlets in the cortical filaments of *Nanjinophycus*) are sufficient to warrant *Nanjinophycus* being accorded generic status, it would not be appropriate to regard this material as representing new species of either of the other three genera.

Affinities

There are a few living algae which are comparable to some extent with *Nanjinophycus*, although none of them is exactly analogous with it. Members of the Chaetangiaceae (Rhodophyta), especially *Galaxaura* Lamouroux, are most similar to *Nanjinophycus*. *Galaxaura* is an erect, calcified alga consisting of cylindrical segments. Internally it has a multiaxial structure formed by outwardly curved filaments which arise from the medulla. Some of its asexual forms have one layer of large cortical cells, which produce stalk cells followed by terminal cells (Chou 1945, pl. 3, figs. 2 and 4) (text-fig. 6). This anatomical structure is very similar to that in *Nanjinophycus*. It is possible that the vesicle in *Nanjinophycus* corresponds to the cortical cell in *Galaxaura* and that the terminal branchlet corresponds to both the stalk and terminal cells. In the sexual forms of *Galaxaura* the male and female reproductive organs develop within the thallus below the surface (text-fig. 7). They are globose in form and connect to the exterior by an orifice. The female conceptacle is usually larger than the male conceptacle. When the conceptacle is mature the sexual cells are released, enlarging the orifice. The resulting depression in the surface of the thallus is very similar to the hollows on *Nanjinophycus*;



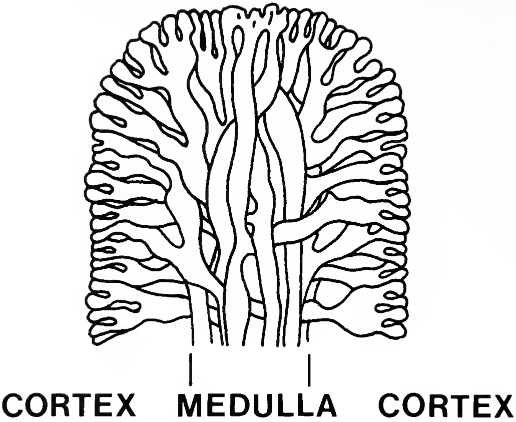
TEXT-FIG. 6. *Galaxaura*, detail of cortical cells (from Svedelius 1945, fig. 20*b*).



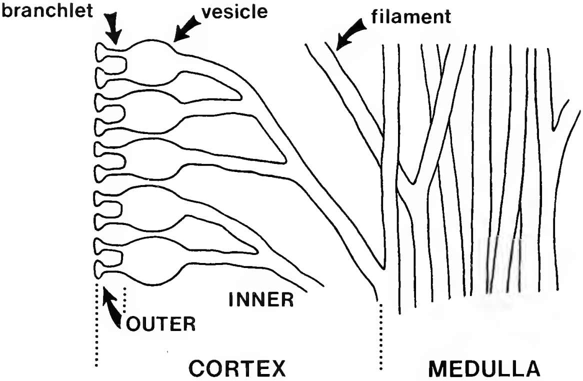
TEXT-FIG. 7. *Galaxaura*, conceptacles (from Svedelius 1945, fig. 11*a–c*). *a*, *c*, female; *b*, male.

we interpret the latter as conceptacles. But it is difficult to say whether they are male or female. In some *Galaxaura* species the conceptacles are concentrated on certain segments of the thallus, usually on those of the terminal parts of the plant. This may explain why only a few of our specimens of *Nanjinophycus* segments bear conceptacles. The cortex of *Galaxaura* is calcified and this preserves the fine reticular network of the surface cells. A similar pattern is seen in *Nanjinophycus*.

Nanjinophycus also resembles some members of the Codiaceae, both in the thallus morphology and

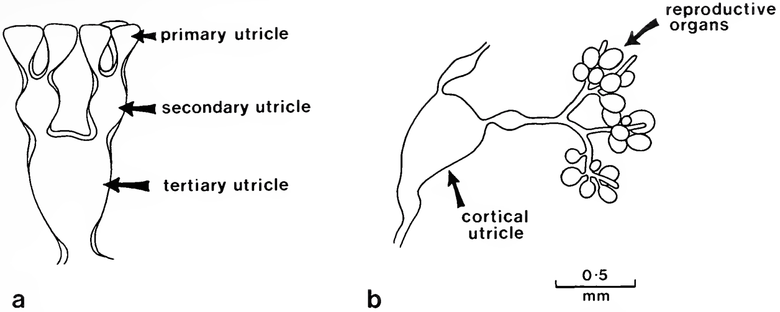


TEXT-FIG. 8. Longitudinal section through part of a *Halimeda* segment showing internal filamentous structure (from Hillis-Colinvaux 1980, fig. 6).

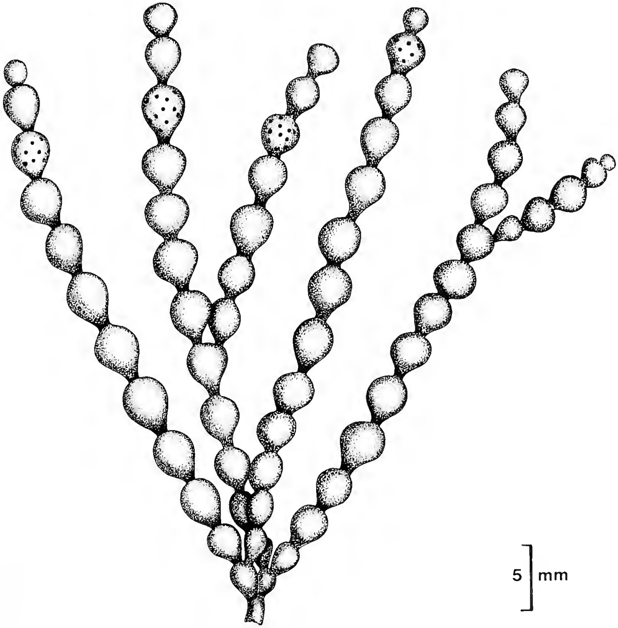


TEXT-FIG. 9. Vegetative construction of *Nanjinophycus*, showing a section of part of a segment from the centre (right) to exterior surface (left).

in internal structure, notably *Halimeda* Lamouroux. *Halimeda* is segmented and calcified. The internal structure is composed of tubular filaments without cross partitions (siphoneous organization), which are differentiated into medulla and cortex (text-fig. 8). The latter is composed of side branches (utricles) which may branch again several times to divide the cortex into a series of layers. Each secondary utricle usually gives rise to 2–4 peripheral (outer) utricles. *Nanjinophycus* also shows differentiation into medulla and cortex (text-fig. 9). The outer cortex of *Nanjinophycus* could, by



TEXT-FIG. 10. (*a*) *Halimeda*, utricles in the cortex (from Hillis-Colinvaux 1980, fig. 7). (*b*) *Halimeda* gametangia forming clusters on filamentous extensions of the cortical utricle (from Egerod 1952, fig. 19*c*).

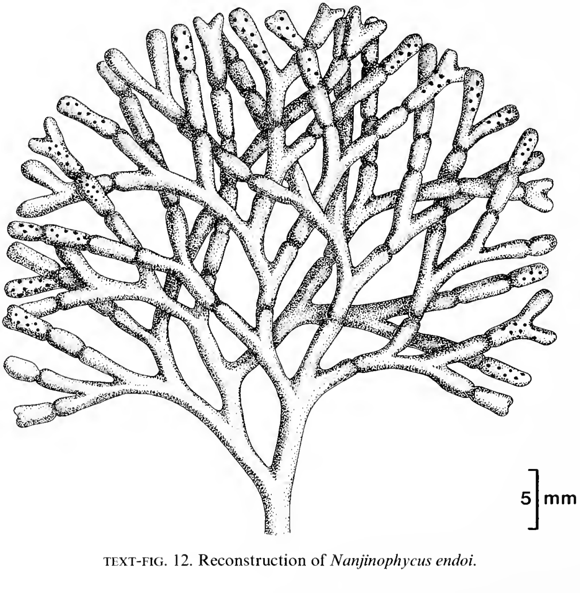


TEXT-FIG. 11. Reconstruction of *Nanjinophycus ovatus*.

analogy, correspond with the peripheral layer of utricles in *Halimeda*. The vesicles in *Nanjinophycus* would then correspond to the secondary utricles of *Halimeda* (text-fig. 10*a*). However, the secondary utricles in *Halimeda* are not usually so obviously swollen as the ovoid to spherical vesicles seen in *Nanjinophycus*. Despite this difference of detail, the general structural pattern is the same. The principal difference between *Nanjinophycus* and *Halimeda* lies in the position and shape of the reproductive organs. In *Halimeda* the gametangia are grape-like clusters on stalks which rise above the surface of the thallus (text-fig. 10*b*). This is quite different from the sporangia-like structure on the surface of *Nanjinophycus*. There is also some difference in the degree of calcification between *Halimeda* and *Nanjinophycus*. In *Halimeda* calcification usually extends into the medulla, but in *Nanjinophycus* it is mainly limited to the cortex (see below).

From the previous comparisons we can see that there are at least two possible interpretations of the affinities of *Nanjinophycus*; either a red algal affinity, in comparison with *Galaxaura*, or a green algal affinity, comparable with that of *Halimeda*. The principal difficulty for a green algal affinity of *Nanjinophycus* is the absence of large conceptacle-like structures in Recent Codiaceae, but we cannot exclude the possibility that *Nanjinophycus* is a green alga. Nevertheless, on the basis of both vegetative structure and organs believed to be reproductive, together with the pattern of calcification, it seems most likely that *Nanjinophycus* is a red alga similar to Recent Chaetangiaceae. In reconstructing the overall form of the thallus of *Nanjinophycus* (text-figs. 11, 12) we have used this analogy with *Galaxaura*.

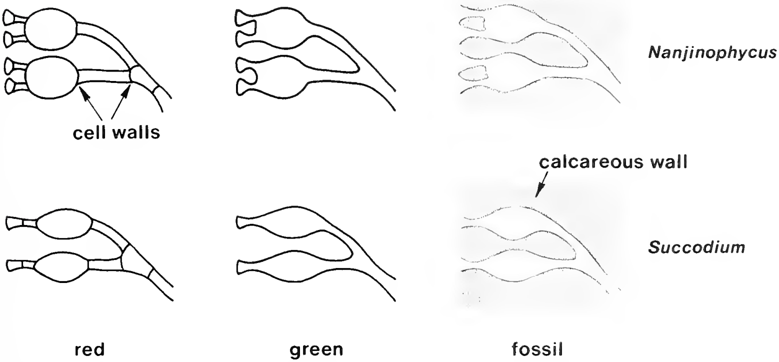
The fundamental reason for the uncertainty regarding the affinity of *Nanjinophycus* is related to the fact that abundant parallelism results in the similarities of general internal structural patterns among algae with different affinities and the algal skeletons alone fail to reveal the critical criteria to distinguish between them. The mode of calcification in *Nanjinophycus* is similar to that shown by



TEXT-FIG. 12. Reconstruction of *Nanjinophycus endoi*.

Galaxaura and *Halimeda*: the $CaCO_3$ is deposited on the surfaces of the cells and in the spaces between the filaments. When the plant dies the soft parts will decay rapidly—first, the cell content and then the cell wall. Only the calcareous skeletons can normally be preserved as fossils. Within this type of calcareous skeleton only the outlines or moulds of the soft parts of the algae are preserved, including both the vegetative and reproductive structures. In these circumstances it is not possible to know the detail of the cell structure—for example, the presence or absence of cross-walls within the filaments, and the development of reproductive organs, not to mention the pigments and food storage organs within the cells. All these features are very important for identification of the systematic position of the alga. Furthermore, even the outer mould does not preserve those parts of the thallus which were not calcified. All this compounds the problem of making anatomical comparisons, as well as more detailed ones, between fossil and Recent algae. Thus, we do not know in this particular material, nor in *Succodium* and other members of this general group, if there are cross-partitions within the filaments. If they did occur we could more confidently assign these specimens to the red algae. If they did not then they are more likely to be green algae (text-fig. 13). Although we tentatively place *Nanjinophycus* in the red algae, a lot of questions remain. For example, we do not know how the cells make up the terminal branchlet in *Nanjinophycus*, nor the external shape of the terminal cell, flat or curved. We do not know if there were any assimilatory filaments on the surface of the terminal cell, nor whether the reproductive organs were male or female. Without more detail about anatomical structure of the alga any assignment of affinity is not conclusive. In order to learn more we must search for specimens in which the soft parts are preserved. These could occur where silicification occurred very early.

In most of the material we have examined, the cortex is completely silicified and it is not possible to recognize a primary discontinuity in the internal structure of the fossil which could reflect the original limit of calcification. However, one specimen of *N. endoi* in thin section shows only partial silicification and the cortex appears as a distinct zone of brownish sparite juxtaposed against the interior clear sparite of the medullary region (Pl. 37, fig. 6). The medulla also clearly shows the traces of filaments. In Recent *Galaxaura* calcification is normally restricted to the cortex and although it varies in degree and location it is relatively constant for each species (Svedelius 1945, 1953). It is



TEXT-FIG. 13. Comparison between possible original organization of cortical filaments in *Nanjinophycus* and *Succodium* and the resulting fossil morphology. If cross-partitions occur but are not calcified the final appearance will be similar to specimens lacking original cross-partitions; yet this feature, if preserved, could help to distinguish between a red and green algal affinity.

therefore likely that the brown sparite cortical zone of *N. endoi* represents the original zone of calcification, and that it was similar in all specimens of this species. In *Galaxaura*, however, the medullary filaments are not usually calcified, although their preservation in *N. endoi* suggests that they had a veneer of carbonate sufficient to preserve their shape and position until the cement filling the interior of the segment was precipitated.

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REFERENCES

CHOU, R. C-Y. 1945. Pacific species of *Galaxaura*. I. Asexual types. *Pap. Mich. Acad. Sci.* **30,** 35-55.

EGEROD, L. E. 1952. An analysis of the siphonous Chlorophyta with special reference to the Siphonocladales, Siphonales and Dasycladales of Hawaii. *Univ. Calif. Publs. Bot.* **25,** 325-454.

ELLIOTT, G. F. 1955. The Permian calcareous alga *Gymnocodium*. *Micropaleontology*, **8,** 29-44.

HILLIS-COLINVAUX, L. 1980. Ecology and taxonomy of *Halimeda*: primary producer of coral reefs. *In* BLAXTER, J. H. S., RUSSELL, F. S. and YOUNG, M. (eds.). *Advances in marine biology*, **17,** Academic Press. 511 pp.

KONISHI, K. 1954. *Succodium*, a new codiacean genus, and its algal associates in the late Permian Kuma Formation of southern Kyushu, Japan. *J. Fac. Sci. Tokyo Univ.*, (2) **9** (11), 225-240.

—— and WRAY, J. L. 1961. *Eugonophyllum*, a new Pennsylvanian and Permian algal genus. *Jl. Paleont.* **35,** 659-666.

KORDE, K. B. 1965. Algae. *In* RUZENCEV, V. E. and SARYCEVA, T. G. (eds.). *The development and alternation of marine organisms at the boundary between the Palaeozoic and Mesozoic*. Palaeont. Inst. USSR, Trudy, **108,** 268-284, 414-429 [In Russian.]

NANJING INSTITUTE OF GEOLOGY AND PALAEONTOLOGY, ACADEMIA SINICA. 1979. *A guide of field excursion in Tangshan, Nanjing*. 21 pp.

NGUYEN, L. T. 1970. Some Permian fossil algae from Vietnam, Cambodia and Laos. *Arch. géol. Viêt-Nam*, **13** (2), 1-42.

PIA, J. 1920. Die Siphoneae Verticillatae vom Karbon bis zur Kreide. *Abh. Zool. bot. Ges. Wien*, **11** (2), 1-263.

—— 1937. Die wichtigsten Kalkalgen des Jungpaläozoikums und ihre geologische Bedeutung. *C.R. 2^e^ Congr. Carb.* (Heerlen, 1935), **2,** 765-856.

RIDING, R. 1977. Problems of affinity in Palaeozoic calcareous algae. *In* FLÜGEL, E. (ed.). *Fossil algae, recent results and developments*. Springer, Berlin. pp. 202-211.

SVEDELIUS, N. 1945. Critical notes on some species of *Galaxaura* from Ceylon. *Ark. Bot.* **32A,** no. 6.

—— 1953. Critical studies on some species of *Galaxaura* from Hawaii. *Nova Acta R. Soc. Scient. Upsal.* ser. iv, **15,** no. 9.

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THE DOMINANT CONIFER OF THE JURASSIC PURBECK FORMATION, ENGLAND

by JANE E. FRANCIS

ABSTRACT. Fossil trees are preserved *in situ* in fossil soils in the Lower Purbeck (Upper Jurassic) strata of Dorset. Silicified tree stumps, still rooted in the soils, stand erect and protrude into the overlying limestones. Numerous trunks and branches lie on the soils, which also contain conifer shoots. The forests were dominated by one kind of conifer with wood, named here as *Protocupressinoxylon purbeckensis* sp. nov., foliage belonging to the species *Cupressinocladus valdensis* (Seward) Seward and with male cones yielding *Classopollis* pollen. A reconstruction of the anatomy and habit of the tree is given. The Lower Purbeck palaeoclimate is discussed using the evidence of tree growth rings and the character of the associated sediments.

THE Lower Purbeck Formation of Dorset represents a sequence of intertidal and supratidal deposits formed during minor transgressive and regressive phases at the edge of a very shallow hypersaline gulf (West 1975). During the first regressive phase the pelletoid silts which were deposited in the lagoon became subaerially exposed and a thin soil developed, now represented by the carbonaceous marl of the Lower Dirt Bed. This soil supported a conifer forest (Strahan 1898; Arkell 1947) which was subsequently drowned by a rapid transgression, recreating extensive tidal flats with large stromatolitic growths (Brown 1963; Pugh 1968). In a second regressive phase gypsum and caliche breccia formed as the area became desiccated in the semi-arid climate (West 1975), and gradually the soil of the Great Dirt Bed formed. This soil incorporated pebbles derived from the underlying lithified limestone including black pebbles which are similar to modern blackened limestone pebbles found on the margins of hypersaline lakes (Ward *et al.* 1970). A closed forest of conifers and cycadophytes became established, bordered by a shallow gulf to the east and an ephemeral inland lake with charophytes in the west (West 1975; Barker *et al.* 1975). This forest was also rapidly submerged by hypersaline water and the tree stumps and fallen logs became covered with algal-bound sediment (Strahan 1898). Hypersaline water eventually covered the whole area and the main Purbeck evaporite deposits formed (West 1964).

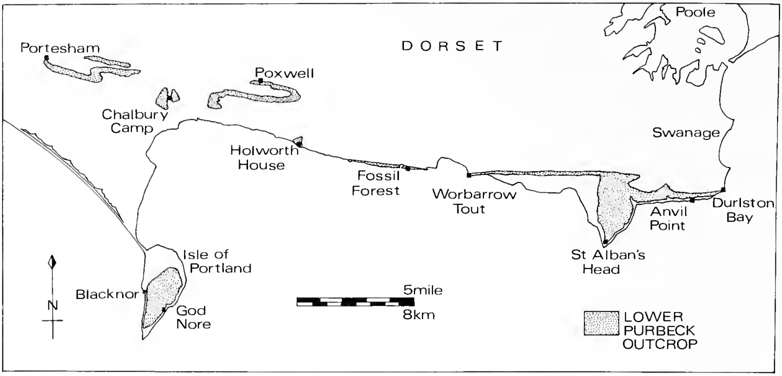
This sequence of events is now represented by algal stromatolitic limestones forming algal heads and non-laminated hummocks, and thinly-bedded pelletoid limestones, some with calcite pseudomorphs after gypsum. Interbedded dark carbonaceous marls of the Lower and Great Dirt Bed represent the former forest soils (text-fig. 2). The erect conifer stumps, fallen trunks, and cycadophyte stems became silicified and remain preserved within circular 'burrs' or domes of stromatolitic limestone (Pl. 38, figs. 2, 4, 5). Silicified wood is abundant in the Lower Dirt Bed of mainland Dorset and in the Great Dirt Bed on both the mainland and the Isle of Portland. Although trees grew in the former dirt bed on Portland they were not petrified but rotted away, leaving tubular cavities within the overlying stromatolitic Hard Cap limestone (text-fig. 2).

At most of the sites examined the conifer foliage is not preserved within the dark, marly dirt beds but an exception is the Great Dirt Bed at God Nore, Portland (text-fig. 1), where the dirt bed is reworked and resedimented. At this site there are a few organic-rich laminae, each of about 10 cm^2 in area, scattered throughout the Great Dirt Bed and on which compressed, fragmentary conifer shoots and male cones were found. No female cones were found. The matrix also yielded a fairly rich miospore assemblage. More complete conifer shoots are preserved in the overlying limestones.

The aim of this paper is to present a reconstruction of the anatomy and habit of the most abundant conifer species which grew in the Lower Purbeck forests.

Valuable information about the 'fossil forests' was recorded by geologists in the nineteenth century,

[Palaeontology, Vol. 26, Part 2, 1983, pp. 277–294, pls. 38–41.]



TEXT-FIG. 1. Map showing the location of some basal Purbeck exposures mentioned in the text.

particularly from quarries on Portland in which fossil trees and soils were being uncovered during a period of extensive quarrying (Webster 1826; Buckland and De La Beche 1836; Fitton 1835 and 1836; Mantell 1854). They discovered erect tree stumps in their original growth positions, often over 1 m in height and penetrating the overlying limestones. Numerous fallen trunks and branches were observed on the fossil soil, some over 10 m in length and 1·3 m in diameter. The erect stumps were shown to have roots which spread laterally through the soil, illustrated in sketches by Fitton (1836) and Buckland and De La Beche (1836). The roots never appear to penetrate the underlying hard limestone but are sharply diverted back at the base of the soil.

Damon (1884*a*) and Mantell (1854), amongst others, agreed that the profusion of fossil wood found on the surface of the Great Dirt Bed clearly indicated that these trees grew in as close proximity as those of a modern forest. Damon (1884*a*) noted, for example, that in a quarry on Portland, 7 erect tree stumps and 2 'Cycadeae' were uncovered in an area of only 'a few square yards'.

The leafy shoots of the trees were noticeably absent from major exposures of the fossil forests (Buckland and De La Beche 1836) though a single specimen of conifer foliage was illustrated by Damon (1884*b*) from the 'Top Cap' limestone overlying the Great Dirt Bed on Portland. It was a small shoot with scale-like leaves, tentatively identified as *Cupressinocladus*. Fitton also found an araucarian cone on the Portland cliffs which was identified as *Araucaria sphaerocarpa* by Carruthers (1866). Silicified stems of cycadophytes (Bennettitales) were often found amongst the fossil trees and were believed by some quarrymen to be fossil crows' nests which had fallen from the branches of the fossil trees! Although less numerous than the conifers these plants occur throughout the area, even where conifers are absent. It was due to the presence of such plants, which were wrongly interpreted as cycads (Cycadales), that Fitton (1835), Buckland (1829), Damon (1884*a*), and others first concluded that a warmer climate than at present prevailed in early Purbeck times since modern cycads occur chiefly in tropical regions. The cycadophyte stems were studied in detail by Buckland (1829) and Carruthers (1870), although their leaves are not described.

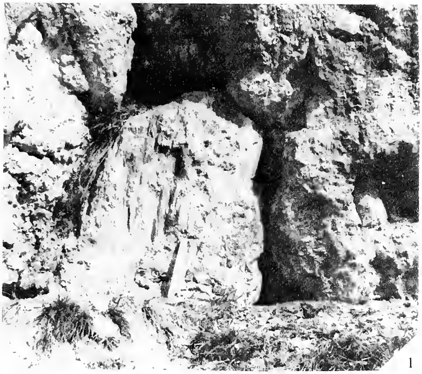
EXPLANATION OF PLATE 38

Fig. 1. Silicified tree stump at Chalbury Camp. Its roots are preserved within the Lower Dirt Bed and the trunk is surrounded by algal stromatolitic limestone of the Hard Cap. Diameter of base of trunk 92 cm.

Figs. 2, 4, 5. 'Burrs' of algal stromatolitic limestone, Soft Cap, Fossil Forest. 2, trough-shaped burr which once encased a fallen trunk. Total length 4·68 m. 4, 5, circular burrs which once surrounded tree stumps. 4, inner diameter 81 cm. 5, inner diameter 78 cm.

Fig. 3. Large silicified trunk reconstructed in the grounds of the Portland Heights Motel, Portland. Approximate height 2 m.

PLATE 38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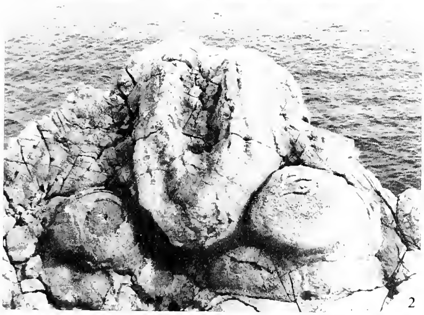
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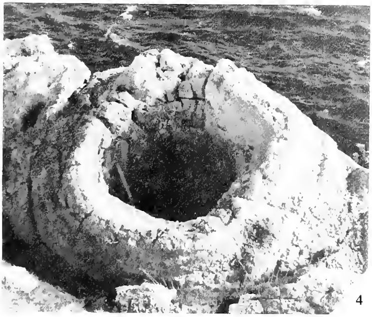
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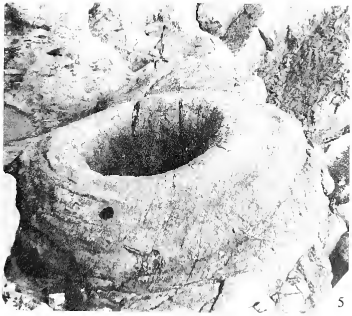
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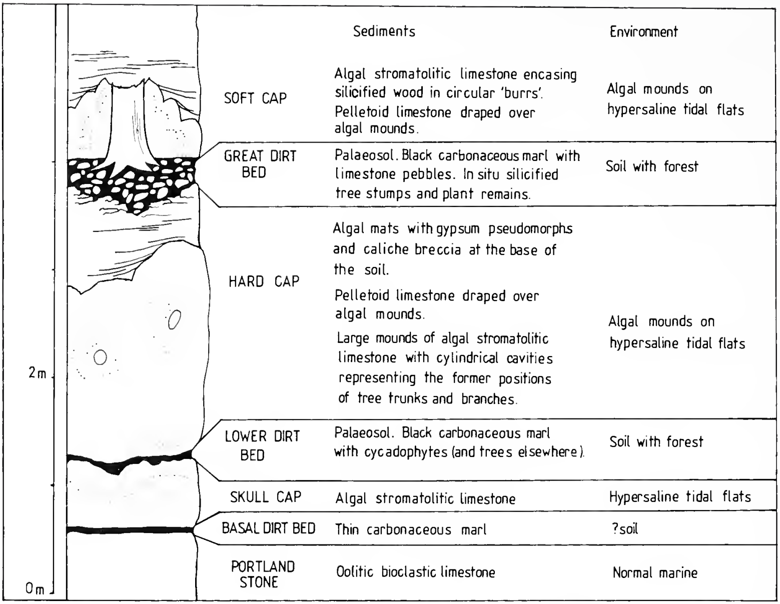
FRANCIS, silicified trees, and 'burrs' of stromatolitic limestone



	Sediments	Environment
SOFT CAP	Algal stromatolitic limestone encasing silicified wood in circular 'burrs'. Pelletoid limestone draped over algal mounds.	Algal mounds on hypersaline tidal flats
GREAT DIRT BED	Palaeosol. Black carbonaceous marl with limestone pebbles. In situ silicified tree stumps and plant remains.	Soil with forest
HARD CAP	Algal mats with gypsum pseudomorphs and caliche breccia at the base of the soil. Pelletoid limestone draped over algal mounds. Large mounds of algal stromatolitic limestone with cylindrical cavities representing the former positions of tree trunks and branches.	Algal mounds on hypersaline tidal flats
LOWER DIRT BED	Palaeosol. Black carbonaceous marl with cycadophytes (and trees elsewhere).	Soil with forest
SKULL CAP	Algal stromatolitic limestone	Hypersaline tidal flats
BASAL DIRT BED	Thin carbonaceous marl	?soil
PORTLAND STONE	Oolitic bioclastic limestone	Normal marine

TEXT-FIG. 2. Generalized section of the basal Purbeck strata on Portland.

Many fragments of plant remains were obtained from the Portesham Charophyte Chert, the western equivalent of the Great Dirt Bed, by Barker *et al.* (1975). These include charophyte fragments, stems of *Equisetum mobergii* (Halle ex. Moller), a small portion of a scale-leaved conifer (*Brachyphyllum* sp.), fragments of silicified wood and fusain, several species of seeds assigned to the genus *Carpolithus* Schlotheim and silicified casts of part of an araucarian cone *Araucarites sizerae*.

Most of the modern work on Purbeckian plants has concerned the miospore assemblages. Couper (1958), Lantz (1958) and Norris (1969) included Purbeck limestones, shales, and clays amongst their samples for miospore analysis and used the spores and pollen for stratigraphic zonation and correlation. Their samples were dominated by *Classopollis* pollen which constituted up to 70% of the miospore assemblages and suggest a forest dominated by *Classopollis*-producing trees, though it would be dangerous to base this interpretation on miospores alone (Chaloner and Muir 1968). They found a few other pollen grains which they attributed to conifers and cycadophytes, and there were some pteridophyte spores thought to belong to the undergrowth.

METHODS

Samples of silicified wood collected for study included portions of *in situ* tree stumps, branches, and roots from both the Lower and Great Dirt Beds at localities shown in text-fig. 1 and isolated specimens from museums and quarry tips, particularly on Portland.

The silicified wood structure was studied in thin-section, requiring three mutually perpendicular sections of each tree to fully demonstrate the anatomy (transverse, radial longitudinal, and tangential longitudinal). Small fusain fragments were obtained from the bulk maceration residue of the dirt beds. These fragments together with cleanly fractured silicified wood, were examined by SEM.

In situ conifer cuticles were picked directly from the intact shoots and male cones on limestone. Dispersed cuticle and pollen was isolated from the Great Dirt Bed matrix by bulk maceration. Small pieces of the soil matrix were subjected to acid digest with hydrochloric and then hydrofluoric acid to remove carbonates and silicates, followed by a final wash with warm hydrochloric acid to remove mineral by-products which obscured the organic matter (see Norris 1969). The cuticle was then separated from the residue by sieving with a 120 μm mesh sieve and was carefully macerated with concentrated nitric acid. Dilute ammonium hydroxide was used to remove humic matter left after oxidation. The cuticle was mounted in glycerine jelly for observation in transmitted light or dried onto stubs for SEM observation.

The fine residue containing pollen was gently macerated as before. Clay minerals of less than 5 μm in size were removed in suspension using a method based upon Stokes' Law (Jackson 1975). The miospore rich residue was then dried on to SEM stubs or mounted in glycerine jelly, a few samples having been stained with Safranine O for examination with the light microscope.

SYSTEMATIC PALAEONTOLOGY

Order CONIFERALES
Family CHEIROLEPIDIACEAE [HIRMERIELLACEAE]
Form-genus PROTOCUPRESSINOXYLON Eckhold 1922 (in part)

Protocupressinoxylon purbeckensis sp. nov.

Plate 39, figs. 1–11

Diagnosis. Growth rings fairly well defined, with a relatively wide zone of early wood and a narrow zone (3–4 cells) of late wood; false rings often present within what appear to be the annual increments. Files of tracheids of uniform appearance; tracheids polygonal or rounded in cross-section; average diameter of lumen 29·4 μm in early wood, 6·2 μm in late wood; wall thickness constant throughout, 9 μm.

Bordered pits on radial walls of tracheids mainly uniseriate (Pl. 39, fig. 11), biseriate opposite arrangement rare; biseriate alternate pitting absent. Pit border and aperture circular (mean diameters 17·2 μm and 6·0 μm respectively); pitting both spaced and contiguous. Contiguously arranged pits have adjacent borders touching and slightly compressed with vertical thickenings.

Rays, seen in tangential longitudinal section (Pl. 39, fig. 8), numerous, often separated by only 3 or 4 tracheids, 2–9 cells deep, mostly 3. Ray cells seen in radial longitudinal section rectangular with 2–7 small pits per crossfield; pits cupressoid with a slit-like aperture within a well developed, round border; aperture inclined at about 45° (Pl. 39, fig. 6), mean diameter 7–8 μm. Horizontal and tangential walls of ray cells thin, unpitted. Wood parenchyma absent.

Resin canals absent, but tracheids often containing a dark resinous deposit throughout the growth ring and ray cells.

Holotype: Silicified trunk, PB.11. is designated as holotype.

Location: Blacknor, Portland.

Horizon: Great Dirt Bed, Lower Purbeck Beds.

Description. Fossil wood with this structure is most common in the dirt beds and constitutes over 90% of all identifiable silicified and fusainized wood samples examined. The state of preservation is very variable in the silicified wood although structural details are particularly enhanced by remaining organic matter outlining cell walls. Fragments of fusain exhibit superbly preserved features, (Pl. 39, figs. 1–3, 5, 6). However, all measurements were taken from silicified wood as fusain exhibits an overall shrinkage of about 30%.

The contiguous pitting of the tracheid walls is the most distinguishable feature of this wood (Pl. 39, fig. 11). The pit borders always touch, sometimes retaining a circular outline, often vertically compressed but never to the extent of acquiring a polygonal outline like the pits of araucarian wood. Pit diameters vary between specimens and range from mean values of 12·5 μm to 17·6 μm, with an overall mean for all the specimens examined of 14·3 μm. Bars of Sanio (cellulose thickenings across the tracheids) are not visible since the pits themselves are so closely packed. Biseriate rows are more common in some samples than others but the pit arrangement is always opposite. No pitting was observed on the tangential tracheid walls.

Pitting was not seen on the horizontal and tangential walls of the ray cells although they looked well enough preserved to show them. 1 to 7 cupressoid pits are visible on each crossfield though 2 or 4 are most common. The pit aperture maintains a constant orientation close to 45° throughout the whole ray and even the whole specimen (Pl. 39, fig. 3). The abundance of resin in this type of wood is particularly noticeable, being present in all cell types as either small globules (2–10 μm in diameter) or as a resinous film coating cell walls. In transverse section the resin-filled cells are scattered throughout the growth ring, not confined to the latewood zone. No resin canals occur anywhere within the wood, either original canals or those which might result from wound reaction.

Form-genus CUPRESSINOCLADUS Seward 1919

Cupressinocladus valdensis (Seward) Seward 1919

Plate 40, figs. 1–13

1895 *Thuites valdensis* Seward, 209, pl. 20, fig. 6.
1919 *Cupressinocladus valdensis* (Seward) Seward, 309.
1960 *Cupressinocladus valdensis* (Seward); Chaloner and Lorch, 236.
1977 *Cupressinocladus valdensis* (Seward); Watson, 742, pl. 97, figs. 6–11.

Holotype: British Museum (Natural History) V.2138. from the Wealden at Ecclesbourne, Hastings.

Material. Conifer shoots and dispersed cuticle were found in the Great Dirt Bed at God Nore, Portland (National Grid map reference SY690697) and in the equivalent bed at Holworth House cliff section (SY762816). More complete shoots from adjacent limestones were studied to discover leaf and branch arrangement. These specimens were obtained from museums and include PB:conf 1 from the Lower Purbeck Beds, Southwell, Portland (Portland Museum), PB:conf 2 from the Purbeck Beds, Lulworth Cove (Southampton University Geology Museum, Day collection,) PB:conf 3 from the Middle Purbeck Beds of Durlston Bay (private collection of R. Coram, Wimborne), V.4033, V.4029, V.2933, and V.2545-shoots from basal Purbeck limestones, Portland (B.M. (N.H) collections).

Description. The most complete shoot, PB:conf 1, (Pl. 40, fig. 11) is 9·6 cm long and exhibits up to 4 orders of branching with branches arising in one plane to produce a flat, frond-like shoot. Branches arise alternately at every node on the main stem and minor branchlets, but appear to be arranged in opposition on the ultimate shoots. Alternate branchlets are straight or slightly curved. The main laterals subtend an angle of about 45° to the main stem and subsequent branches subtend an angle of about 55°. The whole shoot is now strongly compressed and bears small leaves in an opposite and decussate arrangement strongly reminiscent of modern Cupressaceae, such as, for example, *Thuja plicata* D. Don.

EXPLANATION OF PLATE 39

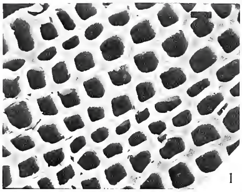
Protocupressinoxylon purbeckensis sp. nov.

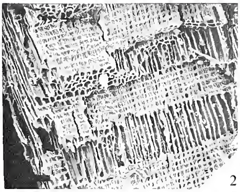
Figs. 1–3, 5, 6. Fusain from the Great Dirt Bed, God Nore, Portland. 1, transverse section. SEM × 130. 2, radial longitudinal section showing tracheids crossed by medullary rays. SEM × 50. 3, medullary ray cells, enlarged from fig. 2. SEM × 200. 5, tangential longitudinal section. SEM × 50. 6, cross-field pits on radial walls of the ray cells. SEM × 1000.

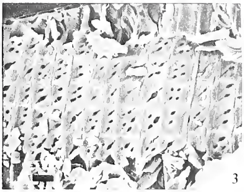
Figs. 4, 10. Silicified wood, PB.24, Great Dirt Bed, Portland. 4, radial longitudinal section showing bordered pits on radial walls of tracheids. SEM × 500. 10, radial longitudinal section showing resin-filled ray cells. Light microscope × 50.

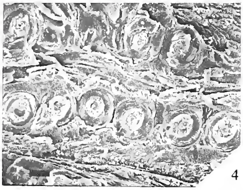
Fig. 7. Silicified wood, PB.52, Great Dirt Bed, Inmosthay Quarry, Portland. Thin section showing small knot. × 3·75.

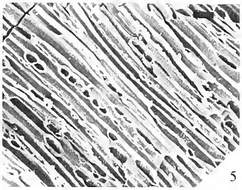
Figs. 8, 9, 11. Silicified wood, Great Dirt Bed, Blacknor, Portland. 8, tangential longitudinal section showing ray cells 2–8 cells deep. Light microscope × 50. 9, transverse section showing variable ring widths. Light microscope × 2·0 11, radial longitudinal section showing uniseriate rows of contiguous bordered pits. Light microscope × 145.

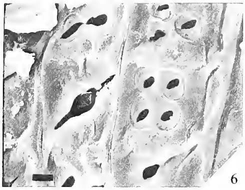


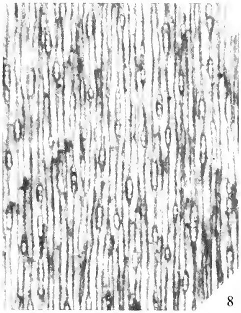


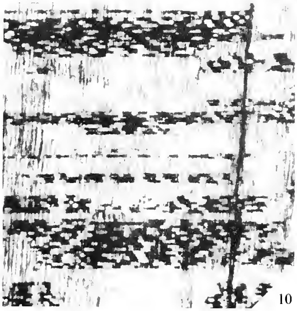


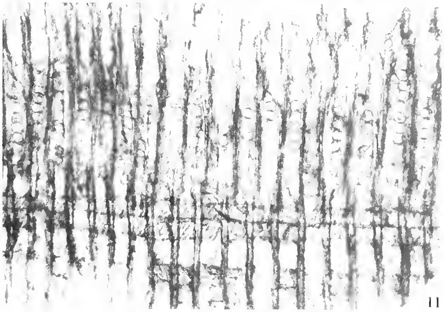












FRANCIS, *Cupressinocladus*

The main axis of this specimen has elongate rectangular leaves 10 mm long, 6 mm wide and pressed close to the stem. Secondary and tertiary branchlets have shorter and narrower leaves which ultimately become square in shape, with a length and breadth of only 1 mm on the youngest shoots. The range in leaf sizes of all specimens is 1 to 10 mm in length, 1 to 6 mm in width. Each leaf on the main shoot has a short, triangular free part and a long decurrent cushion with clear grooves separating it from adjacent cushions.

The abaxial cuticle ranges from 15–20 μm thick. Both the abaxial and adaxial cuticle are covered with short, blunt papillae about 10 μm in height, though on some specimens these are less well-defined and appear merely as a slightly raised area of the cuticle. In the cuticle from the abaxial surface of the free leaf and cushion stomata are arranged in fairly well-defined files and extend over the whole leaf base, including the marginal area. Stomata are, however, absent from a small area at the leaf tip (Pl. 40, fig. 3). The stomatal rows are separated by 2 to 3 epidermal cells and there are 6–8 rows per mm laterally. The stomatal density along each file ranges from 6–9 per mm, giving a mean density of 44 per mm^2.

Each stoma is surrounded by 4–6, but typically 5 subsidiary cells and the whole stomatal apparatus has a diameter of 70–100 μm. Each subsidiary cell bears one broad round papilla which extends into the stomatal pit so that its aperture is nearly filled by the papillae (Pl. 40, figs. 5, 8, 12). The mouth of the pit is commonly polygonal but varies from more or less round to markedly stellate. Some stomata have their openings at surface level though adjacent ones on the same cuticle have a prominent rim (Pl. 40, figs. 8, 12). The guard cells are sometimes present but are thinly cutinized and often do not survive maceration.

The epidermal cells lying between stomata of the same file are isodiametric, 20–35 μm in diameter. However, between stomatal rows the cells are usually elongate (on average 48 μm long) and arranged in longitudinal files 2 to 3 cells wide. The anticlinal walls are 8–10 μm thick. The larger elongate hypodermis cells (mean of 64 μm in length, 37 μm wide) can sometimes be seen between stomatal rows.

The free tip of the leaf is always short. One leaf on the main shoot had a tip 2·6 mm long and a decurrent cushion 7·8 mm long. The adaxial leaf cuticle is like the abaxial but has less regularly arranged stomata and epidermal cells of a more varied shape.

The margin of the free tip of the leaf consists of a sharp border of unicellular hairs, 90–100 μm long, 20 μm wide. These hairs are fused laterally for about three-quarters of their length, leaving only their rounded tips free, (Pl. 40, figs. 4, 7).

Genus CLASSOSTROBUS. Alvin, Spicer and Watson 1978

Classostrobus sp.A

Plate 41, figs. 1, 2, and 4

Description. Three compressed male cones were found amongst the foliage at God Nore. They are oval and 7·5–12 mm long and 6–6·5 mm broad. The microsporophyll heads are rhomboidal, up to 1·5 mm wide and 2·0 mm long, and appear to be spirally arranged. They are poorly preserved and neither microsporophyll stalks or pollen sacs were seen. (Pl. 41, fig. 4). Fragments of microsporophyll cuticle (Pl. 41, fig. 2) resembles *C. valdensis* leaf cuticle, but the stomata are less regularly arranged in files and fewer in number, e.g. 4 per mm. As on the leaves each stoma is surrounded by 5 subsidiary cells surrounding a stellate pit which is filled with 5 broad round papillae. The epidermal cells between adjacent stomata are isodiametric,with a mean width of 47 μm. However, the cells are somewhat elongate in 2–3 longitudinal rows between rows of stomata. Anticlinal walls are about 9 μm thick. Small blunt papillae are irregularly scattered across cuticle surface.

EXPLANATION OF PLATE 40

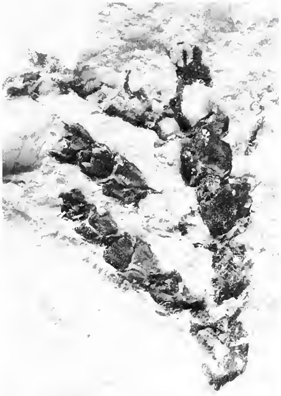
Cupressinocladus valdensis (Seward) Seward

Fig. 1. Shoot from the middle Purbeck Beds, Durlston Bay. PB:conf. 3. × 3.

Figs. 2–10, 12, 13. Cuticle from the Great Dirt Bed, Holworth House, Dorset. 2, single leaf. × 10. 3, triangular leaf tip with stomata in lower part only. SEM × 50. 4, 7, marginal hairs of the leaf sheath. 4, SEM × 100. 7, light microscope × 100. 5, single stoma with strongly papillate subsidiary cells. light microscope × 400. 6, outer surface of abaxial cuticle showing stomatal arrangement and slightly papillate surface. SEM × 50. 8, 12, stomata from the same cuticle showing both level and rimmed apertures. SEM 8, × 300, 12, × 250. 9, inner surface of cuticle. SEM × 50. 10, single stoma from fig. 9. SEM × 250. 13, vertical section of stoma showing papillae inside stomatal pit. SEM × 280.

Fig. 11. Shoot showing alternate branching, PB:conf. 1., basal Purbeck Beds, Portland. × 0·4.

PLATE 40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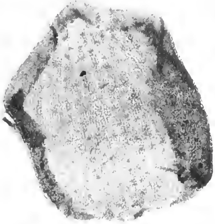
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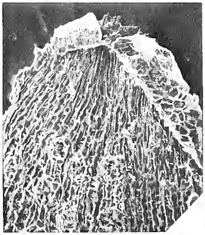
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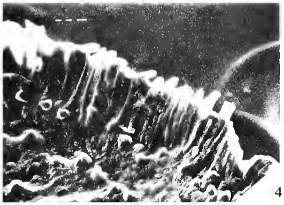
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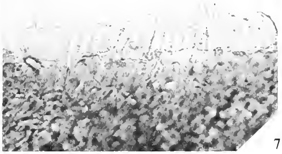
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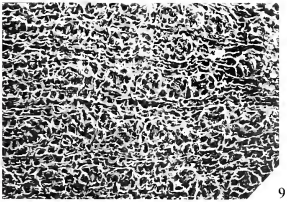
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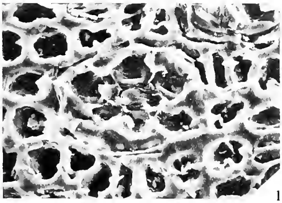
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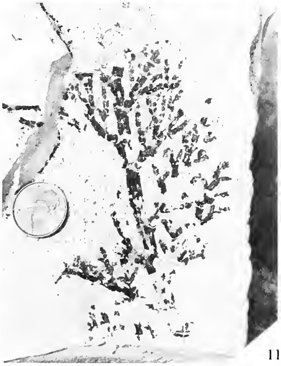
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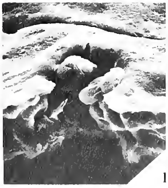
13

FRANCIS, *Protocupressinoxylon*

Although the pollen sacs are missing, isolated pollen grains were found adhering to the cone cuticle (Pl. 41, fig. 7). The pollen grains are spheroidal and slightly flattened at the poles, an equatorial diameter of 25–30 μm being reduced to 20–22 μm in this polar direction. A thickened belt, 6–8 μm wide and about 2 μm thick, encircles the equatorial region of the grain and bears 8–12 striations. Elsewhere the external surface is covered with small irregular granules. The internal structure is vermiculate. A small groove (the rimula) encircles the grain adjacent to the equatorial band on the distal side.

A pore marks the distal pole and is opposed by a triangular or trilete mark at the proximal pole.

Discussion

Wood. The type of wood described above which is the most common in the basal Purbeck Beds is assigned to the form-genus *Protocupressinoxylon* Eckhold on the basis of its mixed arrangement of tracheid pits, uniseriate rays, absence of resin canals but most importantly cross-field pits of cupressoid type.

Tracheid pitting intermediate in character between Araucaroid and Pinoid is common to many form-genera of Mesozoic wood constituting the Protopinaceae (Krausel 1949). In particular *Protocupressinoxylon* Eckhold is very similar to *Protopodocarpoxylon* Eckhold, species of which have recently been described by Lauverjat and Pons (1978) (*P. aveiroense*) from the Lower Cretaceous of Portugal, and wood of this type from the Wealden of the Isle of Wight by Alvin *et al.* (1981). Although in many respects these woods are very similar to that from the Purbeck they are distinguished by the cross-field pitting. In species of *Protopodocarpoxylon* Eckhold the cross-field pits are podocarpoid in the strict sense, with more vertically orientated apertures and are more numerous (up to 13 in *P. aveiroense* Lauverjat and Pons, up to 17 in the Wealden wood of Alvin *et al.* (1981)). In the Purbeck wood the cross-field pits are typically cupressoid (Pl. 39, fig. 6) with fewer, more regularly arranged pits with more horizontal apertures. They are characteristic of the form-genus *Protocupressinoxylon* Eckhold.

Previously described species of *Protocupressinoxylon* Eckhold have been listed by Attims and Crémier (1969). Although several species have similar tracheid pitting and abundance of resin and resemble the Purbeck wood, especially *P. luccombense* (Stopes) Eckhold and *P. vectense* (Barber) Eckhold (both from the Lower Greensand of the Isle of Wight) they possess vertical parenchyma, absent in the Purbeck wood. Species without vertical parenchyma include *P. dockumense* (Torrey) Krausel, *P. koettlitz* (Seward) Eckhold, and *P. malayense* Roggeveen, but are distinguished from the Purbeck wood by dissimilar medullary rays and cross-field pits. *P. chouberti* Attims and *P. aff. chouberti* Attims and Crémier are most similar to the Purbeck wood: vertical parenchyma is absent, growth rings are present, the tracheid pitting is a mixed arrangement of contiguous and separate pits and the cross-field pits are similar. However in *P. chouberti* Attims tangential pitting is present but notably absent in the Purbeck wood and in both these species the rays cells are twice as deep as those in the Purbeck wood. The abundance of resin found in the Purbeck wood was not noted in *P. chouberti* Attims.

The Purbeck wood is thus assigned to the new species, *P. purbeckensis* since in detail its features do not correspond with any previously described species. It is here considered to represent the wood of the Purbeck conifer which bears the *Cupressinocladus* (Seward) Seward foliage.

EXPLANATION OF PLATE 41

Fig. 1. Single shoots of *Cupressinododus valdensis* with male cone. Great Dirt Bed, God Nore Portland. × 1·4.

Fig. 2. Cuticle from cone shown in fig. 4. Outer cuticles of several microsporophylls. Light microscope × 30.

Figs. 3, 5, 7. *Classopollis* pollen associated with the male cone. 3, Grains clearly showing circumequatorial furrow. SEM × 1200. 5, tetrad. Light microscope × 700. 7, single grain showing equatorial striations. Light microscope × 1200.

Fig. 4. Male cone *Classostrobus* sp. indet. PB:cone 1, Great Dirt Bed, God Nore, Portland. × 4.

Fig. 6. Fine rootlets in the Lower Dirt Bed, Sheat Quarry, Portland. × 1·7.


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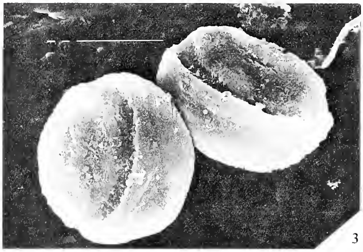
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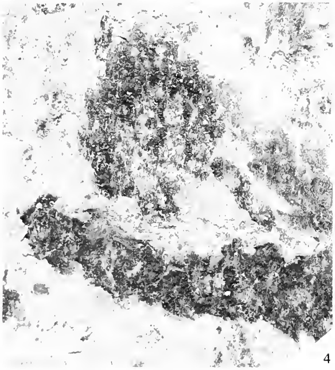
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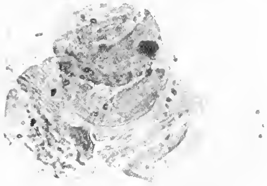
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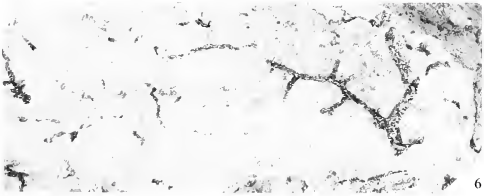
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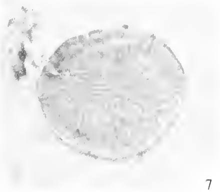
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FRANCIS, *Cupressinocladus*, *Classostrobus*, *Classopollis* and rootlets

Fossil wood of two other genera occur occasionally in the dirt beds. A few samples of fossil wood have unmistakable araucarian-type pitting (PB.8 from Blacknor, Portland and FF/2 from the Great Dirt Bed at the Fossil Forest at Lulworth). This wood has biseriate, even triseriate rows of hexagonal, alternately arranged bordered pits on the tracheid walls and is thus assignable to the genus *Araucarioxylon* Krausel.

One silicified trunk, PB.1 from the cliffs west of Anvil Point (text-fig. 2) and probably from the Lower Dirt Bed, has circular, separate bordered pits in uniseriate rows on the radial walls of the tracheids, small pits on the tangential walls and one or two large, simple pits per crossfield on the ray cell radial walls. Bars of Sanio are also clearly visible. This specimen is assigned to the genus *Circoporoxylon* Krausel.

Foliage. All the intact shoots from the Purbeck limestones mentioned above and the dispersed cuticle from the Great Dirt Bed have identical leaf arrangement in decussate pairs and similar cuticle structure.

The arrangement of leaves in opposite-decussate pairs is a diagnostic feature of the form-genus *Cupressinocladus*, originally erected by Seward in 1919 for vegetative shoots resembling those of modern Cupressaceae, and later emended by Chaloner and Lorch (1960), and Harris (1969). More recently Barnard and Miller (1976) emended it so as to exclude frenelopsid foliage where there are typically no suture lines between adjacent leaf bases. Shoots belonging to this form-genus have been described from the Jurassic and Lower Cretaceous localities worldwide, but the Purbeck specimens appear identical to *C. valdensis* (Seward) Seward from the English Wealden. No single Purbeck shoot has both good cuticle and well-formed branching pattern but the complete description above incorporated details from all specimens, and this agrees with that of the holotype, redescribed by Watson (1977). The cuticles sometimes differ slightly from the holotype in the presence of papillae on the epidermal cells which are absent on the holotype but intermittently present on the Purbeck cuticle. The cuticle surface of the holotype is featureless, the stomatal pits lying level with the surface, but in the Purbeck material stomata with both level apertures and encircling rims occur together in the same specimen.

C. ramonensis Chaloner and Lorch (1960) from the Lower Jurassic of Israel is very similar in appearance to *C. valdensis* (Seward) Seward but was considered distinct by the authors in having thinner cuticle, papillate epidermal cells and an even surface (they found that the stomata had rims on their preparation of *C. valdensis* cuticle). The leaf shape also differs from those of the Purbeck shoots in having a longer and more conspicuous free tip.

Two Lower Cretaceous conifers from Malaya, *C. malaiana* (Kon'no) Barnard and Miller (1976) and *C. acuminifolia* Kon'no (1968) look very similar but since the cuticles are unknown there is no strong evidence for identifying them with *C. valdensis* (Seward) Seward.

Oldham (1976) found *Cupressus*-like foliage in the Wealden marls at Swanage. His specimen 33 CuprCuA, is attributed to *Cupressinocladus* but is most unlike other published species, including the Purbeck shoots for, although the leaves are arranged in pairs, they have shorter decurrent bases so there is no conspicuous suture. The free tips are also much larger and rounder than on other species.

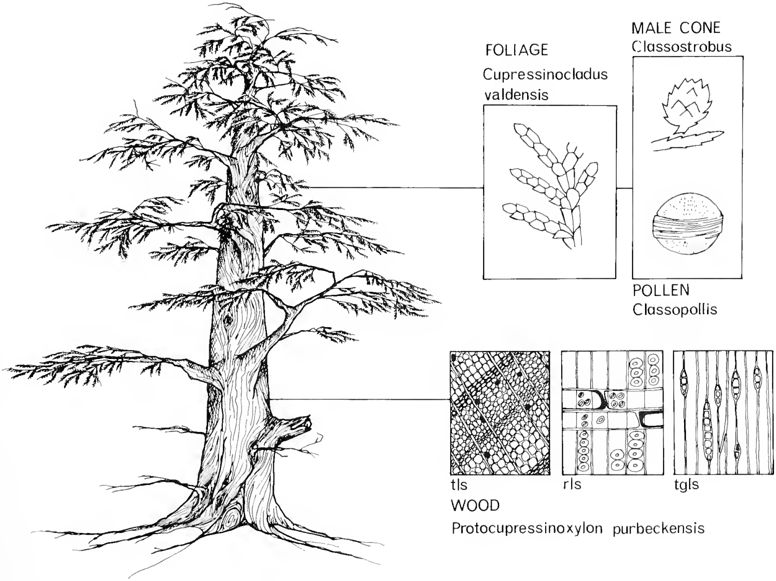
Male cones. The close association of male cones and *Cupressinocladus* foliage in the Great Dirt Bed at God Nore, supported by similarities in the cuticle of the microsporophyll and leaves, strongly suggests that they are part of the same plant. Several species of male cones associated with *Classopollis*-producing conifers have been described and Alvin *et al.* (1978) erected a new genus *Classostrobus* for male cones containing *Classopollis* pollen, and thus attributable to the Cheirolepidiaceae, but which were not specifically in organic contact with the shoots. Two male cones have been associated with *Cupressinocladus foliage: Classostrobus rishra* (Barnard) Alvin *et al.* with *Cupressinocladus pseudoexpansum* Barnard and Miller, and *Masculostrobus harrisianus* Lorch with *C. ramonensis* (Lorch 1968). The Great Dirt Bed cones are similar in shape and appearance to both of these cones, though slightly smaller in size, but lack of internal structure prevents further comparison.

Pollen. The pollen associated with male cones from the Great Dirt Bed is clearly *Classopollis*. In some cases the grains have not collapsed and exhibit remarkably distinct equatorial striations. Although detailed S.E.M. observations have not been made, it seems that the exine is very thin and the internal structure including the striations, is more prominent. Hence, of the many species described and illustrated by Reyre (1970) none is particularly comparable. Collapsed grains exhibit a surface structure of small granules, quite similar to that of *C. noeli* (Reyre) from the Upper Jurassic of Algeria, in the Sahara. Norris (1969) identified the *Classopollis* pollen from the Purbeck strata as belonging to 3 species, *C. torosus* (Reissinger) Balme, *C. echinatus* Burger and *C. hammenii* Burger; the pollen grains from the cone are most similar to *C. torosus*.

RECONSTRUCTION OF THE TYPICAL FOREST TREE

By virtue of the frequent occurrence of individual parts and their close association within the fossil soils, particularly the Great Dirt Bed, the wood, shoots, male cones, and pollen described here are considered to represent parts of one conifer which dominated the Lower Purbeck forests. This conclusion is strengthened by the apparent scarcity of other types of foliage and wood in these strata and agreement in cuticular structure between the male cones and leaves.

A few form-genera of fossil wood have now been attributed to the Cheirolepidiaceae on the basis of their association with cheirolepidiaceous foliage. In particular wood of *Protocupressinoxylon* type was considered by Harris (1979) to represent the wood of *Hirmeriella muensteri* (Schenk) Jung. Wood



TEXT-FIG. 3. Reconstruction of the dominant Purbeck conifer. The width of the base of the trunk represents a diameter of about 1 m.

of *Protopodocarpoxylon* type was associated with *Pseudofrenelopsis parceramosa* (Fontaine) Watson from the Wealden of the Isle of Wight by Alvin *et al.* (1981). Alvin *et al.* (1981) summarized the wood types attributed to the Cheirolepidiaceae. Their common features (contiguous and separate tracheid pitting, cupressoid cross-field pits and resinous tracheids and ray cells) are consistent with the characteristic features of the Purbeck wood.

As shown in text-fig. 3 the Purbeck conifer is considered to have wood of *Protocupressinoxylon purbeckensis* sp. nov., foliage belonging to the species *Cupressinocladus valdensis* (Seward) Seward and males cones (*Classostrobus* sp. A) yielding *Classopollis* Pflug pollen. Although the foliage has been classified as Cupressaceae in the past due to its similar appearance to modern species, *Cupressinocladus valdensis* (Seward) Seward was classified by Watson (1977) as Cheirolepidiaceae. Thus in summary, the affinity of the Purbeck trees to this family is supported by the cheirolepidiaceous-like wood and the *Classostrobus* cone, which on the basis of its *Classopollis* pollen is assignable to the Cheirolepidiaceae.

Additional information regarding the shape, size, and structure of these trees can be deduced from silicified tree stumps, branches, and trunks found in the dirt beds. Branches are seldom found attached to fallen trunks, even very long portions, presumably having broken off on impact with the ground or rotted away. However, at Chalbury Camp a small silicified branch, attached to the main tree stump, is preserved within the same mound of stromatolitic limestone as the rest of the tree (Pl. 38, fig. 1). Just over 1 m of the main upright trunk remains, rooted in the Lower Dirt Bed and attaining a diameter of 92 cm at the base of the trunk. The branch, 8 cm in diameter and 42 cm long, extends upward from the trunk at an angle of about 40°, at a height of only 44 cm from the top of the soil. On the main trunk of this tree, as on many trunk bases, the original positions of branches are indicated by the presence of numerous knots (buried branch bases) of both large and small diameters. Although not all may have penetrated through the sapwood, which has now vanished, some certainly did. The branches arose irregularly with no obvious whorled or spiral arrangement. Nevertheless the evidence suggests even in a full grown tree several branches arose from near the base of the tree, which probably had a more or less monopodial growth form. Radial sections cut across knots in silicified wood verify that the branches subtend an angle of about 40° with the main axis.

Many knots seen in thin section are encircled by cracks which contain soil particles and *Classopollis* pollen embedded in chalcedony. Other cracks with similar matter occur in the trunk wood. These cracks must have been open before silicification, either when the tree was alive or shortly afterwards.

The roots of these conifers are also preserved within the dirt beds. The bases of the erect tree stumps become thickened (but certainly not to the extent of being buttressed) and slightly twisted and then divide into roots spreading laterally through the soil in all directions. Silicified roots up to 10 cm in diameter extend from the base of the large tree into the Lower Dirt Bed at Chalbury Camp. The silicified parts are broken up into lengths of 10–15 cm but are still contained within a continuous lignitic sheath about 3 cm wide. Where the roots taper to less than 3 or 4 cm in width, the siliceous core is lost so the fine rootlets are preserved as lignite only. The root system here can be detected extending radially from the trunk for about 1 metre, though certainly the finer roots have been lost.

It was noticed long ago (Fitton 1836) that the tree roots could not penetrate the underlying hard limestone but were diverted laterally through the soil. The fossil roots appear to have grown down vertically as far as they could go but on meeting the limestone doubled back on themselves before finally extending horizontally through the base of the soil. Compressions of rootlets are present on the surfaces of pale, marly laminae within the Lower Dirt Bed in Sheat Quarry, Portland (SY689698) (Pl. 41, fig. 6). The ultimate branches of these roots are not particularly fine (0·7 mm diameter) and often terminate in small nodule-like swellings (0·6 mm diameter). By comparison with roots of modern trees it seems probable that they were mycorrhizae.

Although only pieces of trunk are preserved, some idea of the height of the Purbeck conifers can be obtained from the dimensions of the remaining silicified parts. Many straight trunks of about 6 m in length, some over 13 m long, have been observed (e.g. Fitton 1836, Mantell 1854) lying on the dirt bed. Dimensions of a tree trunk recorded by Fitton show that it tapers by only 9·5 cm from a diameter of 47·8 cm at the base to a diameter of 38·3 cm at a height of 5·51 m. With monopodial axes of this length trees of over 20 m can be envisaged. The widths of the trunks and tree stumps also suggest that they were large trees; the mean trunk diameter of the sections measured being about 55 cm and the maximum recorded 1·3 m. However, because of the nature of preservation these values represent only part of the heartwood as the outer layers of the tree are always lost. None the less the bases of the tree stumps are often over 1 m in diameter.

Twenty trees showed growth rings which were mostly about 1 mm wide. Using this value and assuming the growth phases were annual, many trees from the Purbeck forests may then have had lifespans of at least 200 years and the largest would have probably been over 700 years of age.

Text-fig. 3 presents a reconstruction of the most common Purbeck conifer, based on the evidence outlined above including data on trunk diameters, frequency of knots, branching angle, etc. Clearly such a diagram involves an imaginative interpretation of the data and where direct evidence is not available comparisons have been made with modern conifers from semi-arid regions, such as *Juniperus oxycedrus* Linnaeus and *Cupressus macrocarpa* Hartweg.

PALAEOECOLOGY OF THE PURBECK FORESTS

The cheirolepidiacean conifer dominating the Lower Purbeck forests was thus a monopodial tree with spreading roots and branches and scale-like foliage, surviving perhaps for hundreds of years in relatively harsh, semi-arid conditions.

The anomalous association between hypersaline sediments on one hand and freshwater faunas, deposits, and large trees on the other could be explained by a strongly seasonal climate. The formation of evaporites suggests that semi-arid conditions prevailed in which gypsum and halite formed from hypersaline brines (West 1975). Algal stromatolites also flourished since the high salinity deterred grazing molluscs which would have destroyed them. However, for part of each year there must have been either sufficient rainfall for freshwater insects, molluscs, ostracods, and trees to thrive or else some other source of freshwater. At a palaeolatitude of about 36° N. (Smith and Briden 1977) a Mediterranean-type of climate seems most likely, with wet winters supplying water for tree growth but with rather long, dry summers in which lake salinity increased sufficiently for the formation of evaporites. This would also account for the ambiguous palaeoenvironment suggested by the lateral equivalent to the Great Dirt Bed at Portesham, represented by a chert horizon in which evaporite pseudomorphs are found with freshwater molluscs, charophytes, land plants, and ostracods. This deposit was suggested by West (1975) to represent a brackish or freshwater lake which, during summer droughts, increased in salinity and allowed halite to precipitate. A recent model for such a situation can be seen in ephemeral continental lakes and coastal lagoons in South Australia (Burne *et al.* 1980). Influenced by the semi-arid Mediterranean-type climate, the lakes become fresh or brackish in winter allowing plants (particularly charophytes), ostracods, and molluscs to thrive. In the summer season the low rainfall and high evaporation rate allows the saline water to become concentrated until gypsum and halite are precipitated. The land surrounding these modern ephemeral lakes is also forested.

This seasonal nature of Purbeck tree growth is clearly reflected in their growth rings. These are narrow and extremely variable in size suggesting that the conditions for growth varied considerably from one year to another. Large uniform cells of the earlywood zone terminate abruptly with a narrow zone of small, thick-walled latewood cells. False rings are also frequent. The picture that emerges is of a strongly seasonal climate in which tree growth was very sensitive to variations in climatic conditions. In some years relatively rapid growth was possible, but in others very little growth was achieved, probably because of low rainfall. A contributing factor must have been the relatively shallow rooting depth of the trees which meant that in a period of no rainfall they would rather rapidly experience the effects of drought. A striking feature of the foliage is the thick cuticle (15–20 μm). This is also consistent with the evidence for a rather xerophytic tree.

The environment suggested for the Purbeck trees is consistent with Vachrameev's view (1970) that the Cheirolepidiaceae were drought-resistant trees or shrubs dominating Upper Jurassic vegetation. Of the many ideas of habitat and form of the trees reviewed by Vachrameev (1970) and Srivastava

(1976), that of a coastal habitat is considered by many palynologists to be most likely. However, a criticism of any interpretation based on miospores alone is that a high concentration of dispersed pollen does not necessarily reflect local macrovegetation. This may be due to sorting in the depositional environment, resistence of particular grains to decay, etc. (See Chaloner 1968, Chaloner and Muir 1968.)

A mangrove-like community on river margins was envisaged by Batten (1974) and Oldham (1976) for *Classopollis*-producing plants in the English Wealden. However, Alvin *et al.* (1981) consider that the Wealden *Pseudofrenelopsis* was a large forest tree which, although living in a climate which seems to have been predominantly warm and moist, was adapted to withstand periods of drought in which it ceased to grow, producing very variable growth-rings.

An environment similar to that suggested for the Lower Purbeck forests can be seen today on Rottnest Island, on the West Australian Coast (Playford and Leech 1977). Here the Rottnest Island Pine (*Callitris preissii*) grows in shallow soils on limestones adjacent to salt lakes which dry out in summer, precipitating halite. Algal stromatolites encrust dead branches and rocks along the lake shores on which gypsum crusts also form. The island lies within the semi-arid, Mediterranean-type climatic zone and has a rainfall of about 700 mm, falling mainly during the winter months. Evidence from the sediments suggest that the mean annual rainfall during the Lower Purbeck was slightly less than this, probably about 400 mm.

SUMMARY

The Lower Purbeck forests were thus dominated by one species of conifer with tall, monopodial trunks, shallow spreading roots, and scale-like foliage. These conifers formed a closed forest bordering an hypersaline gulf, with only a few other conifers of different species and with probably sparse undergrowth. Their variable growth rings reflect growth in response to a seasonal climate which was probably of semi-arid Mediterranean type. The trees and freshwater faunas thrived during periods when freshwater was in ample supply but alternating seasons of drought allowed evaporites to form in the saline lakes.

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REFERENCES

ALVIN, K. L., FRASER, C. J. and SPICER, R. A. 1981. Anatomy and palaeoecology of *Pseudofrenelopsis* and associated conifers in the English Wealden. *Palaeontology*, **24,** 759–778.

—— SPICER, R. A. and WATSON, J. 1978. A *Classopollis*-containing male cone associated with *Pseudofrenelopsis*. Ibid. **21,** 847–856.

ARKELL, W. J. 1947. The geology of the country around Weymouth, Swanage, Corfe and Lulworth. *Mem. geol. Surv. U.K.*, 386 pp.

ATTIMS, Y. and CRÉMIER, F. 1969. Étude de quelques bois fossiles du Mesozoique du Maroc. *Notes et Mém. Serv. Geol. Maroc*, No. **210,** 19–92.

BARKER, D., BROWN, C. E., BUGG, S.C. and COSTIN, J. 1975. Ostracods, land plants and charales from the basal Purbeck Beds of Portesham Quarry, Dorset. *Palaeontology*, **18,** 419–436.

BARNARD, P. D. W. and MILLER, J. C. 1976. Flora of the Shemshak Formation (Elburz, Iran), Part 3: Middle Jurassic (Dogger) plants from Katumbargah, Vasek Gah and Imam Manak. *Palaeontographica*, **B 155,** 31–117.

BATTEN, D. J. 1974. Wealden palaeoecology from the distribution of fossil plants. *Proc. Geol. Ass.* **85,** 433–458.

BROWN, P. R. 1963. Algal limestones and associated sediments in the basal Purbeck of Dorset. *Geol. Mag.*, **100,** 565–573.

BUCKLAND, W. 1829. On the Cycadeoideae, a family of fossil plants found in the oolite quarries of the Isle of Portland. *Trans. geol. Soc. Lond.* **2,** 395-401.

BUCKLAND, W. and DE LA BECHE, H. T. 1836. On the geology of the neighbourhood of Weymouth and the adjacent parts of the coast of Dorset. Ibid. **4,** 1-46.

BURNE, R. V., BAULD, J. and DE DEKKER, P. 1980. Saline lake charophytes and their geological significance. *J. sedim. Petrol.*, **50,** 0281-0293.

CARRUTHERS, W. 1866. On araucarian cones from the secondary beds of Britain. *Geol. Mag.*, **3,** 249-252.

—— 1870. On fossil cycadean stems from the secondary rocks of Britain. *Trans. Linn. Soc.*, **26** (4), 675-708.

CHALONER, W. G., 1968. The palaeoecology of fossil spores. *In* DRAKE, E. T. (ed.) *Evolution and Environment.* Yale University Press, New Haven and London, pp. 125-138.

—— and LORCH, J. 1960. An opposite-leaved conifer from the Jurassic of Israel. *Palaeontology*, **2,** 236-242.

—— and MUIR, M. 1968. Spores and floras. *In* MURCHISON, D. G. and WESTOLL, T. S. (eds.) *Coal and coal-bearing strata.* Oliver & Boyd, London. pp. 127-146.

COUPER, R. A. 1958. British Mesozoic microspores and pollen grains. A systematic and stratigraphic study. *Palaeontographica*, **B 103,** 75-179.

DAMON, R. 1884*a*. *Geology of Weymouth, Portland, and the coast of Dorset, from Swanage to Bridport-on-the-sea; with Natural History and Archaeological Notes.* 2nd edn. Weymouth, 250 pp.

—— 1884*b*. *A supplement (or Atlas) to the Geology of Weymouth, Portland, and the coast of Dorset, consisting of eighteen lithographic plates of fossils, including several new species, with descriptions and notes.* R. F. Damon, Yarmouth.

FITTON, W. H. 1835. Notice on the junction of the Portland and the Purbeck Strata on the Coast of Dorsetshire. *Proc. geol. Soc.*, **2,** 185-187.

—— 1836. Observations on some of the strata between the Chalk and the Oxford Oolite in the southeast of England. *Trans. geol. Soc. Lond.*, **4,** 103-383.

HARRIS, T. M. 1969. Naming a fossil conifer. *J. Sen. Memorial Volume*, 243-252. Calcutta.

—— 1979. *The Yorkshire Jurassic Flora*, 5. *Coniferales.* British Museum (Natural History) London. 166 pp.

JACKSON, M. L. 1975. *Soil Chemical Analysis*—Advanced Course. 2nd edn. Madison, Wisconsin. 895 pp.

KON'NO, E. 1967. Some younger Mesozoic plants from Malaya. Contributions to the Geology and Palaeontology of Southeast Asia, 38. *Geol. Palaeont. S.E. Asia*, **3,** 135-164. Tokyo.

—— 1968. Additions to some younger Mesozoic plants from Malaya. Contributions to the Geology and Palaeontology of Southeast Asia, 48. Ibid. **4,** 139-155. Tokyo.

KRAUSEL, R. 1949. Die fossilen koniferenhölzer. 1. *Palaeontographica*, **B 62,** 185-284.

LANTZ, J. 1958. Étude palynologique de quelques échantillons mésozoiques du Dorset (G.B.). *Rev. Inst. franç. Petr.* **13,** 917-943.

LAUVERJAT, J. and PONS, D. 1978. Le gisement Sénonien d'Esqueira (Portugal): Stratigraphie et flore fossile. *C.r. 103ᵉ. Congr. Socs. sav. Paris Sect. Sci.*, Fasc. 11, 119-137.

LORCH, J. 1968. Some Jurassic conifers from Israel. *J. Linn. Soc.* (*Bot.*), **61,** 177-188.

MANTELL, G. A. 1854. Geological Excursions round the Isle of Wight and along the Adjacent Coast of Dorsetshire; illustrative of the most interesting Geological Phenomena and Organic Remains. 3rd edn. H. G. Bohn, London, xxxi + 356 pp.

NORRIS, G. 1969. Miospores from the Purbeck Beds and marine Upper Jurassic of Southern England. *Palaeontology*, **12,** 574-620.

OLDHAM, T. C. B. 1976. Flora of the Wealden plant debris beds of England. Ibid. **19,** 437-502.

PLAYFORD, P. E. and LEECH, R. E. J. 1977. The geology and hydrology of Rottnest Island. *Geol. Surv. W. Aust.*, Report 6. 98 pp.

PUGH, M. E. 1968. Algae from the Lower Purbeck Limestones of Dorset. *Proc. Geol. Ass.*, **79,** 513-523.

REYRE, Y. 1970. Stereoscan observations on the genus *Classopollis* Pflug 1953. *Palaeontology*, **13,** 302-322.

SEWARD, A. C. 1895. *The Wealden Flora, Part II. Gymnospermae.* Catalogue of Mesozoic plants in the Department of Geology, British Museum (Natural History), xii + 259 pp.

—— 1919. *Fossil Plants.* A Textbook for Students of Botany and Geology 4. Cambridge University Press, 543 pp.

SMITH, A. G. and BRIDEN, J. C. 1977. *Mesozoic and Cenozoic paleocontinental maps.* Cambridge University Press. 63 pp.

SRIVASTAVA, S. K. 1976. The fossil pollen genus *Classopollis*. *Lethaia*, 9, 437-457.

STRAHAN, A. 1898. The Geology of the Isle of Purbeck and Weymouth. *Mem. geol. Surv. U.K.*, 278 pp.

VACHRAMEEV, V. A. 1970. Range and palaeoecology of Mesozoic conifers, the Cheirolepidiaceae. *Paleont. Jour.* **1,** 12-25.

WARD, W. C., FOLK R. L. and WILSON, J. L. 1970. Blackening of eolianite and caliche adjacent to saline lakes, Isla Mujeres, Quintana Roo, Mexico. *J. sedim. Petrol.*, **40,** 548–555.

WATSON, J. 1977. Some Lower Cretaceous conifers of the Cheirolepidiaceae from the U.S.A. and England. *Palaeontology*, **20,** 715–749.

WEBSTER, T. 1826. Observations on the Purbeck and Portland Beds. *Trans. geol. Soc. Lond.*, **2,** 37–44.

WEST, I. M. 1964. Evaporite diagenesis in the Lower Purbeck Beds of Dorset. *Proc. Yorks. geol. Soc.*, **34,** 315–330.

—— 1975. Evaporites and associated sediments of the basal Purbeck Formation (Upper Jurassic) of Dorset. *Proc. Geol. Ass.*, **86,** 205–225.

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NEW BOTHRIOLEPID FISH FROM THE LATE DEVONIAN OF VICTORIA, AUSTRALIA

by J. A. LONG

ABSTRACT. *Bothriolepis gippslandiensis* Hills and four new species (*B. cullodenensis*, *B. fergusoni*, *B. bindareei*, and *B. warreni*) are defined, and synoptic descriptions of their atypical features given. Bothriolepid faunas of Victoria permit biostratigraphic correlation between the Cerberean Volcanics (Taggerty) and the dominantly sedimentary Mt. Howitt Province (Mt. Howitt, Freestone Creek). Radiometric dates, palynological evidence, and the absence of *Remigolepis*, a characteristic Famennian form in the faunas of New South Wales, indicates a Frasnian age for the Victorian faunas. Interrelationships of antiarchs suggest that the bothriolepidoids and asterolepidoids are sister groups. The presence of large lateral pits on the headshield, cristate short armour, ventrolateral scales on the tail, and a primitive pectoral appendage place the Victorian species *B. gippslandiensis*, *B. cullodenensis*, and possibly *B. fergusoni* as the sister group to most other bothriolepids. A revised classification of antiarchs is proposed which places the sinolepids in the new suborder, Sinolepidoidei. The suborder Bothriolepidoidei contains two families: Bothriolepididae Miles and the new family Dianolepididae.

THE aberrant antiarch *Bothriolepis* is known from over fifty described species of nearly world-wide distribution. New finds of *Bothriolepis* in Victoria show that some species differ significantly from the standard bothriolepid morphology which has been well documented by several workers (Stensiö 1931, 1948; Miles 1968; Karatajute-Talimaa 1966; Denison 1941, 1951). The published record of antiarchs in Australia is scant compared to the amount of collected material. Hills first recorded Bothriolepis in Australia in 1929 and subsequently published a series of papers updating descriptions and records of Late Devonian fish faunas (Hills 1929, 1931, 1932, 1936, 1958, 1959). Gilbert-Tomlinson (1968) described fragmentary remains of *Bothriolepis* from the Amadeus Basin, central Australia, but was unable to make a specific determination in this case. Gardiner and Miles (1976) record the genus from the marine carbonates of the Gogo Formation, West Australia, and Young (in Ferguson *et al.* 1979) briefly described bothriolepids from near Eden, New South Wales. Young and Gorter (1981) described a new *Bothriolepis* from the Middle Devonian near Canberra.

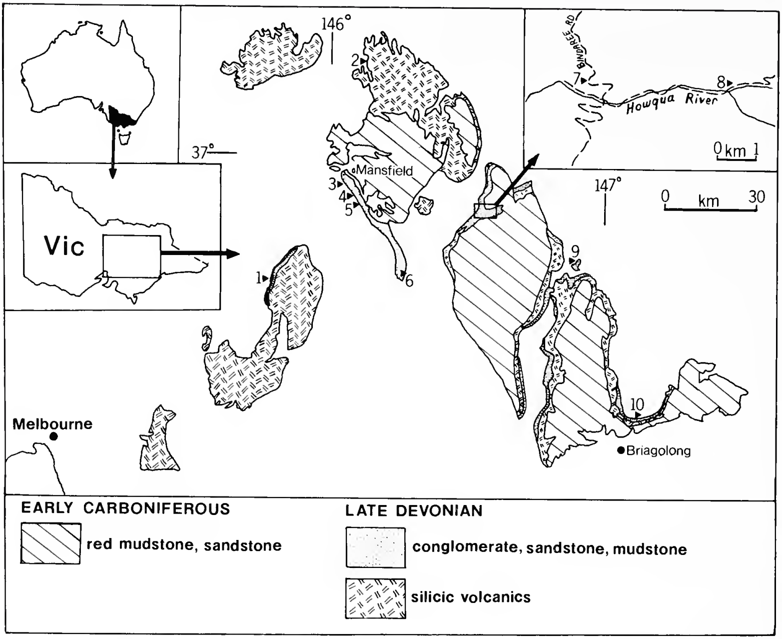
This paper outlines the geological settings and phylogenetic significance of the new species of *Bothriolepis* from the Late Devonian of Victoria. Lengthy systematic descriptions, necessary for biostratigraphic use, will be published separately in the Memoirs of the National Museum of Victoria. Synoptic descriptions are given in the species definitions with unusual morphological features described briefly in the subsequent section.

Specimens prefixed with NMV are housed in the palaeontological collections of the National Museum of Victoria, those preceded by MUGD are kept in the Geology Department of Melbourne University.

LOCALITIES AND FAUNAL LISTS

Text-fig. 1 shows a map of the major Late Devonian fish localities in Victoria. The Mt. Howitt Spur fish site was discovered in the early 1970s and subsequent excavations have yielded hundreds of well preserved, entire fish. The deposit comprises finely varved black anaerobic shales with minor silts and sands indicative of a lacustrine environment (Marsden 1976; Long 1982). The Bindaree Road site was discovered in 1980 and is situated stratigraphically above the main fish beds at Mt. Howitt. This site is of great interest in being geologically younger than the Mt. Howitt fossiliferous shales while containing a fauna identical to that of the Freestone Creek sites.

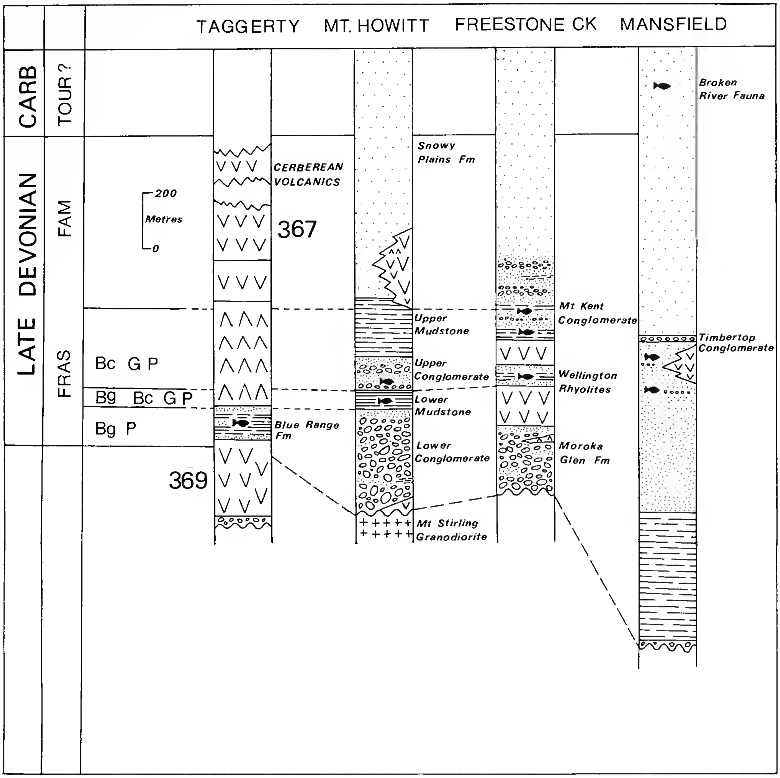
[Palaeontology, Vol. 26, Part 2, 1983, pp. 295-320, pl. 42.]



TEXT-FIG. 1. Locality map for Late Devonian fish sites in Victoria. Generalized geology from the 1:1000000 Victorian Geology mapsheet (Department of Minerals and Energy, Melbourne). 1. Blue Hills, near Taggerty. 2. Tatong. 3. Amphitheatre ridge, South Blue Range. 4. SEC transmission line cutting, South Blue Range. 5. Delatite River. 6. Jamieson Road cutting. 7. Bindaree Road cutting. 8. Mt. Howitt Spur. 9. Snowy Bluff. 10. Freestone Creek localities. Sites 4–6 and 9 were recently discovered and their faunas have not yet been studied in detail. These sites are not discussed in the text.

Stratigraphical and faunal relationships of the Late Devonian fish bearing successions in Victoria are shown in text-fig. 2. The geological settings of these localities are outlined in Marsden (1976) with a discussion of taphonomy in Long (1982). Faunal lists for these sites given by Marsden (1976, p. 122) have been extended by recent collecting (Long, in press).

Hills (1931) records *Bothriolepis gippslandiensis* Hills from Freestone Creek, and Talent (1975) based correlations upon this identification. Hills, however, studied a limited collection of quite small fish plates from this region, being much smaller than the average sized plates from Taggerty. Large headshields and trunkplates from several sites in the Freestone Creek region indicate that *B. gippslandiensis* is not present in the faunas from the Wellington Rhyolite sediments or the basal section of the Mt. Kent Conglomerate. Instead, the new species *B. cullodenensis* and *B. warreni* are present. New material from Taggerty has clarified the cranial morphology of *B. gippslandiensis* enabling identification of the species at Mt. Howitt. A large number of specimens from Mt. Howitt show *B. gippslandiensis* in all stages of growth. This clarifies the misconceptions concerning the



TEXT-FIG. 2. Biostratigraphic correlation of Late Devonian sequences in Victoria. Radiometric dates from Williams *et. al.* (1983). Geology from Marsden 1976. Bc. *Bothriolepis cullodenensis* n. sp. Bg. *B. gippslandiensis* Hills. G. *Groenlandaspis*. P. *Phyllolepis*.

Freestone Creek fossils and permits the species to be determined even from juvenile material. The suggested presence of *Remigolepis* (by Stensiö, in Hills 1932, p. 855) at Taggerty is based on a single mixilateral plate. Young (1974, p. 254) has questioned this identification and there is no doubt that the specimen (MUGD 1886) is attributable to *B. gippslandiensis* by means of its ornamentation and proportions.

FAUNAL LISTS

Mt. Howitt Spur

Placoderms	*Bothriolepis gippslandiensis*, *B. cullodenensis* n. sp., *B. fergusoni* n. sp., *Phyllolepis* sp., *Groenlandaspis*, sp.

Mt. Howitt Spur (*cont.*)

Acanthodians	at least three forms have been recognized, all probably belonging to the family Acanthodiiformes (Marsden 1976, p. 122).
Dipnoans	two forms occur, both short snouted (ibid.).
Crossopterygians	an osteolepid crossopterygian is present.
Palaeoniscids	at least one type of palaeoniscid is present which has both cheirolepid and stegotrachelid affinities.

Bindaree Road

Placoderms	*Bothriolepis cullodenensis* n. sp., *B. bindareei* n. sp., *B. warreni* n. sp., *Groenlandaspis* sp., *Phyllolepis* sp.
Others	isolated dipnoan scales, an acanthodian fin spine, isolated palaeoniscid bones.

Freestone Creek

Placoderms	*Bothriolepis cullodenensis* n. sp., *B. warreni* n. sp., *Bothriolepis* sp. indet., *Groenlandaspis* sp., *Phyllolepis*, sp.
Others	*Striacanthus sicaeformis* (Hills 1931). Dipnoan and crossopterygian (osteolepid?) scales. Isolated palaeoniscid dermal bones.

Blue Hills, Taggerty

Placoderms	*Bothriolepis gippslandiensis*, *Phyllolepis*, sp.
Others	The dipnoan *Dipterus* (*Eoctenodus* Hills 1929).

South Blue Range, Mansfield

Placoderms	*Bothriolepis* sp., *Phyllolepis* sp. (Hills 1936), *Groenlandaspis* sp.

Tatong

Indeterminable placoderm fragments, including a bothriolepidoid pectoral appendage bone.

Genoa River

Bothriolepis sp. (Professor J. Warren, pers. comm.); crossopterygians, amphibian footprints (Warren and Wakefield 1972).

Mt. Tambo

A small tuberculated fish plate (Marsden, 1976, p. 122).

BIOSTRATIGRAPHY AND THE AGE OF FAUNAS

The Late Devonian freshwater fish faunas of Victoria can be subdivided into three relative age categories using the entry and disappearance of key placoderm taxa, as shown in text-fig. 2.

The Taggerty Fauna contains *Bothriolepis gippslandiensis* and *Phyllolepis* sp., both of which occur at Mt. Howitt. Radiometric dates above and below the fish bearing strata at Taggerty indicate an early Frasnian age (Richards and Singleton 1981; Williams *et al.* 1983). The absence of characteristic Famennian forms such as *Groenlandaspis* and *Remigolepis* supports the older age assessment. Young (1974) reviewed the age ranges of biostratigraphically useful placoderms and places the Australian entry of *Groenlandaspis* and *Remigolepis* close to the Frasnian Famennian boundary. *Phyllolepis*, a Famennian zone fossil in European successions (Bendix-Almgreen 1976; Denison 1978, p. 42), occurs in the Frasnian Boyd Volcanic Complex (Fergusson *et al.* 1979, p. 103) and at Braidwood, where the fish fossils underlie a marine intercalation of at least Fransian age (Dr A. Ritchie, pers. comm.).

The Mt. Howitt Fauna is regarded as Frasnian by Marsden (1976) on comparison with the dipnoans from Escuminac Bay, Canada. The presence of *B. gippslandiensis* and a similar form of *Phyllolepis* from this locality and Taggerty indicates the close age affinity of these faunas. The presence of *Groenlandaspis* at Mt Howitt suggests that this fauna is slightly younger than the Taggerty Fauna, possibly still within the Frasnian if the exclusion of *Remigolepis* is considered. The entry of *B. cullodenensis* with *B. gippslandiensis* at Mt. Howitt is an important event which permits correlation with the Freestone Creek Fauna over 80 km to the south-east. Talent (1975, in Boucot) gives a Frasnian age to the Freestone Creek Fauna on palynological data.

The Bindaree Road Fauna is found within the Upper Conglomerate unit (Marsden, 1976) stratigraphically superpositioned on the Mt. Howitt Fauna. The disappearance of *B. gippslandiensis* with the abundance of high crested *B. cullodenensis* makes this fauna identical to that of Freestone Creek. *Phyllolepis* and *Groenlandaspis* occur in both these faunas although specific identifications have not yet been clarified.

The absence of *Remigolepis* from the Victorian faunas indicates that either they are all Frasnian in age or that the genus did not extend its range far enough to reach the state. The appearance of *Groenlandaspis* may be earlier in this state than indicated by Young (1974), preceding *Remigolepis*, and if the age proximity of the Taggerty and Mt. Howitt Faunas is correct, a Frasnian appearance of *Groenlandaspis* is most probable. Groenlandaspids have been recorded from the Middle Devonian of Mt. Grenfell, western New South Wales (Dr. A. Ritchie, pers. comm.), suggesting an even earlier entry for the genus.

The South Blue Range Fauna is believed to be contemporary with the Mt. Howitt and Freestone Creek Faunas on the common presence of *Bothriolepis* sp., *Phyllolepis* sp., and *Groenlandaspis* sp. Further collecting from this site is necessary for more accurate age assessment to be made. Comparisons with the volcanics from this succession with the Toombullup Rhyodacite in the Tolmie Igneous Complex indicates that the fish bearing horizon would be younger than the Givetian age obtained on the Tolmie volcanics (Richards and Singleton 1981; Dr. John Clemens,[1] pers. comm. concerning the petrographical and geochemical similarities between the igneous rocks). This reinforces the Frasnian age assessment for the Victorian faunas discussed above.

Fragmentary placoderm remains collected from the basal conglomerates in the Tolmie Igneous Complex (Brown 1961) are inferred to be Givetian age from the radiometric dates on the volcanics higher in the sequence (Richards and Singleton 1981). Re-examination of this material has turned up a bothriolepidoid pectoral appendage bone. Absence of the charcteristic ornament of *Phyllolepis* supports the early age assigned to this site, yet on the paucity of the present collection it would be unethical to make statements concerning faunal correlations.

The Genoa River and Mt. Tambo fish sites do not have large enough faunas at this stage to make age assessments. Warren and Wakefield (1972) have compared the red mudstone succession of the Genoa River Beds to the similar lithologies occurring around Eden, although only Late Devonian age status was assigned.

Correlations with the Middle and Late Devonian fish faunas of New South Wales are shown in text-fig. 3, incorporating all relevant radiometric dates and marine invertebrate faunas. The present age ranges of the placoderms discussed above are shown in text-fig. 4, modified from Young (1974).

SYSTEMATIC PALAEONTOLOGY

The following species will be described in detail in a separate paper as this work is primarily of local interest for its use in biostratigraphy. Synoptic descriptions are presented here in the species definition. Plate measurements are taken from points designated in Stensiö (1948, pp. 11–16). External measurements refer to the dimensions of a plate as seen in the articulated armour hence excluding overlap areas.

Genus BOTHRIOLEPIS Eichwald 1840, designated by Woodward 1891

Type species. Bothriolepis ornata Eichwald.

Diagnosis. See Young and Gorter 1981, p. 93.

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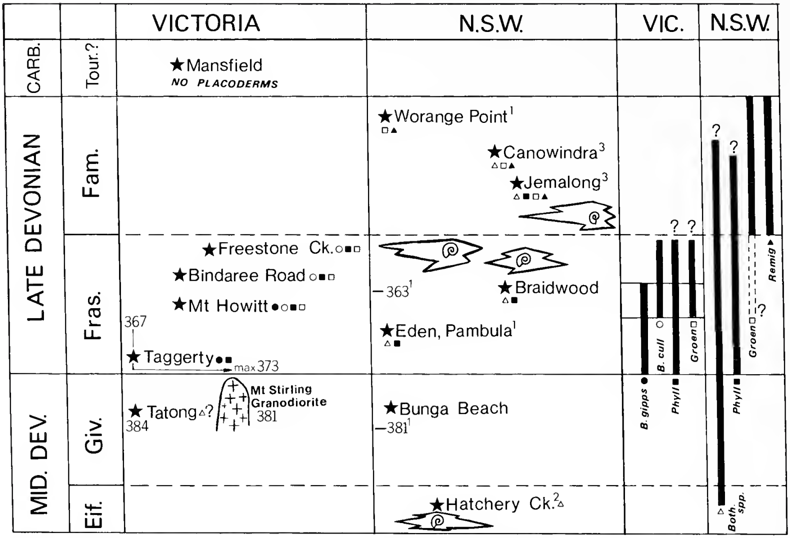
[1] Current address: Dept. Chemistry, Arizona State University, Tempe, Arizona 85281, U.S.A.



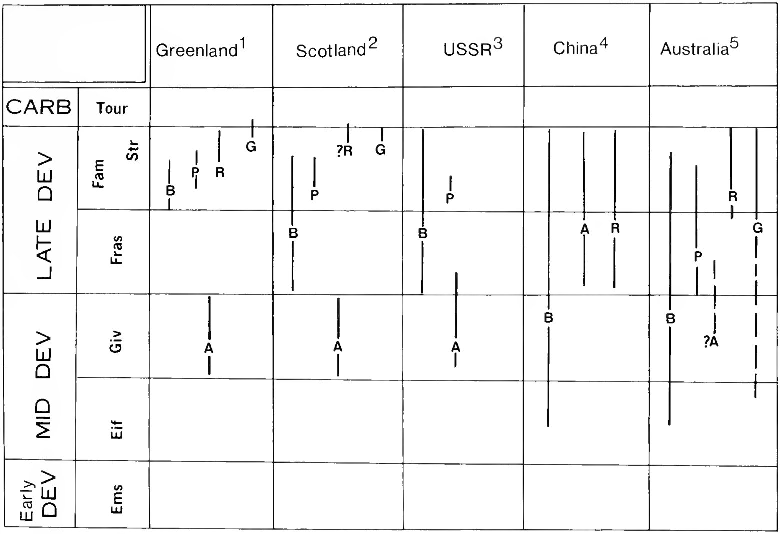
TEXT-FIG. 3. Correlation between Devonian fish faunas from Victoria and New South Wales. 1. Fergusson *et. al.* 1979. 2. Young and Gorter, 1981. 3. Campbell and Bell 1977. Marine invertebrate horizons are discussed in the above references.

Bothriolepis gippslandiensis Hills 1929

Plate 42, fig. 10; text-figs. 5, 6, 8, 9, 12, 13

1929	*Bothriolepis gipplandiensis* Hills, pp. 195–197, text-fig. 2, p. 118, fig. 8.
1931	*Bothriolepis gippslandiensis* Hills, pp. 214–222, text figs. 5, 7, plate 11, figs. 1–6.
1932	*Remigolepis* sp. Hills, p. 855.
1948	*Bothriolepis gippslandiensis* Stensiö, pp. 74, 77, 516–521, text-figs. 264, 265.
1968	*Bothriolepis gippslandiensis* Gilbert-Tomlinson, pp. 191, 193, 199; 206, 209.
1969b	*Hillsaspis gippslandiensis* Stensiö, pp. 515, 516, 669, text-fig. 210D.
1978	*Hillsaspis gippslandiensis* Denison, pp. 109, 111, 112, text-fig. 86D, G.
1981	*Bothriolepis gippslandiensis* Young and Gorter, p. 93.

Diagnosis. A *Bothriolepis* with a maximum mid-dorsal armour length of about 170 mm. Anterior median dorsal and posterior median dorsal plates bear a well-developed, smooth median dorsal crest which is higher on the posterior median dorsal plate. Trunkshield broad and moderately high vaulted, the dorsal walls enclosing an angle of at least 90° and meeting the lateral walls at 120–130°. Headshield weakly vaulted with a breadth/length index around 135 or 145–160 for flattened specimens. Postpineal plate is symmetrical about a transverse plane through the lateral corners in maturity. Orbital fenestra broad and short, the length being under half the breadth. Lateral pits on the ventral surface of the headshield are large but shallow. Anterior median dorsal plate having an anterior breadth around 1·2 times the extent of the posterior margin. Anterior dorsolateral plate square with a dorsal lamina having an external height/length index around 60. Pectoral appendages



TEXT-FIG. 4. Age ranges of biostratigraphically useful placoderms. 1. Bendix-Almgreen 1976. 2. Miles 1968. 3. Young 1974. 4. P'an Kiang 1981. 5. Young 1974; Campbell and Bell 1977.

broad, the proximal segment having a breadth/length index up to 30 and being about 1·5 times the length of the distal segment. Central ventral plate 2 has short contact with the mesial marginal plate 2. Tail has two rows of large ventrolateral scales with minute dermal denticles covering the flanks. A single dorsal fin is preceded by an anterior fin spine. Ornament of coarse, short blunt ridges with tubercles developed prominently on the headshield and lateral laminae.

Holotype. This is a small juvenile headshield collected from the Blue Hills, near Taggerty by Hills (Hills 1929, pp. 195–197, plate xviii, fig. 8). MUGD 776. Figured in Young and Gorter 1981, plate 2, fig. 3.

Material studied. The original material collected by Hills from Taggerty (Hills 1929, 1931); new material from the Mt. Howitt site collected by Professor J. Warren and Dr. M. Marsden; new material collected from Taggerty by the writer and friends. A complete listing of specimens will be published in another paper dealing with the detailed systematics.

Remarks. This species was first recorded from Taggerty in 1929 and later recognized from the Freestone Creek area (Hills 1931). The material studied by Hills from the latter site consisted entirely of small trunkshield and rare headshield plates belonging to a population of juveniles. This is ascertained by the reticulate ornament and juvenile state of the sensory canal system (Stensiö 1948, pp. 211–212). Recent additions to the Freestone Creek collection have shown that the mature plates from this site are all referable to at least two new species *B. cullodenensis* and *B. warreni*. The presence of *B. gippslandiensis* has not been confirmed from this region.

Stensiö (1969b, p. 515) erected the new genus *Hillsaspis* for *B. gippslandiensis* because of the nuchal plate not participating in the orbital fenestra. Recently Young and Gorter (1981, p. 93) re-examined the holotype and found orbital facets to be present on the nuchal plate, demonstrating the condition which is usual for *Bothriolepis*. The well-preserved Mt. Howitt specimens confirm this observation for the species in all stages of growth. Although this species and other new species described below differ from *B. canadensis* in the structure of the tail, it would be confusing to alter the generic status of those species on this character alone, as this feature is very rarely preserved on other species. In the relative shapes and sizes of the dermal plates, *B. gippslandiensis* resembled other species and is here retained within the genus.

B. gippslandiensis is distinguished from all other species of *Bothriolepis* by having a broad headshield with large, shallow lateral pits and a broad, short orbital fenestra; a broad, laterally symmetric postpineal plate; and bearing a smooth median dorsal crest on the relatively high trunkshield.

Bothriolepis cullodenensis sp. nov.

Plate 42, figs. 4, 6, 8, 9, 11; text-figs. 5, 6, 9, 13

1931 *Bothriolepis gippslandiensis* Hills, p. 220, fig. 7, no. 3.

Derivation of Name. From the town of Culloden, 7 km north of Briagolong where the fossils are found. The name was coined by Mr. P. Kenley of the Victorian Mines Department, who collected and informally described material from the region.

Diagnosis. A cristate *Bothriolepis* reaching an estimated dorsal armour length of at least 200 mm. Trunkshield moderately high vaulted with the dorsal walls enclosing an angle of 90° and meeting the lateral walls at 125°. The headshield is elongate, having an external breadth/length index of 100–118 or 120–138 when flattened in a plane. Orbital fenestra large. Ventral surface of the headshield characterized by possessing large, deep lateral pits and paired premedian pits separated by a prominent vertical ridge. Premedian plate narrow, rectangular in shape. Anterior median dorsal and posterior median dorsal plates bear a well-developed median dorsal crest which may extend as high as the anterior median dorsal plate is long and may be serrated along the posterior edge. The anterior median dorsal plate bears a prominent ventral lamina formed by the merging postlevator cristae. The posterior median dorsal plate bears a semicircular ridge anterior to the narrow posterior ventral pit, and has well-developed lateral processes. Mixilateral plate with a strongly convexed external ventral margin. Anterior ventrolateral and posterior ventrolateral plates with high lateral laminae, up to 0·6 times the plate length in height. Posterior ventrolateral plate with a well-marked posteromesial angle. Pectoral fin having the central ventral plate 2 contacting the mesial marginal plate 2, as in *B. gippslandiensis*. Tail of similar structure to *B. gippslandiensis*. Ornamentation of short linear ridges and tubercles, often forming a concentric grid-like pattern.

Holotype. A large near complete headshield from the upper Freestone Creek locality. NMV P31296.

EXPLANATION OF PLATE 42

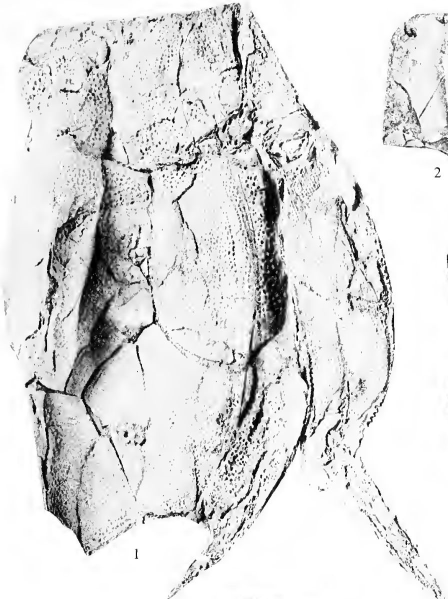
Fig. 1. *Bothriolepis fergusoni* sp. nov. Holotype, almost complete armour in dorsal view, × 1. NMV P157152.

Figs. 2, 3. *B. warreni* sp. nov. 2. Holotype, anterior median dorsal plate in dorsal view. NMV P158767. × 2. 3. Anterior median dorsal plate in ventral view. NMV P158770. × 2.

Figs. 4, 6, 8, 9, 11. *B. cullodenensis* sp. nov. 4. Holotype, headshield in dorsal view. NMV P31296. × 1. 6. Headshield in ventral view. NMV P157226. × 1. 8. Anterior median dorsal plate in dorsolateral view. NMV P158764. × 2. 9. Anterior median dorsal plate in ventral view. NMV P158765. × 1. 11. Posterior median dorsal plate in ventral view. NMV P157207. × 1.

Figs. 5, 7. *B. bindareei* sp. nov. Holotype, anterior dorsolateral plate, internal (5) and external (7) aspects. NMV P157195. × 2.

Fig. 10. *B. gippslandiensis* Hills tail. NMV P157149. × 1. P157152, P157149 from Mt. Howitt. P158767 from the lower site at Freestone Creek. P31296, P157226, P158764, P158765, P157207 from the upper site at Freestone Creek. P158770, P157195 from the Bindaree Road locality. All latex casts whitened with ammonium chloride sublimate.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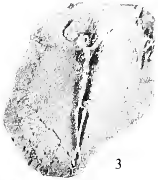
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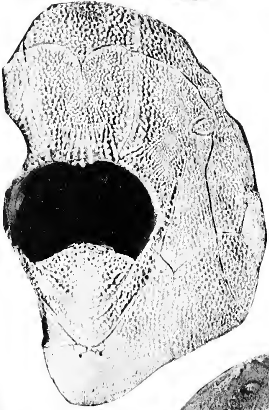
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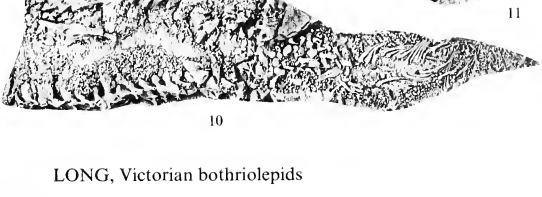
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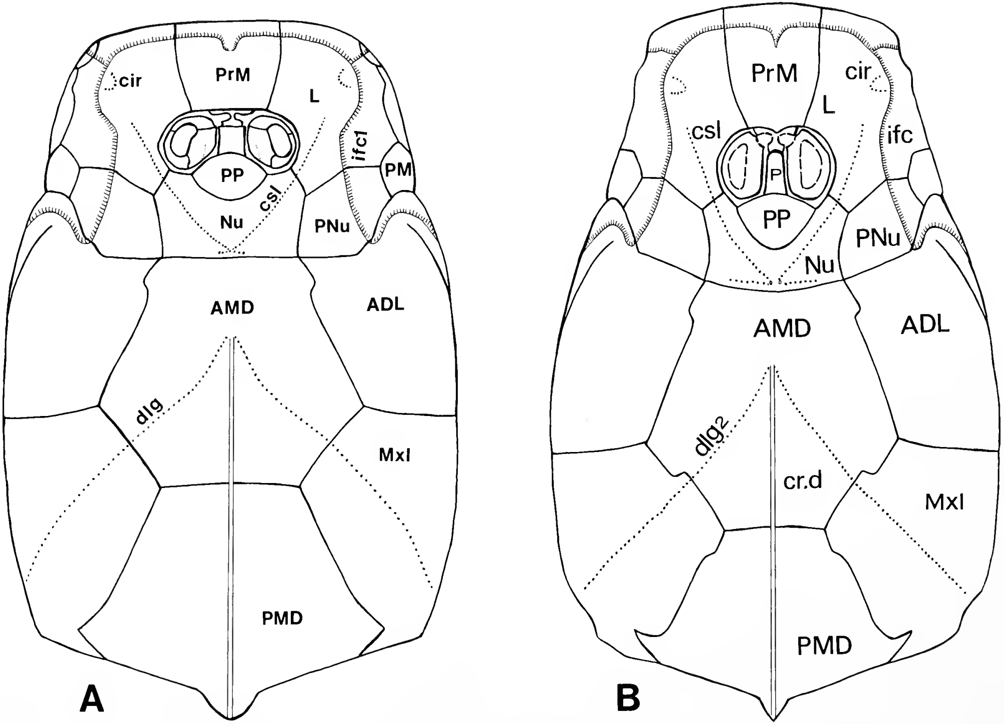
LONG, Victorian bothriolepids



TEXT-FIG. 5. Restoration of armours in dorsal view. A. *Bothriolepis gippslandiensis* Hills. B. *B. cullodenensis* sp. nov. Natural size.

Material studied. Entire articulated specimens and incomplete specimens from Mt. Howitt; isolated plates and semi-articulated specimens from Bindaree Road; isolated plates and articulated headshields from Freestone Creek.

Remarks. Two varieties are found within this species, distinguished only by the relative height and shape of the median dorsal crest, and their stratigraphic positions. From the lower Mt. Howitt Spur site all specimens bear a low, smooth crest and in the topmost horizons the crest is high and posteriorly serrated. Specimens from the Bindaree Road and Freestone Creek localities all bear a high crest in maturity. Aside from this difference the two varieties are morphologically identical and hence regarded as conspecific. It is highly probable that a continuum of crest heights is exhibited by the species with the younger forms being selective for a higher crest. Alternatively crest height could reflect sexual dimorphism, though more material is necessary before any qantitative analysis of this hypothesis could be attempted.

Bothriolepis cullodenensis is distinguished from all other species of *Bothriolepis* by the long, narrow headshield with the large orbital fenestra; possessing large, deep lateral pits and paired premedian pits on the visceral surface; by the well-developed high median dorsal crest; and by possessing a crescentic transverse ridge on the visceral surface of the posterior median dorsal plate.

Bothriolepis fergusoni sp. nov.

Plate 42, fig. 1; text-figs. 7, 13

Derivation of name. After the geologist W. M. Ferguson who not only found fish remains in the Grampians (Ferguson 1917) but also collected material from Freestone Creek (Ferguson 1937).

Diagnosis. A *Bothriolepis* with a mid-dorsal armour length of at least 120 mm, probably much larger. Trunk armour low and narrow with a slight median dorsal crest developed, dorsal and lateral walls meeting at about 100°. Headshield broad, arched both rostrocaudally and transversely, with a short preorbital division. Preorbital recess semilunar with the floor extending well beneath the broad orbital fenestra. Premedian plate broad with a breadth/length index close to 100. Nuchal plate having an external length/breadth index around 80. Anterior median dorsal plate with a flat breadth/length index around 96, the anterior margin being 1·8 times the extent of the posterior margin. Posterior median dorsal plate slightly smaller than the anterior median dorsal plate, lacking lateral processes. Anterior dorsolateral plate having a dorsal lamina under half as high as long, forming a strongly curved external suture with the mixilateral plate. Pectoral appendage slender with noticeable incurvature; the distal segment is striated. Ornament of variable coarseness, changing from a finely reticulate pattern to coarser ridges on a single plate.

Holotype. An almost complete individual, lacking the preorbital division of the headshield. NMV P157152.

Material studied. All from Mt. Howitt, five specimens.

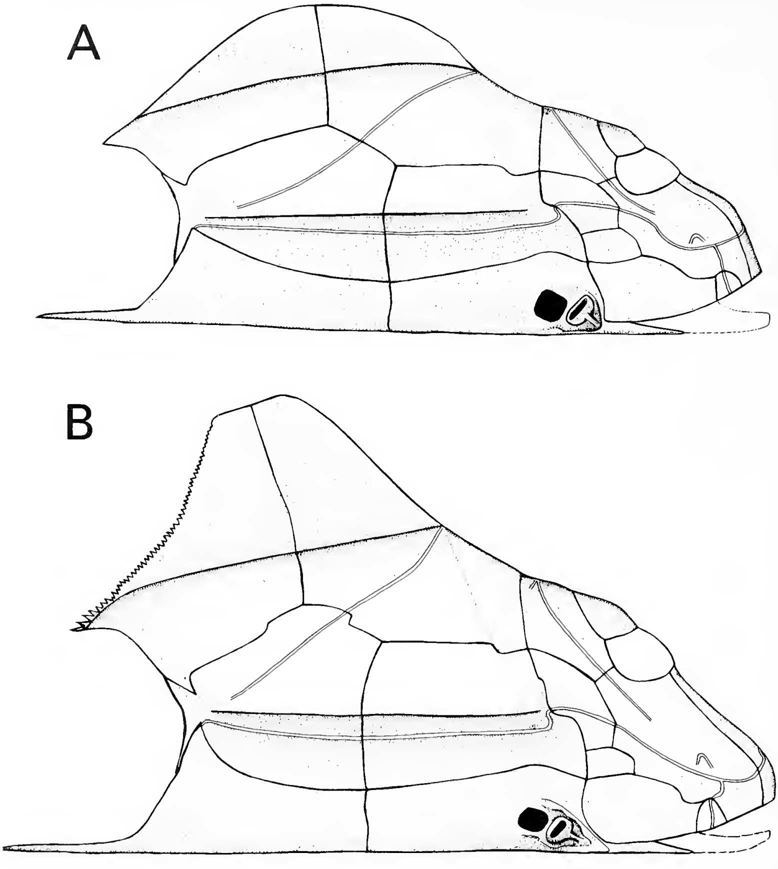
Remarks. Bothriolepis fergusoni is distinguished from all other species of *Bothriolepis* by possessing a headshield having a broad orbital fenestra, and large but shallow lateral pits in conjunction with a narrow, long trunkshield having an anterior median dorsal plate which is broad anteriorly and narrow posteriorly.

Bothriolepis bindareei sp. nov.

Plate 42, figs. 5, 7.

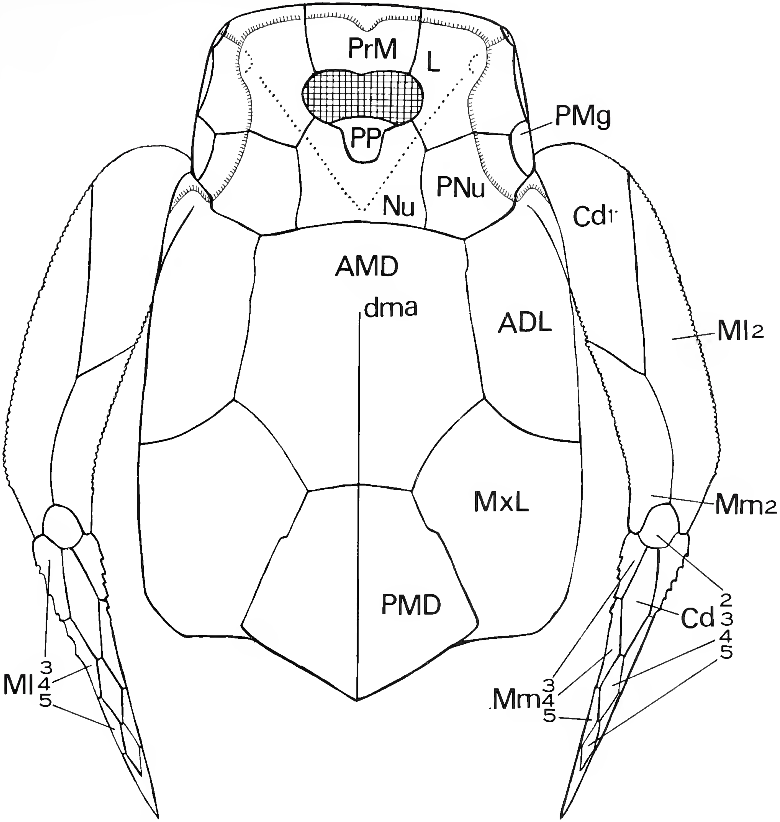
Derivation of name. From the Bindaree Road cutting, second bend up from the junction of the Howqua River track, where the specimens were found. 'Bindaree' is Aboriginal for river which also coincides with the shallow stream environment the species inhabited.

Diagnosis. A *Bothriolepis* with an estimated maximum dorsal armour length of 60 mm. Nuchal plate has an external length/breadth index of 65 and is broadest across the anterolateral corners.



TEXT-FIG. 6. Restoration of armours in lateral view. A. *Bothriolepis gippslandiensis* Hills. B. *B. cullodenensis* sp. nov. Natural size.

Trunkshield short and high. The anterior dorsolateral plate is broader than long, having a breadth/length index of 135. The mixilateral plate is of similar proportions to the anterior dorsolateral plate, the dorsal lamina being equally as high as long. Dorsal and lateral laminae meet at 135°. Posterior ventrolateral plate with a lateral lamina having a height/length index around 75. Ornamentation tubercular on the lateral lamina, being reticulate with tubercular swellings at nodes on the dorsal surface.



TEXT-FIG. 7. *Bothriolepis fergusoni* sp. nov. Restoration of armour in dorsal view. About half natural size.

Holotype. An almost complete anterior dorsolateral plate from the Bindaree Road cutting. NMV P157195.

Material studied. Five isolated plates from Bindaree Road.

Remarks. A new species, *B. bindareei*, is proposed for a few plates displaying proportions quite different from any other known species of the genus. It is retained within the genus *Bothriolepis* because of the anterior dorsolateral, mixilateral, and posterior ventrolateral plates being of proportionate size relative to each other for the genus, and because the nuchal plate bears orbital facets.

Bothriolepis warreni sp. nov.

Plate 42, figs. 2, 3

Derivation of name. After Professor J. W. Warren (Zoology, Monash).

Diagnosis. A *Bothriolepis* with an estimated mid-dorsal length of the trunkshield reaching at least 35 mm. Lateral plate having a breadth/length index close to 80, lacking lateral pits. Trunkshield fairly flat with the dorsal walls enclosing an angle of about 140° at the tergal angle and meeting the lateral walls at 90°. Median dorsal ridge developed as a raised keel. Anterior median dorsal plate having a breadth/length index close to 85 with a short posterior margin. Posterior median dorsal plate having a breadth/length index around 140, with well-developed lateral processes. Mixilateral plate narrow, the dorsal lamina having an estimated breadth/length index of 36, the lateral lamina having a height/length index around 30. Ornament of radiating isolated tubercles on the dorsal surfaces, being sparser or absent on the lateral walls.

Holotype. The almost complete dorsal impression of an anterior median dorsal plate, from the lower site at Freestone Creek. NMV P158767.

Material studied. Ten isolated plates.

Remarks. This species resembles *B. verrucosa* (Young and Gorter 1981) in possessing ornamentation of isolated tubercles, but is distinguished from that species by the absence of the transverse crescentic ridge and stronger development of the median ventral ridge and groove on the anterior median dorsal plate, and by the proportions of the posterior medial dorsal plate. The tubercles of *B. verrucosa* are seen to be coarser and more densely packed around the centres of ossification than for *B. warreni.*

UNUSUAL MORPHOLOGICAL FEATURES OF THE VICTORIAN BOTHRIOLEPIDS

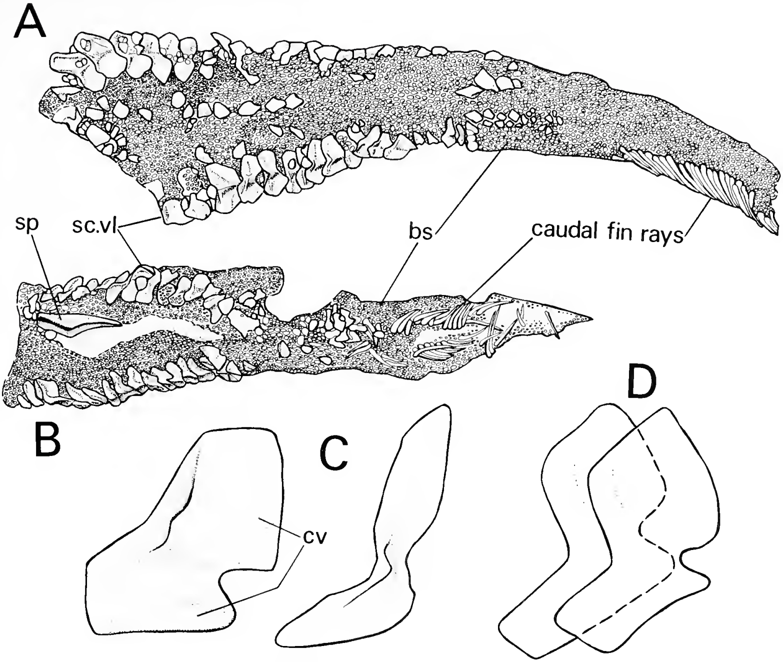
Although the morphology of bothriolepids has been thoroughly treated by Stensiö (1931, 1948) and Miles (1968), a few noteworthy points of interest are seen on the Victorian specimens, such as the structure of the tail, and on the ventral surfaces of the headshield and trunkshield.

The tail of *B. canadensis* is presently the only well-known example of this feature on bothriolepids (Stensiö 1948). In *B. gippslandiensis* and *B. cullodenensis* the tail is characterized by the two large ventrolateral scale rows with minute body scales covering the flanks (plate 42, text-fig. 8). A single dorsal fin is indicated by the prominent fin spine which is probably a composite scale structure as in *Pterichthyodes* (Hemmings 1978, p. 37). As the material is studied from latex casts the internal construction of the scales is unknown. No evidence of pelvic fins could be observed in the material, including radiographs of unprepared specimens. This implies that either the pelvic fins were naked or not present. A final point concerning the tail is that in juveniles the ratio of tail length to armour length is proportionately greater. A restoration of *B. gippslandiensis* is shown in text-fig. 12.

The ventral surface of the headshields of *B. gippslandiensis*, *B. cullodenensis*, and *B. fergusoni* show the development of large lateral pits (prespiracular pit of Stensiö). In *B. cullodenensis* this feature is of greater area and depth than for the other species (plate 42, fig. 6). Stensiö (1948, p. 61) notes that in *B. canadensis* these pits may invariably be absent, and in all other species they are weakly developed if present.

The premedian plate of *B. cullodenensis* has a pair of oval depressions separated by a median vertical ridge (plate 42, fig. 6) on the ventral surface. Similar structures are encountered in other antiarchs, for example *Microbrachius* (Hemmings 1978, p. 45) although it is not clear if they are strictly homologous.

The ventral surface of the anterior median dorsal plate of *B. gippslandiensis* has been described by Hills (1931) and Stensiö (1948, p. 519) as bearing a prominent horizontal lamina which floored the levator fossa. This feature is even better developed in *B. cullodenensis* where a strong but short median vertical ridge supports the crescentic lamina formed by the merged postlevator cristae. The posterior median dorsal plate of this species (plate 42, text-fig. 9) has a peculiar crescentic ridge in the



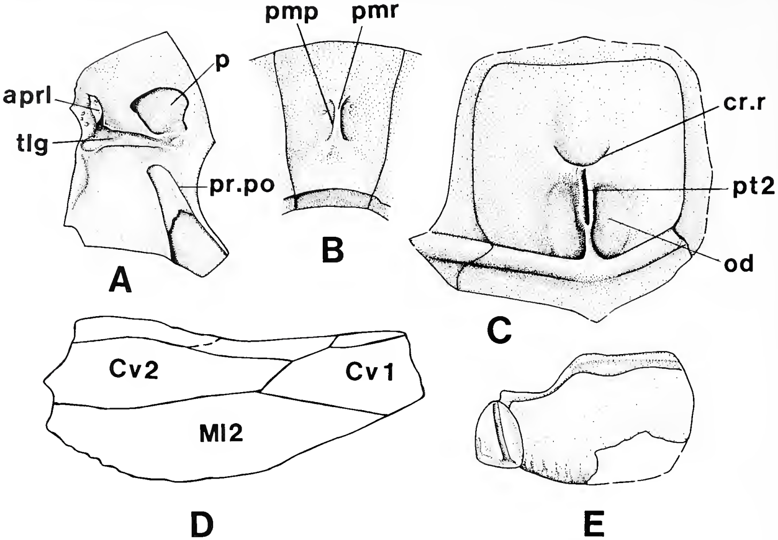
TEXT-FIG. 8. *Bothriolepis gippslandiensis* Hills. Tail and squamation. A. NMV P157170. B. NMV P157149. Natural size. C. internal lateral view and anterior view of a ventrolateral scale from NMV P157170. D. Overlap relations of scales. C, D. × 6. From Mt. Howitt. bs. body scales. cv. overlap areas. scvl. ventrolateral scales. sp. dorsal fin spine.

centre of the ventral surface, immediately anterior to the narrow posterior ventral process which contains the posterior ventral pit.

Without going into more detailed descriptions of the new species, the following morphological features are worthy of note: the extralateral plates of *B. gippslandiensis* and *B. cullodenensis* are broader and shorter than for other species whose extralateral plates are essentially similar to that of *B. canadensis* (Stensiö 1948, p. 89); the central ventral plate 1 and mesial marginal plate 2 of the pectoral appendages of *B. gippslandiensis* and *B. cullodenensis* have extensive contact, similar to *B. verrucosa* (Young and Gorter 1981, p. 101); the preorbital region of the headshield of *B. fergusoni* is very short by comparison with other species.

INTERRELATIONSHIPS OF ANTIARCHS

In order to evaluate the taxonomic position of the Victorian bothriolepids it is first necessary to consider the relationship of *Bothriolepis* to other antiarchs. Young (1981, p. 238) has put forward

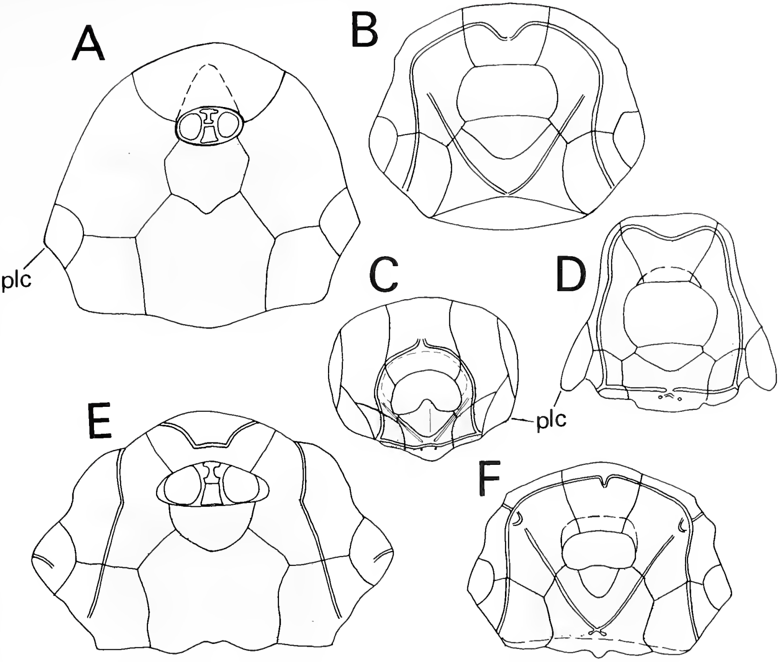


TEXT-FIG. 9. A–C. *Bothriolepis cullodenensis* sp. nov. A. Lateral plate, NMV P158762. B. Premedian plate, CPC 54651. C. Posterior median dorsal plate, NMV P157207. D, E, *B. gippslandiensis* Hills. D. Incomplete proximal segment of pectoral appendage in ventral view, NMV P160702. E. Extralateral and prelateral plates, NMV P157168. All ×2. A–C. Freestone Creek. D. Taggerty. E. Mt. Howitt. Aprl. prelateral plate attachment area. cr.r. Crescentic ridge. CV1, 2. Central ventral plates 1, 2. Ml. 2. lateral marginal plate 2. Od. ovoid depression. p. lateral pit. pmp. premedian pit. pmr. premedian ridge. pr.po. postorbital process. pt2. posterior median ventral pit. tlg. transverse groove.

a cladogram of antiarchan interrelationships using biogeographic data. I intend to outline the morphological evidence for this hypothesis before discussing the interrelationships of bothriolepids.

I accept the hypothesis of Miles and Young (1977, p. 133) that antiarchs are the sister group of euarthrodires (*sensu* Young 1979, p. 344), and that antiarchs and euarthrodires are the sister group of *Phyllolepis*. Antiarchs are specialized in possessing a posterior median dorsal plate, mid-dorsal orbital fenestra and a cranio-thoracic articulation having the trochlea on the paranuchal plate. The premedian plate is believed to be acquired independently in antiarchs and some rhenanids (Miles and Young, 1977, p. 135).

Yunnanolepidoids (Zhang Guorui 1978, p. 184) are the most primitive of the antiarchs (*ibid.* p. 186, Young 1981, p. 236) and may be separated from all other genera by the absence of a true brachial process. They are specialized amongst antiarchs in possessing an external rhombic depression (Zhang Guorui 1978, p. 184) and a subpremedian ridge (Zhang Mi-man 1980, p. 180). A specialization of yunnanolepidoids which is retained in bothriolepidoids (see 'Classification') but lost in asterolepidoids (*sensu* Hemmings 1978, p. 3) is the well-formed median ventral pits of the trunkshield. Euarthrodires primitively possess a ventral ridge on the median dorsal plate (Miles and Dennis 1979, p. 43) which is developed into a carinal process in higher forms (*ibid.* p. 48), but lack the pits seen in antiarchs.



TEXT-FIG. 10. Headshields of various antiarchs. A. *Sinolepis* restored with long obstantic margins, modified from Liu and P'an 1958. B. *Dianolepis*, from pl. 2 in Chang 1965. C. *Microbrachius*, from Hemmings 1978. D. *Pterichthyodes*, from Hemmings 1978. E. *Yunnanolepis* from Zhang Mi-man 1980. F. *Bothriolepis canadensis*, from Stensiö 1948. Inferred endocranial outlines stippled. Not to scale. plc. posterolateral corner.

Sinolepids are similar to yunnanolepidoids in retaining a long occipital (preorbital) division of the headshield, small, anteriorly situated orbital fenestra and short, flaired premedian plate. They are more specialized than yunnanolepidoids in possessing a brachial process. The brachial process of *Sinolepis* has not been described by Liu and P'an (1958), but is assumed to be present because of the well-developed pectoral appendages. An antiarch from Grenfell, New South Wales, which may be a sinolepid (Young 1981, p. 237) lacks the brachial process on all specimens of the anterior ventrolateral plate. However, the proximal bones of the pectoral fin show an articular region for the brachial process, suggesting that this feature was originally present. A thin *pars pedalis* is present on the anterior ventrolateral plate which indicates that the brachial process may have had weak connection to the trunkshield, consequently breaking off easily after death.

Although *Sinolepis* is restored with the preobstantic corners situated on the posterior margin of the headshield, closer examination of the plates in Liu and P'an (1958, pls. 3, 5, figs. 1*a*, *b*; 6, figs. 1*a*, *b*) indicates that the postmarginal plate has a more anterior position on the headshield (text-fig. 29). The obstantic margin is developed essentially as in *Yunnanolepis* but is relatively shorter in *Sinolepis*.

Sinolepis resembles *Yunnanolepis chii* (Liu 1963, p. 40; Zhang Guorui 1978, p. 156) in having broad overlap areas on headshield plates, which may further remove the yunnanolepidoids and sinolepids from other antiarchs which typically possess short overlap areas. The long pectoral appendages and short trunkshield comprising equally sized squarish plates are interpreted as parallelisms. This is evidenced by the long pectoral appendages of bothriolepids which are more specialized than *Sinolepis* in several characters discussed below. The development of a short trunkshield relative to headshield size is a trend in some antiarchs which parallels the euarthrodires (Miles 1969, p. 131), although is not as clearly defined.

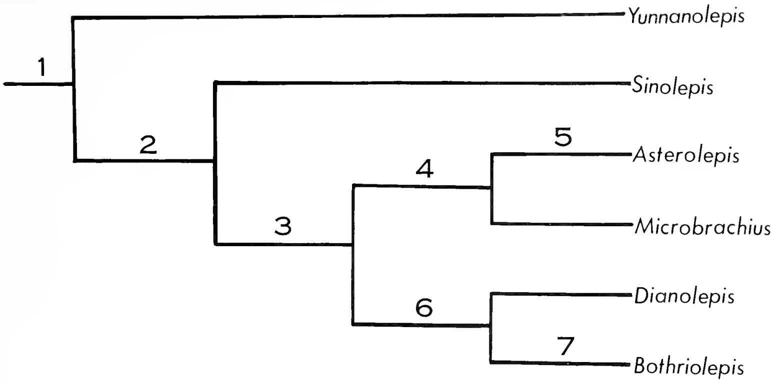
Asterolepidoids, *Microbrachius* and bothriolepidoids are united by the possession of a short occipital region on the headshield, enlarged orbital fenestrae and reduced overlap areas between headshield plates (text-fig. 29). Asterolepidoids are a monophyletic group united by the acquisition of a short, posteriorly facing obstantic margin with the preobstantic corners close to the posterior margin of the headshield. They are also specialized in the loss of median ventral pits on the trunkshield, although this character is variably developed. *Pterichthyodes* (Hemmings 1978, p. 24), *Byssacanthus* (Karatajute-Talimaa 1960, p. 296) and *Sherbonaspis* (Young and Gorter 1981, p. 105) have lost the pits entirely, whereas *Asterolepis* (Karatajute-Talimaa 1963, fig. 45) and *Microbrachius* (Hemmings 1978, p. 51) retain the posterior median ventral pit. The single extralateral plate in the cheek of asterlepidoids is paralleled in *Sinolepis*. *Microbrachius* is here classified as an asterolepidoid, in agreement with Miles (1968, p. 3) because of the obstantic margins and loss of the anterior ventral pit. *Microbrachius* parallels the bothriolepidoids in the development of spines on the distal segment of the pectoral appendage and the well-formed central sensory line canals, and parallels *Sinolepis* and Grossilepis in the shape of the trunkshield plates.

Bothriolepidoids are the sister group of the asterolepidoids and are united as a monophyletic group by having anteriorly extended postorbital processes with a narrow otico-occipital region on the endocranium (restored from the impressions on the ventral surface of the headshield), and a prelateral plate. They retain the primitive condition of having the preobstantic corners anterior to the posterior margin of the headshield with a long obstantic margin. *Wudinlepis* is provisionally included in this suborder because of the anterior preobstantic corners in conjunction with the short occipital region of the headshield. *Dianolepis* is included within the suborder because of the anteriorally extended postorbital processes which meet the paranuchal plate closer to the orbital fenestra than to the postmarginal plate (Chang 1965, pl. 2, fig. 2). This indicates that the otico-occipital region would be proportionally narrow to headshield breadth as in *Bothriolepis*. *Pterichthyodes* has extended postorbital processes yet retains a proportionally broad otico-occipital region as in other asterolepidoids (Hemmings 1978, p. 13). Chang does not state that a prelateral plate is present on *Dianolepis*. However, close examination of fig. 2, pl. 2 (Chang 1965) shows a broad attachment area anterior to the transverse lateral groove, similar to the prelateral attachment area on *Bothriolepis*. The attachment area for the anterior division of the extralateral plate in asterolepidoids is typically rostrocaudally elongate, as in *Pterichthyodes*, *Microbrachius*, *Asterolepis*, and *Sherbonaspis*. The bothriolepidoid affinity of *Dianolepis* is further suggested by the postpineal plate which is more convex posteriorly than anteriorly, well-developed central sensory canals and relatively broad lateral plate. *Bothriolepis* and *Grossilepis* are united by having the postpineal plate not contacting the lateral plates, and possibly by the presence of a well-developed median occipital crista on the posterior ventral face of the headshield.

INTERRELATIONSHIPS OF BOTHRIOLEPIDS

Of over sixty described species of *Bothriolepis* and further specimens awaiting description, only twenty-five or so are known by headshields and trunkshields, and only in *B. canadensis*, *B. gippslandiensis*, and *B. cullodenensis* is the squamation and structure of the tail known. In the following discussion only these species or particularly relevant species such as *B. verrucosa* are considered.

B. verrucosa is the most primitive species in possessing a small axillary foramen, weakly developed



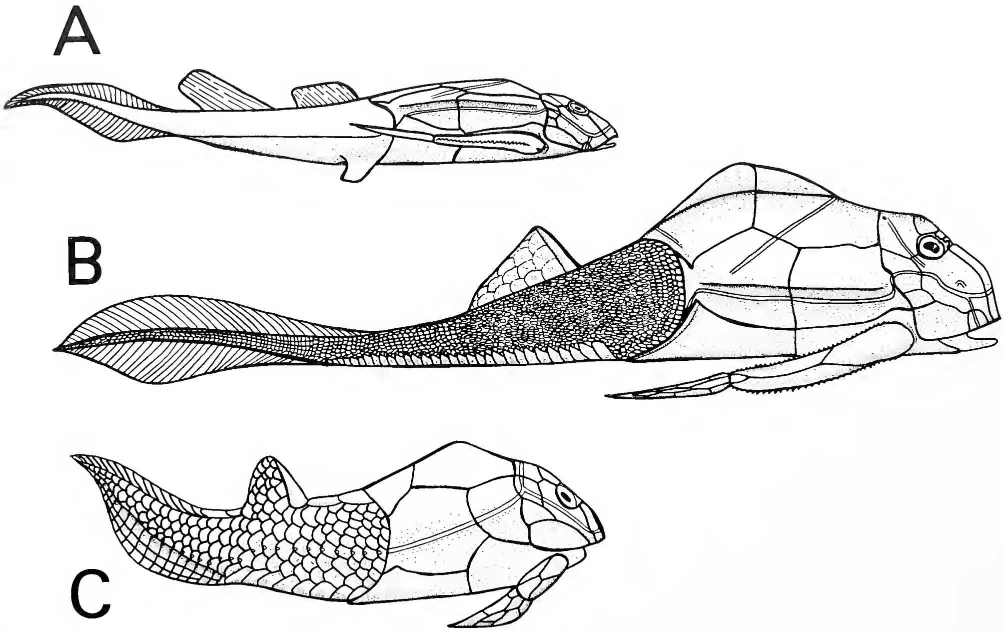
TEXT-FIG. 11. Hypothesis of antiarchan interrelationships. Numbered synapomorphies: 1. Possessing a posterior median dorsal plate, eyes and nares meet mid-dorsally on the headshield and are situated within an orbital fenestra. 2. Acquisition of a brachial process and axillary foramen. 3. Shortened postorbital division of exocranium, enlarged orbital fenestra. 4. Preobstantic corners of headshield situated on or close to the posterior margin, loss of the anterior cheek element (prelateral). 5. Loss of anterior median ventral pit on the dorsal wall of the trunkshield, or both anterior and posterior pits. 6. Otico-occipital depression of headshield proportionally narrow with well-developed postorbital processes. 7. Postpineal plate loses contact with the lateral plates. Each genus is representative of the respective family.

median occipital crista and having the central ventral plate 1 contacting the mesial marginal plate 2. This species is specialized in the development of a crescentic ridge on the anterior median dorsal plate.

All other bothriolepids, including *Grossilepis*, are united by the possession of a large axillary foramen and a well-developed median occipital crista. Two major lines of descent are apparent: one comprising certain Victorian species described herein, the other containing all other well-known species.

B. gippslandiensis, *B. cullodenensis*, and *B. fergusoni* are specialized in possessing large lateral pits on the headshield. *B. gippslandiensis* and *B. cullodenensis* are further specialized in the development of short, high trunkshields which bear median dorsal crests, and short, broad levator fossae which are floored by merged postlevator cristae. The crescentic ridge of *B. verrucosa* arises from the posterior margins of the postlevator thickenings (Young and Gorter, 1981, p. 95) whereas in *B. gippslandiensis* and *B. cullodenensis* the postlevator cristae merge to form a bony lamina which is situated more anteriorly than in *B. verrucosa*. *B. fergusoni* is parenthetically included in the cladogram with the other Victorian species because some morphological features are not clear (as in the central surface of the anterior median dorsal plate, and the ventral aspect of the pectoral appendage). If the floored levator fossa is used to united *B. verrucosa* with the Victorian species then the large axillary foramen and well-formed median occipital crista would have to be independently acquired in *B. gippslandiensis*, *B. cullodenensis*, and all other bothriolepids. This is less parsimonious than the independent acquisitions of one character (the floored levator fossa) in the Victorian forms.

The rest of the bothriolepids may be united by having the central ventral plate 1 and mesial marginal plate 2 barely touching in the pectoral appendage. Examination of material of the Gogo *Bothriolepis* in the Australian Museum, Sydney, shows that this condition and the primitive condition seen in *B. verrucosa* and the relevant Victorian species can occur within a single species (personal observation). Hoewever, as this is the only species displaying this kind of variation, and this



TEXT-FIG. 12. Comparison of the tail of *Bothriolepis canadensis* (A) with *B. gippslandiensis* (B) and *Pterichthyodes* (C). A, after Stensiö 1948. Hemmings 1978. Not to scale.

is observed in one specimen only, it is assumed that the contact relationship of the central ventral plate 2 and the mesial marginal plate 1 is not typically variable for other species of *Bothriolepis*.

The tail of *B. canadensis* has little scale covering (Stensiö 1948, p. 167) whereas large ventrolateral scales and minute body scales cover the tails of *B. gippslandiensis*, *B. cullodenensis*, and presumably *B. fergusoni*. The tail of antiarchs is primitively covered by large scales, as in *Yunnanolepis*, *Sinolepis*, *Pterichthyodes*, *Asterolepis* (Stensiö 1969, p. 656), and *Remigolepis* (Dr. A. Ritchie, pers. comm.). The reduced squamation of *B. canadensis* is therefore apomorphic relative to the Victorian species (text-fig. 12). *Bothriolepis* sp. from Canowindra, New South Wales, also possesses the reduced squamation of *B. canadensis* (personal observation), and it is possible that many of the typical Euramerican species may have had little scale cover on the tail. This character may further separate the Victorian species when more is known of the tail of other *Bothriolepis* species. The use of this character in the cladogram implies that *B. verrucosa* had some degree of scale cover on the tail. However, as material of this species occurs as isolated plates it would be difficult to test this hypothesis.

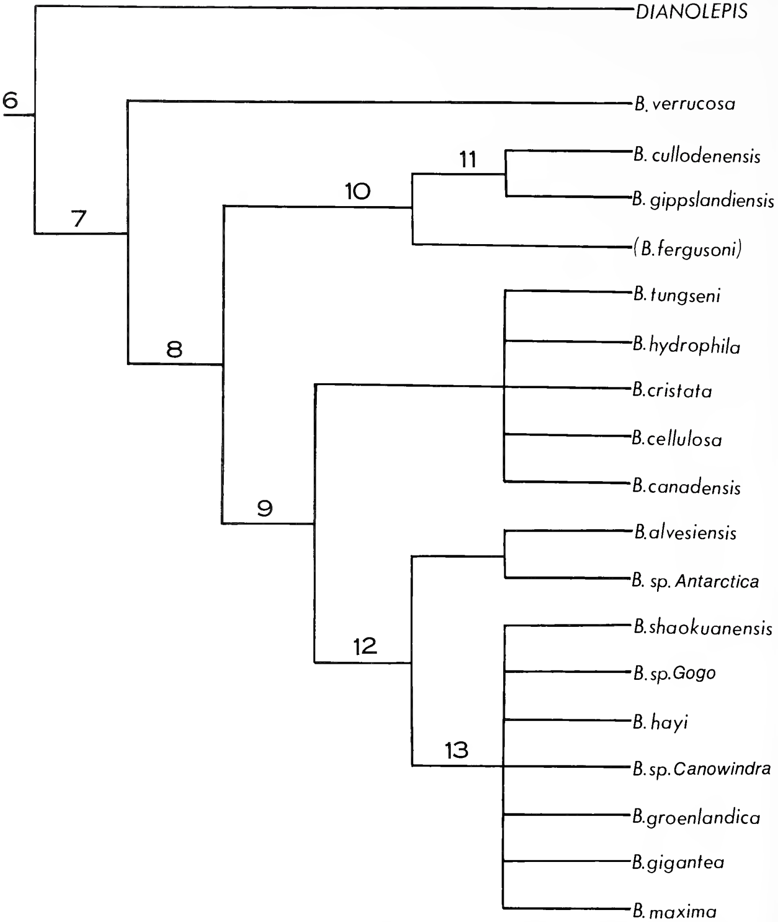
The preorbital recess is primitively developed in antiarchs in a semicircular shape, as in *Pterichthyodes* (Hemmings 1978, p. 14) and *Asterolepis* (Stensiö 1948, p. 52). The trifid preorbital recess is unique to certain species of *Bothriolepis* and is more complex than the semicircular type in having extended medial and lateral divisions. *B. alvesiensis* and a species from Antartica (Dr. G. Young, pers. comm.) possess a preorbital recess which has an extended medial division with simple lateral divisions, intermediate between the two prevalent types. *B. tungseni* from the Eifelian of China is the oldest known species and has a semicircular preorbital recess (Chang 1965, p. 9). However, *B. shaokuanensis* from the Givetian of China (Liu 1963) possesses a trifid preorbital recess, indicating that the two varieties appeared close together in time.

The bothriolepid diversity gave rise to much parallelism. *B. gippslandiensis* and *B. tungseni* possess postpineal plates with strongly convex anterior margins and broad orbital fenestrae. *B. tungseni*, *B. fergusoni*, *B. hayi*, *B. nitida*, and *Bothriolepis* sp., Antarctica (Dr. G. Young, pers. comm.), possess striae on the distal segment of the pectoral appendage. *B. verrucosa* and *B. paradoxa* possess a shallow depression in the centre of the supraotic thickening of the nuchal plate. *B. cristata* and *B. groenlandica* possess a median vertical ridge on the premedian plate (Miles 1968, p. 57), but the ridge developed on the premedian of *B. hayi* is more like that of *B. cullodenensis* in being outside of the preorbital recess. The development of median dorsal crests on *B. gippslandiensis* and *B. cristata* is another example of parallelism. The shape of the headshield in bothriolepids varies from being narrow with a strongly convex rostal margin (*B. cullodenensis*, *B. tungseni*, *B. alvesiensis*, *B. shaokuanensis*) to being broader with a fairly straight rostral margin (*B. gippslandiensis*, *B. canadensis*, *B. gigantea*, *B. hicklingi*, *B. leptocheira*, *B. maxima*). The early appearance of *B. tungseni* and *B. shaokuanensis* suggests that the straight rostral margin was independently developed in bothriolepids possessing semicircular and trifid preorbital recesses. The straight rostral margin is seen on the most specialized of the bothriolepids, those possessing trifid preorbital recesses and attaining large size (*B. gigantea*, *B. maxima*). *B. maxima* is specialized in possessing a relatively narrow, long orbital fenestra and a large posterior ventral pit situated centrally on the posterior median dorsal plate (Gross 1948, p. 446).

Extremes on bothriolepid diversity are exemplified by such forms as *B. kwangtungensis* which had unusually narrow, flat armour (P'an Kiang 1964) and *B. bindareei* which had very high, short armour. Size ranges of *Bothriolepis* armours vary from 60 mm (*B. verrucosa*) to 500 mm (*B. maxima*), being the largest of the antiarchs.

CLASSIFICATION

The classification of antiarchs by Miles (1968, p. 3) agrees with that of Gross (1965, p. 13) in using the exoskeletal characteristics of the armour as a whole, rather than the structure of the pectoral fin (Stensiö 1931, 1948, 1969). However, unlike Gross, Miles erected a new suborder for the Lower Devonian yunnanolepids. Zhang Guorui (1978) and Zhang Mi-man (1980) have recently shown that the primitive organization of the group deserves subordinal rank. Hemmings (1978, p. 3) placed the enigmatic families Sinolepidae (Liu and P'an 1958) and Microbrachiidae (Miles 1968) within the



TEXT-FIG. 13. Hypothesis of bothriolepid interrelationships. Numbered synapomorphies: 6, 7 see text fig. 11. 8. Median occipital crista well developed, axillary foramen enlarged. 9. Mesial marginal plate 2 barely touches central ventral plate 1, squamation on tail reduced. 10. Large lateral pits on ventral surface of headshield. 11. Armour short, high, cristate. Cristae (forming horizontal laminae). 12. Preorbital recess with an enlarged median division. 13. Preorbital recess with extended lateral divisions. These species represent the well-known types of the genus. Material of *Bothriolepis* sp. from Gogo, Western Australia, Canowindra, New South Wales, and Antarctica kept in the Australian Museum, Sydney and the Bureau of Mineral Resources, Canberra.

suborder Bothriolepidoidei (Miles 1968), though this is refuted by Young and Gorter (1981, p. 93) who retain the single family Bothriolepididae within the suborder. Young and Gorter have given new definitions of the suborder Bothriolepidoidei which incorporates the postpineal plate not contacting the lateral plates as a diagnostic feature. In defining the Asterolepidoidei Young and Gorter (*ibid*, p. 100) use the characters 'antiarchs with the posterolateral angle of the headshield situated at or just in front of the posterior margin . . . prelateral plate absent'. These statements exclude *Dianolepis* from either suborders (see above for comments concerning the possible presence of a prelateral plate in *Dianolepis*), yet it is suggested that the genus does not belong in the Bothriolepidoidei so is more closely allied to the asterolepidoids. I have proposed a closer affinity between *Dianolepis* and *Bothriolepis* and include these genera with *Grossilepis* in the Bothriolepidoidei. *Dianolepis* is here referred to its own family, Dianolepididae, on the basis of the postpineal plate contacting the lateral plates. The following classification of antiarchs recognizes *Sinolepis* as the sister group to both asterolepidoids and bothriolepidoids and places the genus in its own suborder, the Sinolepidoidei. *Xichonolepis* (Zhang Guorui, 1980) is classified as an asterolepidoid but in possessing well-developed median ventral pits on the trunkshield and a single mixilateral plate this genus is more closely allied to *Sinolepis*. In view of the fragmentary nature of *Xichonolepis*, the genus is provisionally included within the new suborder. Sinolepid remains may also be present from Australia. An antiarch having rectangular median dorsal plates with well-developed median ventral pits and an unusually long nuchal plate has been found from the Mt. Grenfell area in New South Wales (Dr. A. Ritchie, pers. comm.).

The classification of antiarchs presented here is fundamentally similar to that of Miles (1968) with modifications concerning the systematic status of sinolepids and the genus *Dianolepis*. It has not been reorganized as a cladistic classification for the following reasons: (1) inadequate knowledge of asterolepidoid interrelationships; (2) the possibility of decreasing the number of current species of *Bothriolepis* by recognition of morphotypic groups; and finally (3) the need of further data on many of the poorly known Chinese forms. When these problems have been dealt with then perhaps a revised classification of the Antiarcha can be confidently attempted.

Order ANTIARCHA Cope 1885

Suborder YUNNANOLEPIDOIDEI Miles 1968

Diagnosis. As in Zhang Guorui 1978 (in Chinese).

Family YUNNANOLEPIDAE Zhang Guorui 1978

Diagnosis. As in above.

Genera *Yunnanolepis*, *Phymolepis*, ?*Zhanjilepis*

Family QUIJINOLEPIDAE

Diagnosis. As in above.

Genus *Quijinolepis*

Suborder SINOLEPIDOIDEI

Diagnosis. Antiarchs having a headshield with a relatively long postorbital region. Trunkshield with well-developed median ventral pits on the dorsal wall; brachial process present.

Family SINOLEPIDAE Liu and P'an 1958

Diagnosis. As above.

Genera *Sinolepis*, ?*Xichonolepis*

Suborder BOTHRIOLEPIDOIDEI Miles 1968

Diagnosis. Antiarchs having a short postorbital region on the headshield; postpineal plate separated or almost separated from the lateral plates; otico-occipital depression narrow relative to headshield breadth; prelateral plate present. Anterior median dorsal plate with a broad anterior margin; single mixilateral plate replacing posterior dorsal and posterior dorsolateral plates. Semilunar plate unpaired.

Family DIANOLEPIDIDAE

Diagnosis. Bothriolepidoids with the postpineal plate contacting the lateral plates.

Genera *Dianolepis*, ?*Wudinolepis*

Family BOTHRIOLEPIDIDAE Cope 1886

Diagnosis. Bothriolepidoids having the postpineal plate excluded from the lateral plates. Preorbital recess well developed. Pectoral appendages extending beyond trunkshield when adducted; dorsal central plate 2 small, not contacting dorsal central plate 1.

Genera *Bothriolepis*, *Grossilepis*

Suborder ASTEROLEPIDOIDEI Miles 1968

Diagnosis. Antiarchs having a short postorbital region on the headshield; preobstantic corners situated on or close to the posterior margin of the headshield. Prelateral plate absent. Otico-occipital depression broad. Postpineal plate contacting lateral plates, usually broad in proportion to its length. Median ventral pits poorly developed or absent.

Family ASTEROLEPIDIDAE Miles 1968; Traquair 1888

Diagnosis. Asterolepidoids having a low trunkshield; preorbital division of headshield very short. Orbital fenestra large.

Genera *Asterolepis*, *Remigolepis*

Family PTERICHTHYODIDAE Stensiö 1948

Diagnosis. As in Young and Gorter 1981, p. 100.

Genera *Pterichyodes*, *Sherbonaspis*, *Stegolepis*, *Gerdalepis*, *Lepadolepis*, *Grossaspis*, *Byssacanthus*

Family MICROBRACHIIDAE Miles 1968

Diagnosis. As in Hemmings 1978, p. 42.

Genus *Microbrachius*

All other general *Incertae sedis*.

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REFERENCES

BENDIX-ALMGREEN, S. E. 1976. Palaeovertebrate Faunas of Greenland. *In* ESCHER, A., STUART WATT, W. (eds.), *The Geology of Greenland.* Geol. Surv. Greenland. 537–552.

BROWN, M. C. 1961. The geology of the Tatong-Tolmie area. Univ. Melb., M.Sc. thesis (unpubl.)

CAMPBELL, K. S W. and BELL, M. 1977. A primitive amphibian from the Late Devonian of New South Wales. *Alcheringa* **1.** 369–381.

CHANG KUO-JUI 1965. New Antiarchs from the Middle Devonian of Yunnan. *Vertebr. Palasiat.* **9,** 1–9.

COPE, E. D. 1885. The position of *Pterichthys* in the system. *American Naturalist*, **19,** 289–291.

—— 1886. An interesting connecting genus of Chordata. **20,** 1027–1031.

DENISON, R. H. 1941. The soft anatomy of *Bothriolepis. J. Palaeont.* **15,** 535–561.

—— 1951. Late Devonian freshwater fishes from the Western United States. *Fieldiana, Geol.* **11,** 219–261.

—— 1978. Placodermi. *In* SCHULTZE, H.-P. (ed.), *Handbook of Palaeoichthyology*, Vol. 2. G. Fischer, Stuttgart, 1–128.

EICHWALD, E. I. von 1840. Die Thier-und Pflanzenreste des alten rothen Sandsteins und Bergkalks in Novgorodschen Gouvernement. *Bulletin de l'Académie (impériale) des sciences de Saint-Petersbourg*, **7,** 78–91.

FERGUSON, W. H. 1917. The discovery of fossils in the Grampians Sandstones with general notes on the formation. *Rec. geol. Surv. Vic.* **4,** 5–9.

—— 1937. Fossil fish, Briagolong district. Ibid. **5,** 506–507.

FERGUSSON, C. L. *et. al.* 1979. The Upper Devonian Boyd Volcanic Complex, Eden, New South Wales. *J. Geol. Soc. Aust.* **26,** 87–105.

GARDINER, B. J. and MILES, R. S. 1976. Devonian Fishes of the Gogo Formation, Western Australia. *Colloques. Internat. Centre Nat. Rech. Sci.* **218,** 73–79.

GILBERT-TOMLINSON, J. 1968. A new record of *Bothriolepis* from the Northern Territory of Australia. *Palaeontology Papers. Bull.* **80,** BMR, Canberra, 191–226.

GROSS, W. 1948. *Bothriolepis maxima. In* STENSIÖ, E. A. 1948. (see below).

—— 1965. Über die Placodermem-Guttungen *Asterolepis* und *Tiaraspis* aus dem Devon Belgiens und einen fraglichen *Tiaraspis* — Rest aus dem Devon Spitzbergens. *Bull Inst. R. Sci. Nat. Belg.* **41,** 1–19.

HEMMINGS, S. K. 1978. The Old Red Sandstone Antiarchs of Scotland: *Pterichthyodes* and *Microbrachius. Palaeontogr. Soc. (Monogr.)*, **131,** no. 551, 1–64.

HILLS, E. S. 1929. The geology and palaeontography of the Cathedral Range and Blue Hills in northwestern Gippsland. *Proc. R. Soc. Vict.* **41,** 176–201.

—— 1931. The Upper Devonian fishes of Victoria, Australia, and their bearing on the stratigraphy of the state. *Geol. Mag.* **68,** 206–31.

—— 1932. Upper Devonian fishes from New South Wales. *Geol. Soc. Quart. Journ. Lond.* **88,** 850–858.

—— 1936. Records and descriptions of some Australian Devonian fishes. *Proc. R. Soc. Vict.* **48,** 161–171.

—— 1958. A brief review of Australian fossil vertebrates. *In* WESTOLL, T. S. (ed.), *Studies on fossil vertebrates.* Athlone Press, London.

—— 1959. Record of *Bothriolepis* and *Phyllolepis* (Upper Devonian) from the Northern Territory of Australia. *Proc. R. Soc. N.S.W.* **92,** 174–175.

KARATATUTE-TALIMAA, V. N. 1960. *Byssacanthus dilatatus* (Eichw.) from the Middle Devonian of the U.S.S.R. *Collectanea Acta Geologica Lithuania*, 293–305.

—— 1963. Genus *Asterolepis* from the Devonian of the Russian platform. In GRIGELIS, A. and KARATAJUTE-TALIMAA, V. (eds.), *The Data of the Geology of the Lithuania.* Geological and Geographical Institute of the Academy of Sciences of the Lithuanian SSR, Vilnius.

—— 1966. Bothriolepids of the Sventoji horizon of the east Baltic area. *Palaeontologiya Stratigrafiya Pribaltiki. belorussi*, **1,** 191–279.

LIU TUNG-SEN and P'AN KIANG 1958. Devonian fishes from the Wutung series near Nanking, China. *Palaeont. Sinica*, **141,** 1–41. (In Chinese and English.)

LIU YU-HAI 1963. On the Antiarchi from Chutsing. *Vertebr. Palasiat.* **7,** 39–46.

LONG, J. A. 1982. Late Devonian Fish Taphonomy in Victoria. *In* RICH, P. V. and THOMPSON, E. M. (eds.), *The Fossil Vertebrate Record of Australasia*, 120–127. Monash Press, Melbourne.

—— Devonian Fishes in Victoria. *Proc. R. Soc. Vict.* (in press).

MARSDEN, M. A. H. 1976. Upper Devonian Carboniferous. *In* DOUGLAS, J. G. and FERGUSON, J. A. (eds.), Geology of Victoria. *Geol. Soc. Aust. Spec. Pub.* **5,** 77–124.

MILES, R. S. 1968. The Old Red Sandstone Antiarchs of Scotland. Family Bothriolepididae. *Palaeontogr. Soc.* (*Monograph*), **122,** 1-130.

—— 1969. Features of placoderm diversification and the evolution of the arthrodire feeding mechanism. *Trans. Roy. Soc. Edinburgh*, **68,** 123-170.

—— and DENNIS, K. 1979. A primitive eubrachythoracid arthrodire from Gogo, Western Australia. *J. Linn. Soc.* (*Zool.*), **66,** 31-62.

—— and YOUNG, G. C. 1977. Placoderm interrelationships reconsidered in the light of new ptyctodontids from Gogo, Western Australia. *In* ANDREWS, S. M., MILES, R. S., WALKER, A. D. (eds.), *Problems in Vertebrate Evolution. Linn. Soc. Lond. Symposium Series*, **4,** 123-198. Academic Press, London and New York.

P'AN KIANG 1964. Some Devonian and Carboniferous fishes from South China. *Acta palaeontologica Sinica*, **12,** 139-183. (In Chinese and English.)

—— 1981. Devonian Antiarch biostratigraphy of China. *Geol. Mag.* **118,** 69-75.

RICHARDS, J. R. and SINGLETON, O. P. S. 1981. Palaeozoic Victoria, Australia: Igneous Rocks, Ages and their Interpretation. *J. geol. Soc. Aust.* **28,** 395-422.

STENSIÖ, E. A. 1931. Upper Devonian Vertebrates from East Greenland collected by the Danish Greenland Expeditions in 1929 and 1930. *Medd. om. Groenl.* **86,** 1-212.

—— 1948. On the Placodermi of the Upper Devonian of East Greenland. 2. Antiarchi: subfamily Bothriolepinae. With an attempt at a revision of the previously described species of that family. Ibid. 139 (*Palaeozoologica Groenlandica*, 2), 1-622.

—— 1969. Elasmobranchiomorphi Placodermata Arthrodires. *In* PIVETEAU, J. (ed.), *Traité de Paleontologie*, **4** (2), 71-692. Masson, Paris.

TALENT, J. A. 1975. *In* BOUCOT, A. J. (ed). *Evolution and Extinction Rate Controls*. Elsevier, Amsterdam.

TRAQUAIR, R. M. 1888. Notes on the nomenclature of the fishes of the Old Red Sandstone of Great Britain. *Geol. Mag.* (3), **5,** 507-517.

WARREN, J. W. and WAKEFIELD, N. A. 1972. Trackways of tetrapod vertebrates from the Upper Devonian of Victoria, Australia. *Nature*, **238,** 467-470.

WILLIAMS, I. S., TETLEY, N. W., COMPSTON, W. and MCDOUGALL, I. 1983. A Comparison of K-Ar and R6-Sr ages of rapidly cooled igneous rocks: two points in the Palaeozoic time scale re-evaluated (in the press).

WOODWARD, A. S. 1981. *Catalogue of the fossil fishes in the British Museum* (*Natural History*), **2,** London.

YOUNG, G. C. 1974. Stratigraphic occurrences of some Placoderm fishes in the Middle and Late Devonian. *Newslett. Strat.* **3,** 243-261.

—— 1979. New information on the structure and relationships of *Buchanosteus* (Placodermi, Euarthrodira) from the Early Devonian of New South Wales. *J. Linn. Soc.* (*Zool.*), **66,** 309-352.

—— 1981. Biogeography of Devonian Vertebrates. *Alcheringa*, **5,** 225-243.

—— and GORTER, J. D. 1981. A new fish fauna of Middle Devonian age from the Taemas/Wee Jasper region of New South Wales. *BMR Bull.* **209,** 83-147.

ZHANG GUORUI, 1978. The antiarchs from the Early Devonian of Yunnan. *Vertebr. Palasiat.* **16,** 147-186. (In Chinese with English summary.)

—— 1980. New Material of *Xichonolepis qujingensis* and discussion on some of its morphological characteristics. Ibid. **18,** 272-280. (In Chinese with English summary.)

ZHANG, MI-MAN 1980. Preliminary note on a Lower Devonian Antiarch from Yunnan, China. Ibid. **18,** 179-190.

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DISTRIBUTION MAPS OF RECENT DINOFLAGELLATE CYSTS IN BOTTOM SEDIMENTS FROM THE NORTH ATLANTIC OCEAN AND ADJACENT SEAS

by REX HARLAND

ABSTRACT. Distribution maps have been drawn for forty-two extant species of dinoflagellate cysts recovered from bottom sediments in the North Atlantic Ocean and adjacent seas. Data have been compiled from published and unpublished work for a total of one hundred and forty-two sample stations. The maps clearly show the influence of the North Atlantic circulation pattern, and areas of convergence, on the patterns of dinoflagellate cyst distribution. Areas of concentrations of cyst species are noted and discussed, as are the differing distribution patterns of several cysts that have at some time been referable to a single thecate species. The differences of distribution between neritic and oceanic cyst assemblages is clearly demarcated. Finally a tentative broad ecological classification of cyst types is attempted. *Impagidinium aculeatum* (Wall) and *I. sphaericum* (Wall) are proposed as new combinations.

THE analysis of dinoflagellate cysts in Quaternary and Recent sediments from the offshore region of the British Isles has been underway at the Institute of Geological Sciences (IGS) for several years. The work has concentrated upon the areas of the North Sea and offshore western Scotland and England, where the IGS has drilled several boreholes and taken many vibrocores that have yielded good sequences of marine Quaternary sediments. The overall intention was to eludicate the Quaternary history, as recorded in these marine sediments, and to relate the various biostratigraphical events to the commonly understood climatic patterns. Indeed over the past few years several such sequences have been analysed and a number of climatic events recognized. These events are usually characterized, in the dinoflagellate cyst record, by a series of 'favourable' and 'unfavourable' units, in terms of productivity and diversity, within sediments that would, under normal circumstances, be expected to yield consistently good dinoflagellate cyst assemblages. This work has been related to foraminiferal analyses of the same strata and some of the results are published (Harland 1973, 1974, 1977, 1978; Binns *et al.* 1974; Hughes *et al.* 1977; Gregory *et al.* 1978; Harland *et al.* 1978; Gregory and Harland 1978). The Quaternary climatic history as recorded in marine continental shelf sediments is beginning to emerge and work in this area is still underway.

It has, however, been somewhat worrying that the ability to interpret the Quaternary record has been hampered by a lack of knowledge concerning the distributions of modern dinoflagellate cysts in bottom sediments in the North Atlantic area, i.e. the dinoflagellate cyst thanatocoenosis. Indeed there is also a lack of knowledge of the synecology of living dinoflagellate cysts and their relationships to natural phytoplankton populations. Research by such workers as Anderson and Wall (1978), Dale (1976, 1977, 1978), and Reid (1975, 1977, 1978) has assisted in the understanding of the ecology of living cysts, and that of Dodge (1977), Dodge and Hart-Jones (1974, 1977), Holligan (1979, 1981), and Holligan *et al.* (1980), has been of value in understanding the ecology of phytoplankton populations particularly in British waters, but nevertheless much more data need collecting and analysis.

In the course of the work at IGS it became clear that one of the areas where more information was urgently required was the nature of the dinoflagellate cysts thanatocoenosis in the North Atlantic Ocean, and more particularly in the northern part of the North Atlantic. Although a number of

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works on dinoflagellate cyst distributions had been published there are no maps available showing the percentage distributions of the various dinoflagellate cyst species. Such maps are commonly published for other organisms, including planktonic and benthonic foraminiferans, diatoms, and radiolarians, for the North Atlantic region and other oceans of the world. This appeared to be a fact that could be rectified and one which had direct application to the interpretation of the Quaternary dinoflagellate cyst record, since it is clear that in the fossil record a thanatocoenosis is all the information available. This study and compilation is hopefully a step in linking the fossil record to the modern thanatocoenosis thence to the biocoenosis and finally to a full understanding of the ecology of dinoflagellates and their cysts.

HISTORY OF STUDY

The study of the modern dinoflagellate cyst thanatocoenosis in the North Atlantic began with the pioneering thesis of Williams (1965), the results of which were published in 1971. He used principal component analysis on data from thirty-five sites in the North Atlantic and recognized a number of 'facies' which could be related to such surface conditions as water mass configurations and current distributions. Also recognized was the fact that certain species appeared to be concentrated in particular areas. Graham and Bronikowsky (1944) had also noted a link between the distribution of the thecate dinoflagellate species and water mass configurations.

Reid (1972*a*) followed this work in a thesis which described the distribution of dinoflagellate cyst species in Recent intertidal sediments around the British Isles. Cluster analysis was used on some sixty-eight samples and again close relationships were seen between the dinoflagellate cyst thanatocoenosis and the various water masses around the British Isles. This work was subsequently published in a series of papers (Reid 1972*b*, 1974, 1975, 1977).

In 1976 Dale published on some of the primary factors that influence the composition of cyst assemblages in bottom sediments. His study compared the integrated phytoplankton records in the Trondheimsfjord area of Norway with the assemblages preserved in the sediments. These observations are discussed more fully later in relation to the results of the present study, as they indicate a number of constraints that must be understood and taken into account in the interpretation of this kind of data and research.

A little later Morzadec-Kerfourn (1977) recognized, in a series of offshore sediment samples from Brittany, an onshore–offshore differentiation. An oceanic realm characterized by such cysts as *Impagidinium aculeatum* (Wall) and *Spiniferites bulloideus* (Deflandre and Cookson), a coastal realm with *S. bentori* (Rossignol) and an estuarine realm with *Lingulodinium machaerophorum* (Deflandre and Cookson) were noted.

In the same year Reid and Harland attempted a summary of current knowledge on the distribution of dinoflagellate cysts in the North Atlantic. They concluded that the cyst thanatocoenosis is dependent upon a number of interrelated factors that include: (1) latitude—encompassing factors of solar radiation, temperature, and climate, so in essence giving rise to a series of latitudinal biogeographical zones; (2) water depth—as exemplified by the onshore–offshore differentiation; (3) water mass—including interaction of water masses, e.g. convergence, upwelling, bathymetry, current distribution, all at many differing scales of occurrence; and (4) sedimentary factors—selective concentration etc.

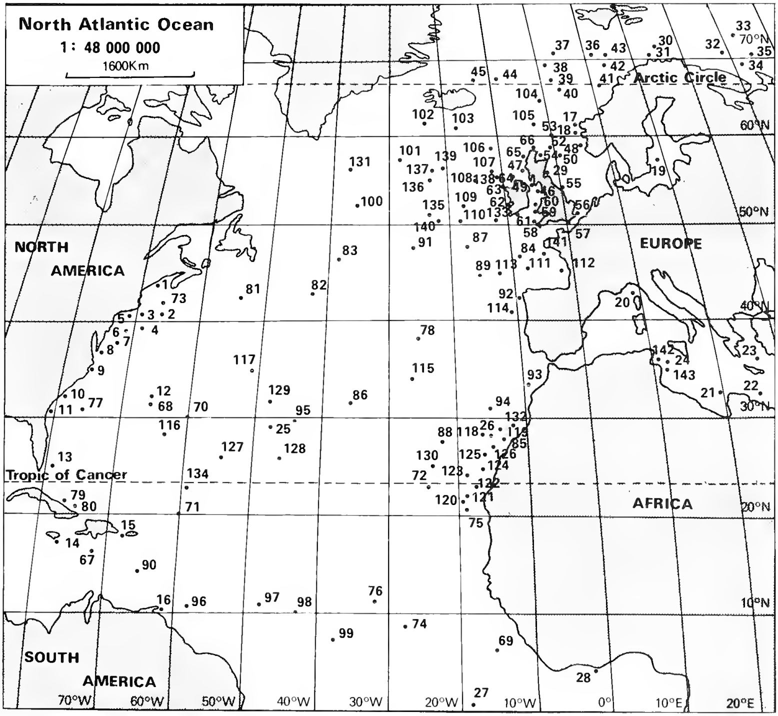
At much the same time Wall *et al.* (1977) published a major piece of work that analysed the cyst thanatocoenosis of one hundred and sixty-eight samples in the North and South Atlantic and Pacific Oceans. Using Q-mode factor analysis, cluster analysis, and a species diversity index they also recognized onshore to offshore and latitudinal variations in distributions involving both individual taxa, and associations of species. This largely confirmed the conclusions of Reid and Harland (1977) but Wall *et al.* (1977) also proposed an ecological classification for the extant cyst species and suggested that the genesis of such ecological species groups in nature can be interpreted by use of stability–predictability concepts where surface water masses are taken to be unique hydrographic niches with their own stability and predictability characteristics.

Most recently Turon (1980) has studied Recent dinoflagellate cysts in the north-east Atlantic and related their distributions to environmental factors such as temperature and the hydrographic structure of the water.

It is clear from this review that although the major factors appear to have been identified, the distribution of individual species is not documented nor has the thanatocoenosis been linked to the biocoenosis except perhaps, in part, by the work of Reid (1978) and Dale (in press).

MATERIALS AND METHODS

The present study has involved the compilation of data from the doctoral theses of D. B. Williams (1965) and P. C. Reid (1972*a*), with their permission and helpful assistance; from the published work of Wall *et al.* (1977), Morzadec-Kerfourn (1977, 1979), and Turon (1980), who have also been most helpful in supplying some of the original data; and the incorporation of some of my own records



TEXT-FIG. 1. North Atlantic Ocean at a 1 : 48 000 000 scale drawn on a modified cylindrical projection showing the approximate location of the one hundred and forty-two samples.

held at the Institute of Geological Sciences (IGS), Leeds. In addition the British Museum (Natural History) supplied many more samples to assist in filling some of the more obvious gaps. In total the assemblages from one hundred and forty-two samples have been utilized of which forty-nine are attributable directly to me. Appendix I lists the samples, their localities, authors responsible for the data, and the various registered catalogue numbers. Those registered in the IGS collections can be examined at the IGS, Leeds.

All the samples have undergone standard palynological preparation techniques although those processed at Leeds have not been given any oxidation, to avoid the loss of peridiniacean cysts (Dale 1976). In general therefore there is some bias toward the gonyaulacacean cysts, and no attempt has been made to isolate calcareous cysts. This is comparable to techniques employed in our studies on Quaternary sediments and hopefully makes the results compatible.

The data are expressed in terms of percentage, the common factor in all the data sets, and in most cases are based upon a count of over 100 specimens and in many cases over 250 specimens. The complete data set on which this study is based is held by the Palaeontology Unit, IGS, Leeds where it is open to inspection. Persons requiring copies of the data should contact the author.

The recorded dinoflagellate cyst species are illustrated in the plates and the palaeontological cyst species name and the biological thecate species names are given. Appendix II lists all the considered species and their thecate cyst relationships where known. Recent work on the *Protoperidinium* species has indicated a possible way of compromising the two schemes (Harland 1982), and this is used herein, but no similar scheme exists for gonyaulacacean cysts as yet.

The base map used to plot the cyst distributions is on the 1:48000000 scale and is a modified cylindrical projection, so some distortion particularly towards the North Pole is apparent. The base map showing all the sample stations sequentially numbered is illustrated in text-fig. 1 so that this together with Appendix I will show sample positions and the author responsible for the original counts. Text-fig. 2 shows the main geographical areas mentioned in the text.

CYST SPECIES DISTRIBUTIONS

The forty-two cyst species of this study have had maps drawn of their individual distributions. Contours were drawn on the following intervals: up to and including 10%; > 10 to 50%; greater than 50%. The distributions reflect, of course, the scope of the sampling and no doubt additional samples will modify the maps presented here. The number at the beginning of each entry refers to the reference number in Appendix II.

EXPLANATION OF PLATE 43

All photomicrographs were taken by Nomarski interference contrast and are illustrated at a magnification of × 500.

Figs. 1, 2. *Achomosphaera andalousiense* Jan du Chêne, Specimen MPK 1213. 1, dorsal view showing the P archeopyle. 2, ventral view showing morphology of the distal tips of the processes.

Figs. 3, 4. *Bitectatodinium tepikiense* Wilson, Specimen MPK 2959. 3, dorsal view showing the 2 P archeopyle. 4, ventral view showing nature of the cyst surface.

Figs. 5, 6. *Lingulodinium machaerophorum* (Deflandre and Cookson) Wall, Specimen MPK 1225. 5, ventral view showing the morphology of the processes. 6, dorsal view showing some archeopyle sutures.

Figs. 7, 8. *Nematosphaeropsis labyrinthea* (Ostenfeld) Reid, Specimen MPK 2963. 7, ?oblique dorsal view showing the nature of the trabeculae. 8, ?oblique ventral view.

Figs. 9, 10. *Operculodinium centrocarpum* (Deflandre and Cookson) Wall, Specimen MPK 2962. 9, dorsal view showing P archeopyle. 10, ventral view showing the process morphology.

Figs. 11, 12. *O. israelianum* (Rossignol) Wall, Specimen MPK 3117. 11, dorsal view showing a broad P archeopyle. 12, ventral view showing the operculum and process morphology.

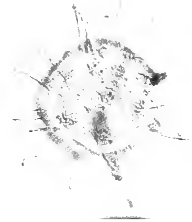
PLATE 43


1


2


3


4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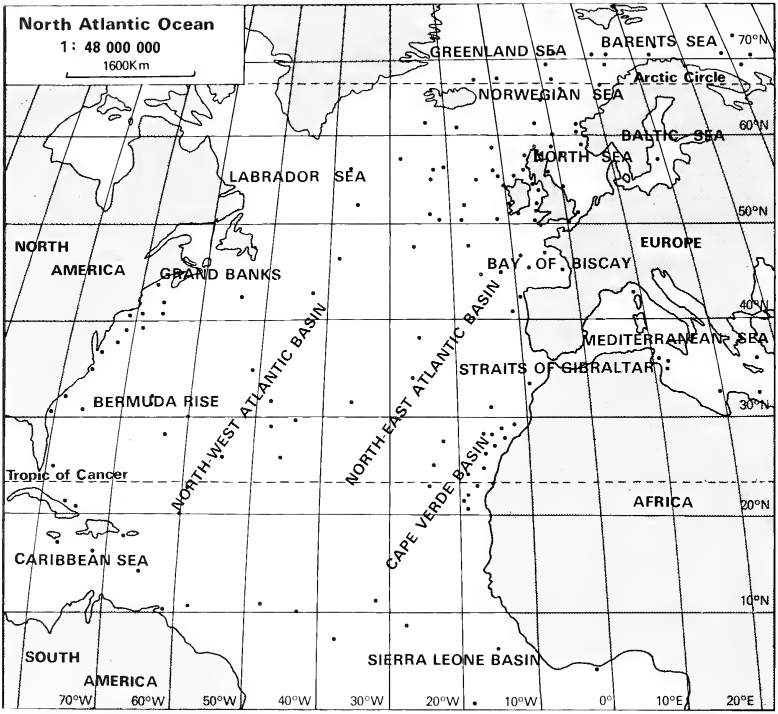
12

HARLAND, Recent dinoflagellates



TEXT-FIG. 2. North Atlantic Ocean showing major geographical features.

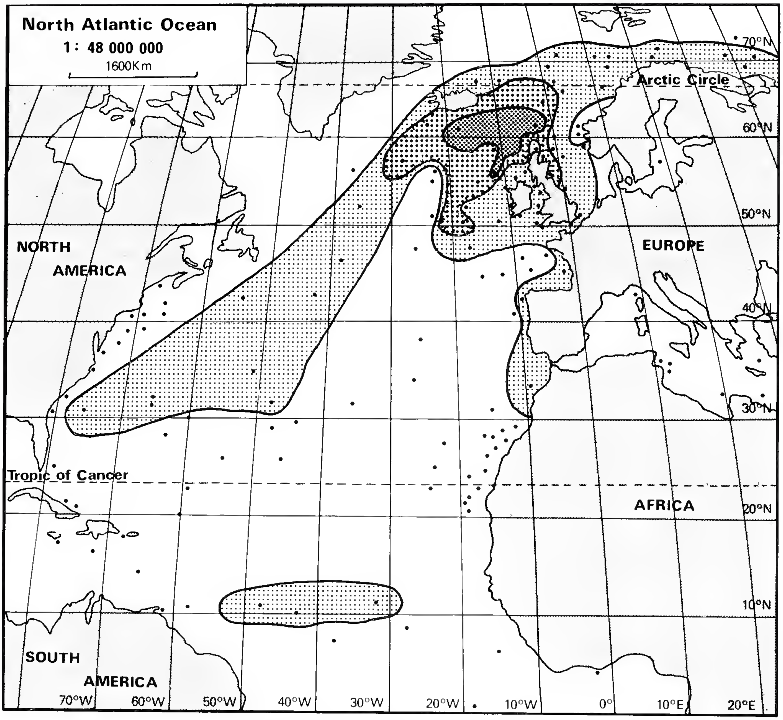
Gonyaulacacean Cysts

1 *Achomosphaera andalousiense* Jan du Chêne 1977

Plate 43, figs. 1, 2

Taxonomic Comments. This cyst, attributable to *Gonyaulax* sp. indet., was first described from the Miocene by Jan du Chêne (1977). It was also described by Harland (1977) as *Spiniferites septentrionalis* sp. nov., a junior synonym. The attribution to *Achomosphaera* Evitt is arbitrary, based upon the lack of parasutures, and in my opinion is artificial serving little useful purpose.

Distribution. In one sample, 133, off the south-west coast of Ireland. It is possibly a reworked occurrence as its restricted distribution and its abundance in older Quaternary sediments would suggest. In Quaternary sequences it may indicate a pre-Flandrian or even possibly a pre-Ipswichian age, but further study is required.



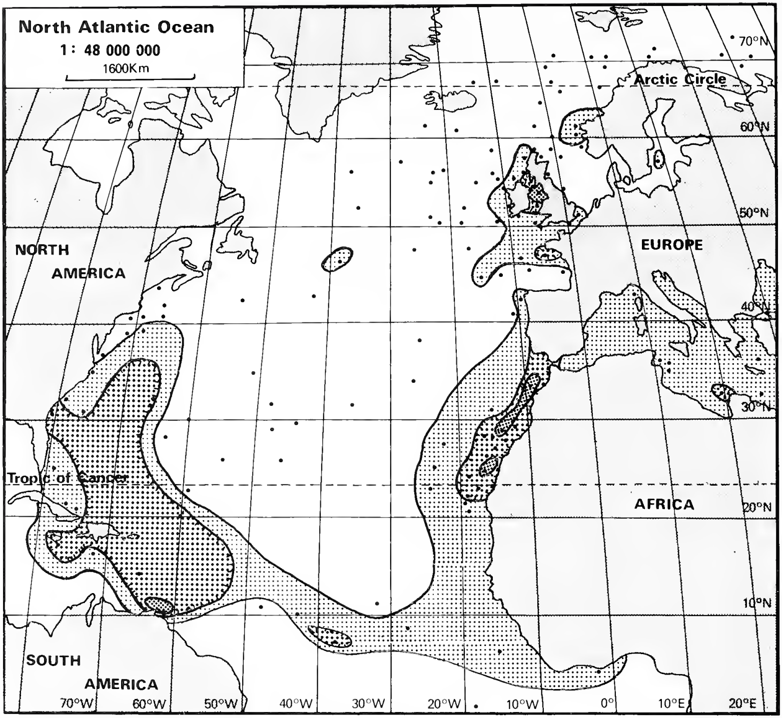
TEXT-FIG. 3. Distribution of *Bitectatodinium tepikiense* Wilson. Light stipple indicates up to and including 10% occurrence, medium stipple > 10% to 50% occurrence and coarse stipple greater than 50% occurrence.

2 *Bitectatodinium tepikiense* Wilson 1973

Text-fig. 3; Plate 43, figs. 3, 4

Taxonomic Comments. A well-known form and one of the many cyst types attributable to *Gonyaulax spinifera* (Claparède and Lachmann) Diesing. It is very similar to the cyst species *Tectatodinium pellitum* Wall but is distinguished by the possession of a 2P archeopyle.

Distribution. A north-temperate to arctic distribution across the North Atlantic with an area of concentration between Iceland and Scotland. It also occurs to the west of the Iberian Peninsula and toward the equator along latitude 10° N. between 50° and 30° W. Wall *et al.* (1977) recorded this species from an estuarine environment which led them to classify it with that environment. *B. tepikiense* is a common component in Quaternary sequences about the area of the British Isles. Its distribution appears to be particularly associated with the North Atlantic Current and the Iceland–Faeroes–Scotland ridge. The disparate occurrence off South America may indicate the presence of a separate taxonomic entity.



TEXT-FIG. 4. Distribution of *Lingulodinium machaerophorum* (Deflandre and Cookson) Wall. Ornament as before.

3 *Lingulodinium machaerophorum* (Deflandre and Cookson) Wall 1967

Text-fig. 4; Plate 43, figs. 5, 6

Taxonomic Comments. This, the well-known cyst of *Gonyaulax polyedra* Stein, is a variable form especially in relation to archeopyle development and the ratio of the length of processes to the cyst diameter (Harland 1977).

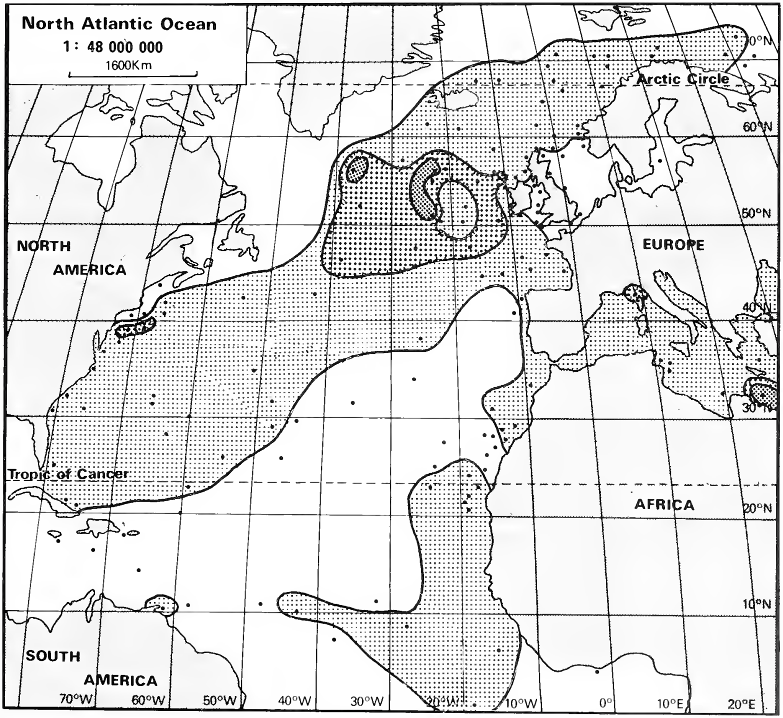
Distribution. This cyst appears to have a distribution in the southern part of the North Atlantic, Caribbean, off the west coast of Africa, Mediterranean, and off the west coast of the British Isles. Areas of concentration include the Caribbean, off the north-west African coast, and in the Irish Sea. It appears to be associated with the South Equatorial Current. It is often associated with estuarine low-salinity environments (Wall *et al.* 1977) as portrayed here in the Irish Sea but it also seems associated with highly saline waters, e.g. off the west coast of Africa. The species may be, therefore, tolerant of marine salinities both less and greater than normal. Williams (1971) had already pointed out the facies associated with the Straits of Gibralter and north-west Africa. Wall *et al.* (1977) also note that the possession of differences in archeopyle morphology are not evenly distributed such that there may be some ecophenotypic variations. *L. machaerophorum* occurs rarely in offshore Quaternary sediments except in the Irish Sea where it appears to have been established sometime in the middle Flandrian.

4 *Nematosphaeropsis labyrinthea* (Ostenfeld) Reid 1974

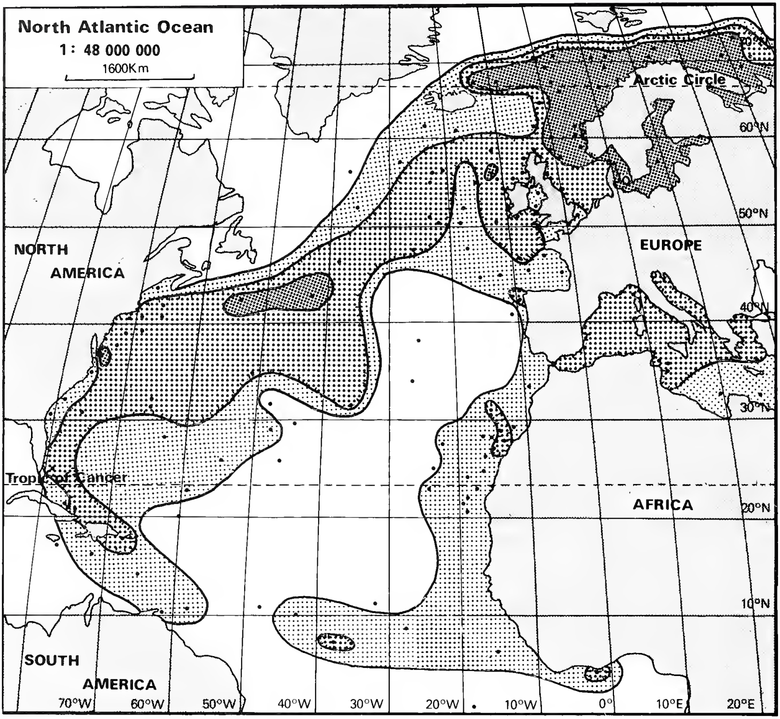
Text-fig. 5; Plate 43, figs. 7, 8

Taxonomic Comments. This cyst, another of *Gonyaulax spinifera* (Claparède and Lachmann) Diesing, is well known but unfortunately usually appears somewhat distorted making any detailed examination difficult. The specimen in Plate 43, fig. 7 clearly shows some double trabeculae but often even these are difficult to observe and therefore may indicate an assignment to the genus *Cannosphaeropsis* O. Wetzel.

Distribution. Widespread in the North Atlantic especially associated with the North Atlantic Current but also in the Mediterranean and off parts of the west coast of Africa. Areas of concentration include the eastern Mediterranean and off the west coast of Ireland at about the region where the North Atlantic Current and East Atlantic gyre separate. This cyst is more rarely seen in offshore British Quaternary sequences.



TEXT-FIG. 5. Distribution of *Nematosphaeropsis labyrinthea* (Ostenfeld) Reid. Ornament as before.



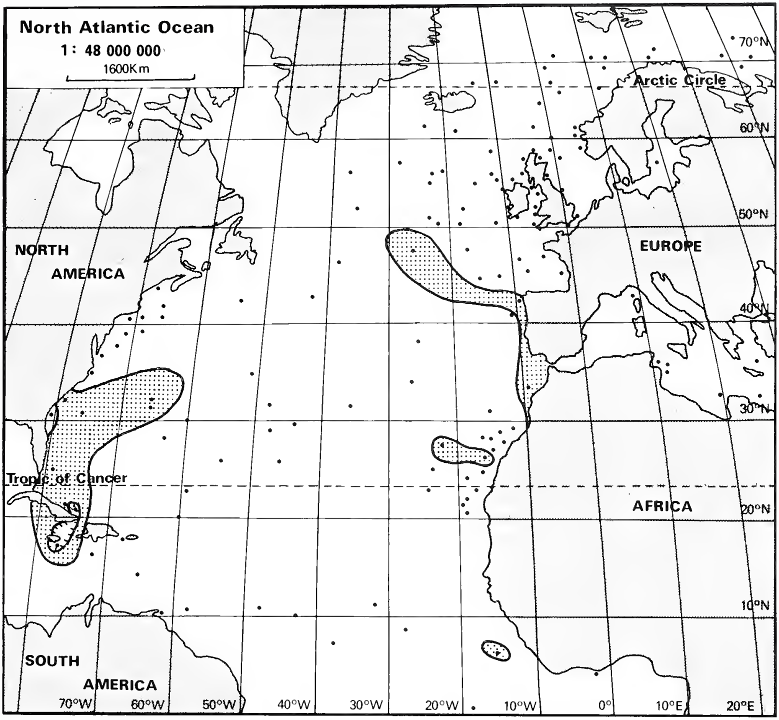
TEXT-FIG. 6. Distribution of *Operculodinium centrocarpum* (Deflandre and Cookson) Wall. Ornament as before.

5 *Operculodinium centrocarpum* (Deflandre and Cookson) Wall 1967

Text-fig. 6; Plate 43, figs. 9, 10

Taxonomic Comments. This, the cyst of *Gonyaulax grindleyi* (Reinecke) Von Stosch, has been described and seen many times (Harland 1977).

Distribution. A widespread North Atlantic cyst from the Caribbean in the south-west to the Barents Sea in the north-east, including the Mediterranean and off the west coast of Africa. Particular areas of concentration occur off Newfoundland and in the Norwegian and Barents Seas. It appears to be associated with the North Atlantic Current but does not occur in the central-eastern side of the ocean. *O. centrocarpum* can certainly be regarded as an ubiquitous cyst but also possibly as somewhat of a pioneer species in north-temperate to arctic environments where the assemblages are almost monospecific. It is a cyst form that is extremely common in British offshore Quaternary sediments. The distribution presented here agrees well with that given by Wall *et al.* (1977) especially in terms of its disposition in the outer neritic region.



TEXT-FIG. 7. Distribution of *Operculodinium israelianum* (Rossignol) Wall. Ornament as before.

6 *Operculodinium israelianum* (Rossignol) Wall 1967

Text-fig. 7; Plate 43, figs. 11, 12

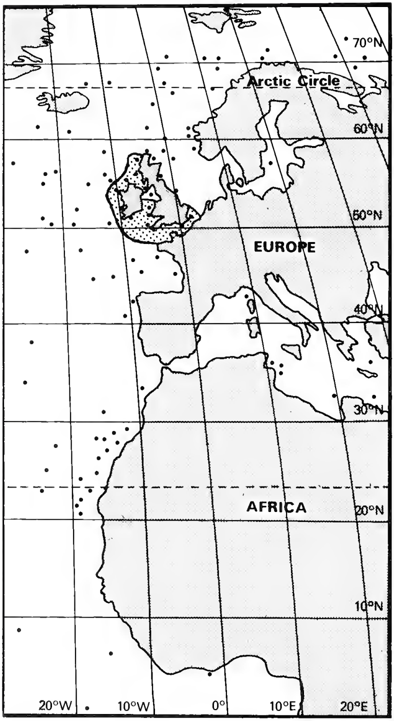
Taxonomic Comments. This cyst may also be produced by *G. grindleyi* (Reinecke) Von Stosch but to my knowledge no incubation studies have been carried out to establish a relationship with any thecate species. It differs from *O. centrocarpum* in size, being larger, and in having a much broader P archaeopyle and shorter, squat processes.

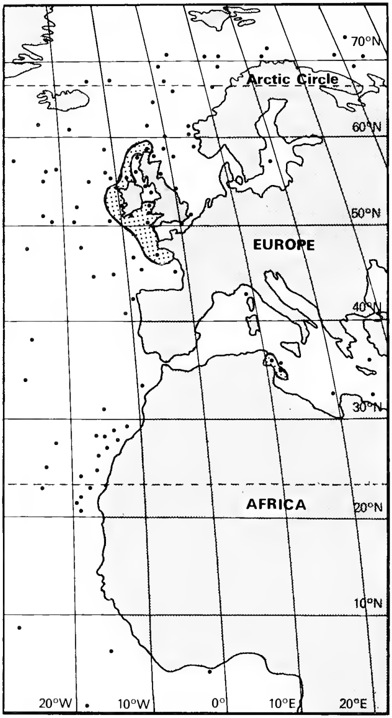
Distribution. O. israelianum has a much more restricted distribution than *O. centrocarpum* being confined to the Caribbean, off the Iberian Peninsular and off the west coast of Africa. Its major centre of concentration appears to be the Caribbean. This species is of particular interest in that the early Pleistocene marine sediments of the British Isles contain *O. israelianum* in abundance at a time when the environmental evidence was suggestive of a 'glacial' climate (Wall and Dale 1968*a*). This is in marked contrast to what is known of its present distribution and further study is needed to explain the discrepancy.

7 *Spiniferites belerius* Reid 1974

Text-fig. 8; Plate 44, figs. 1, 2

Taxonomic Comments. This may be the cyst of *Gonyaulax scrippsae* Kofoid but it has not been incubated, to my knowledge, so that the suggestion of a relationship to a thecate form is probably premature. It is a form not easily recognized in Recent sediments as it is particularly small and may, more often than not, be included in the category *Spiniferites* sp. indet. herein.





TEXT-FIG. 8 (*left*). Distribution of *Spiniferites belerius* Reid. Ornament as before.

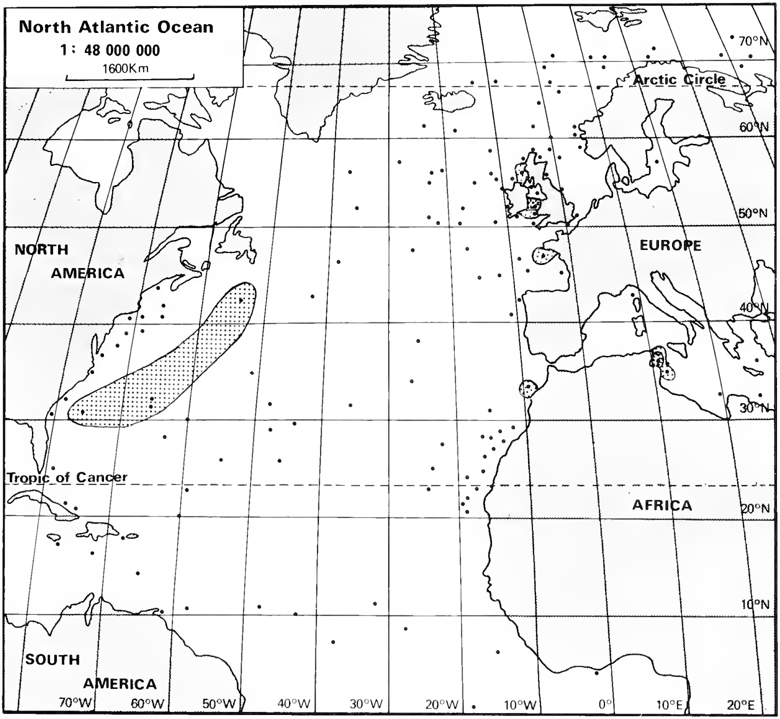
TEXT-FIG. 9 (*right*). Distribution of *Spiniferites delicatus* Reid. Ornament as before.

Distribution. Restricted distribution around the western side of the British Isles excluding the Irish Sea. It is not a species that has been recognized elsewhere, but it does occur in Quaternary sequences although its identification can be difficult. Its restricted distribution pattern may be largely as a result of these identification difficulties.

8 *Spiniferites bentori* (Rossignol) Wall and Dale 1970

Text-fig. 10; Plate 44, figs. 3, 4

Taxonomic Comments. This cyst of *Gonyaulax digitalis* (Pouchet) Kofoid is fairly distinctive, but is a species of some intraspecific variability especially in relation to the length of the processes, and includes a form sometimes referred to as *Spiniferites nodosus* Wall.



TEXT-FIG. 10. Distribution of *Spiniferites bentori* (Rossignol) Wall and Dale. Ornament as before.

Distribution. Restricted to the offshore area of the eastern seaboard of the United States, the western side of the British Isles, plus one or two isolated occurrences. Wall *et al.* (1977) recognized two morphotypes within this species which probably account for the disparate distribution between the United States and European occurrences. Reid (1972*b*) regarded *S. bentori* as being prominent in enclosed bays with rather localized temperature and salinity conditions. It has been seen as an early component in sediments associated with the Flandrian marine transgression in the Irish Sea area (Pantin 1978).

9 *Spiniferites delicatus* Reid 1974

Text-fig. 9; Plate 44, figs. 5, 6

Taxonomic Comments. This the cyst of a *Gonyaulax* sp. indet. is fairly readily distinguished by its process morphology, petaloid distal tips, and high granular membranous parasutural membranes. It is not a cyst that is commonly recognized.

Distribution. Restricted to the western side of the British Isles, but its distribution may reflect a failure to identify it. It was first identified in British intertidal sediments and described by Reid (1974). It has only rarely been seen in offshore marine Quaternary sequences.

10 *Spiniferites elongatus* Reid 1974

Text-fig. 11; Plate 44, figs. 7–10

Taxonomic Comments. This cyst species is attributable to *Gonvaulax spinifera* (Claparède and Lachmann) Diesing. There is, however, some evidence to suggest that the *Spiniferites* cysts may not all belong to *G. spinifera sensu stricto* but to another related type. It was first recognized as a distinct morphotype by Wall and Dale (1968*b*) and by Harland and Downie (1969). *S. elongatus* in the present study also includes those forms named *S. frigidus* in Harland *et al.* (1980) (Plate 44, figs. 9, 10) and a description of the variation within these species in north-temperate and arctic waters is in preparation by Harland and Sharp. The importance of elongate *Spiniferites* species in northern waters has already been noted (Harland 1982*b*).

Distribution. A somewhat restricted distribution, confined to the north-eastern seaboards of the United States and around the British Isles and Norwegian and Barents Sea. Some isolated occurrences in the Mediterranean and off the west coast of Africa. Areas of concentration occur in the western Atlantic and in the Norwegian and Barents Sea, the latter mostly formed by the *S. frigidus* morphotype.

This cyst is often found in offshore marine Quaternary sediments albeit in small percentages. Its distribution suggests that it may be quite useful in recognizing colder north-temperate to arctic environments, but it does not appear to be an estuarine type (Wall *et al.* 1977) as has been suggested, on the present evidence.

EXPLANATION OF PLATE 44

All photomicrographs were taken with Nomarski interference contrast, unless otherwise stated, and are illustrated at a magnification of × 500.

Figs. 1, 2. *Spiniferites belerius* Reid, photomicrographs kindly supplied by P. C. Reid. 1, dorsal view showing the archeopyle. 2, median view showing somewhat atypically developed antapical membrane. Photographed in plain light.

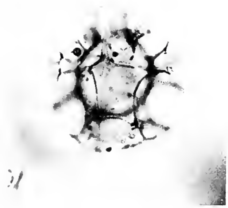
Figs. 3, 4. *S. bentori* (Rossignol) Wall and Dale, Specimen MPK 1216. 3, median view showing apical horn and nature of the processes. 4, ventral view showing well-developed narrow, rectangular 1''' paraplate.

Figs. 5, 6. *S. delicatus* Reid, Specimen MPK 1222. 5, oblique dorsal view showing the archeopyle. 6, high dorsal view showing the distinctive nature of the process tips.

Figs. 7, and 8. *S. elongatus* Reid, Specimen MPK 2579. 7, oblique dorsal view showing the archeopyle. 8, ventral view showing the sulcus and sulcal paratabulation.

Figs. 9, 10. *S. frigidus* Harland and Reid, Specimen MPK 2424. 9, dorsal view showing the archeopyle. 10, ventral view showing the 1' and 4' apical paraplates. This species is included in the *S. elongatus* counts as it is regarded as a part of the variation for the species.

Figs. 11, 12. *S. lazus* Reid, Specimen MPK 1204. 11, oblique dorsal view showing the archeopyle. 12, oblique ventral view.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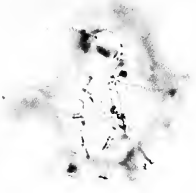
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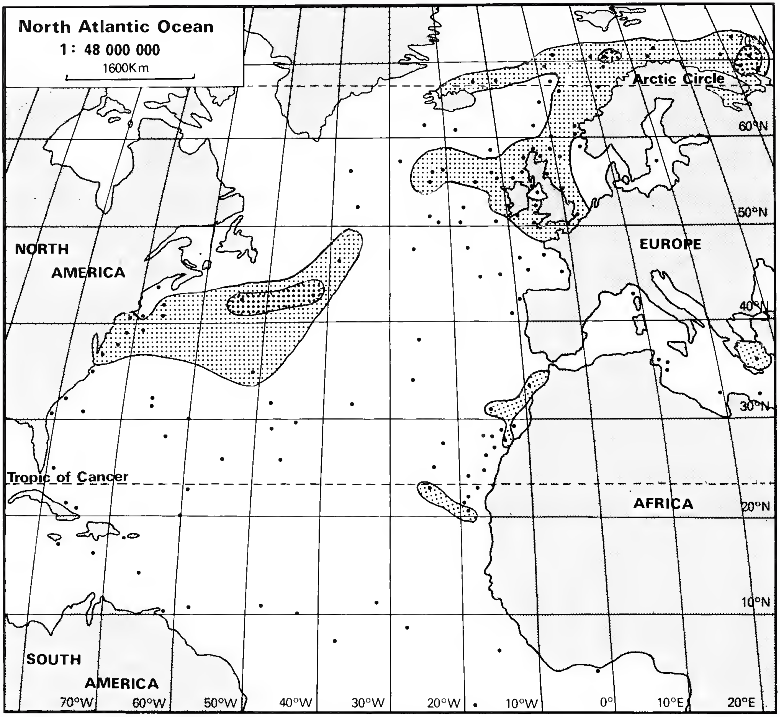
HARLAND, Recent dinoflagellates



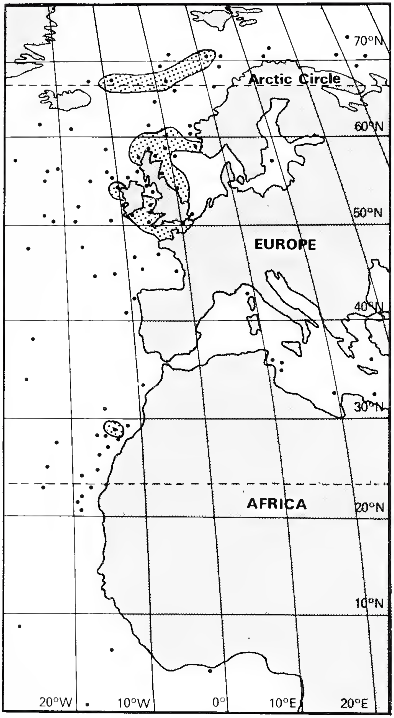
TEXT-FIG. 11. Distribution of *Spiniferites elongatus* Reid. Ornament as before.

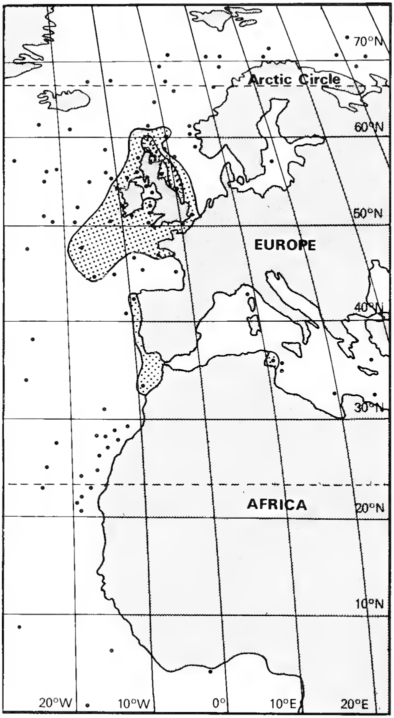
11 *Spiniferites lazus* Reid 1974

Text-fig. 12; Plate 44, figs. 11, 12

Taxonomic Comments. A well-known cyst in sediments around the United Kingdom, it is attributable to *Gonyaulax* sp. indet. as no incubation experiments have been carried out to relate it to a thecate species. This cyst is morphologically characterized by the perforate 'lace-like' periphragm at the bases of the processes, and its rather asymmetrical appearance.

Distribution. Restricted to offshore British Isles, the Norwegian Sea, and an isolated occurrence off the north-west coast of Africa. In no case was it recorded in percentages above 10%. This cyst is interesting, however, in that in some Quaternary sequences it has been recorded up to 50% of the assemblage. It appears, in general, to be a north-temperate cyst species and of possible particular environmental significance.





TEXT-FIG. 12 (*left*). Distribution of *Spiniferites lazus* Reid. Ornament as before.

TEXT-FIG. 13 (*right*). Distribution of *Spiniferites membranaceus* (Rossignol) Sarjeant. Ornament as before.

12 *Spiniferites membranaceus* (Rossignol) Sargeant 1970

Text-fig. 13; Plate 45, figs. 3, 4

Taxonomic Comments. Another well-known cyst type of *Gonyaulax spinifera* (Claparède and Lachmann) Diesing. It is characterized by membranous processes particularly at the antapical and paracingulum regions. Wall *et al*. (1977) drew attention to their belief that the *S. membranaceus* as described by Reid (1974) and herein is not conspecific with that of Rossignol (1964). This probably explains the rather restricted distribution recorded here, in temperate waters, and the isolated occurrences in more tropical waters (samples 67 and 117 not shown on the map) may in fact be the other morphotype. *S. membranaceus sensu* Reid is the only form known to the author. It is also a very variable cyst species.

Distribution. Restricted to areas around the British Isles, into the eastern Atlantic, and off the Iberian peninsula. Isolated occurrences were also recorded in the Caribbean, western Atlantic, and Mediterranean. A centre of concentration is noted off the north-eastern coast of England. This species is occasionally seen in offshore marine Quaternary sequences. Further work is obviously needed to clearly separate the two morphotypes, as it probably has potential in recognizing particular enviroments.

13 *Spiniferites mirabilis* (Rossignol) Sargeant 1970

Text-fig. 14; Plate 45, figs. 1, 2

Taxonomic Comments. Another cyst of *G. spinifera* (Claparède and Lachmann) Diesing, *S. mirabilis* is characterized by its large size and distinctive antapical membrane. It is occasionally confused with *S. membranaceus*.

Distribution. A widespread distribution in the western Atlantic off the eastern seaboard of the United States and into the Caribbean, in the eastern Atlantic off the British Isles, Iberia and the north-west coast of Africa, the Norwegian Sea, and Mediterranean. It has an area of concentration off the Iberian peninsula apparently associated with the eastern Atlantic gyre. It is a cyst seen occasionally in Quaternary sequences around the British Isles but more commonly in Quaternary sediments in the Bay of Biscay area.

14 *Spiniferites ramosus* (Ehrenberg) Mantell 1854

Text-fig. 15; Plate 45, figs. 5, 6

Taxonomic Comments. This is the cyst of *Gonyaulax scrippsae* Kofoid which in some publications is referred to as *S. bulloideus* (Deflandre and Cookson) Sarjeant 1970. This taxonomic problem is discussed by Harland (1977) and the separation of this cyst from *S. ramosus sensu* Wall 1965 explained. It is a cyst characterized by a typical *Spiniferites* morphology with simple processes without membranes etc. and no particular outstanding feature.

Distribution. Fairly widespread but not in the central North Atlantic. *S. ramosus* occurs down the eastern seaboard of the United States, in the Caribbean, Mediterranean, around the British Isles, in the Baltic and Norwegian Sea. Areas of concentration occur off the United States, Caribbean, and in the Mediterranean. There are some isolated occurrences off north-east South America and north-west Africa. In general it appears to be a more neritic cyst type. It is fairly common in marine Quaternary sequences.

EXPLANATION OF PLATE 45

All photomicrographs were taken using Nomarski interference contrast, unless otherwise stated, and are illustrated at a magnification of × 500.

Figs. 1, 2. *Spiniferites mirabilis* (Rossignol) Sarjeant, Specimen MPK 1626. 1, dorsal view showing the archeopyle. 2, median view showing the large antapical membrane.

Figs. 3, 4. *S. membranaceus* (Rossignol) Sarjeant, Specimen MPK 1208. 3, dorsal view showing the archeopyle. 4, median view showing the nature of the antapical membrane.

Figs. 5, 6. *S. ramosus* (Ehrenberg) Loeblich and Loeblich, Specimen MPK 1205. 5, dorsal view showing the archeopyle. 6, ventral view. Photographed in plain light.

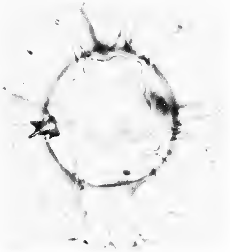
Fig. 7. *S. scabratus* Wall. Photograph kindly supplied by D. Wall, oblique dorsal view. Photographed in plain light.

Fig. 8. *S. ramosus sensu* Wall. Photograph kindly supplied by D. Wall, median view showing the nature of the processes. Photographed in plain light.

Fig. 9. *Tectatodinium pellitum* Wall, Specimen MPK 1628, oblique dorsal view showing the archeopyle.

Fig. 10. *Polysphaeridium zoharyi* (Rossignol) Bujak *et al.* Photograph kindly supplied by D. Wall, polar view. Photographed in plain light.

Fig. 11. *Tuberculodinium vancampoae* (Rossignol) Wall. Photograph kindly supplied by D. Wall, antapical view showing the archeopyle. Photographed in plain light.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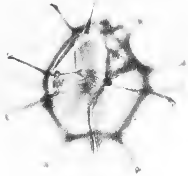
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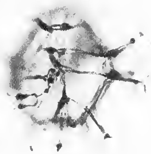
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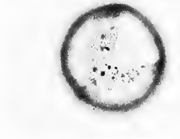
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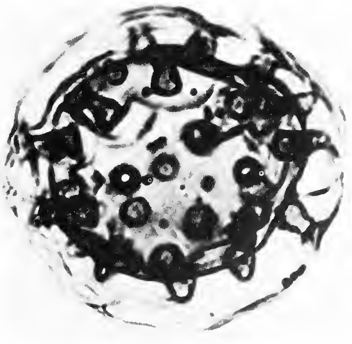
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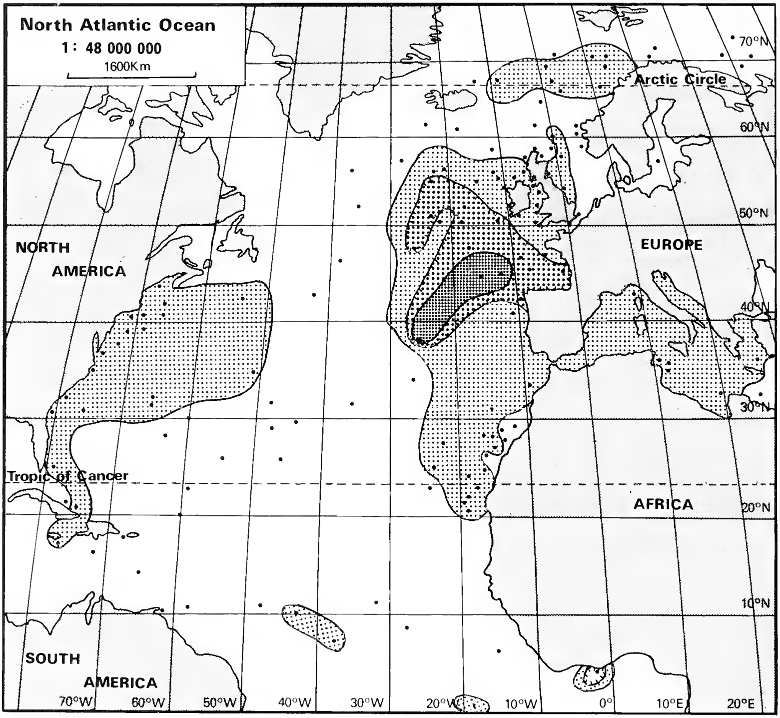
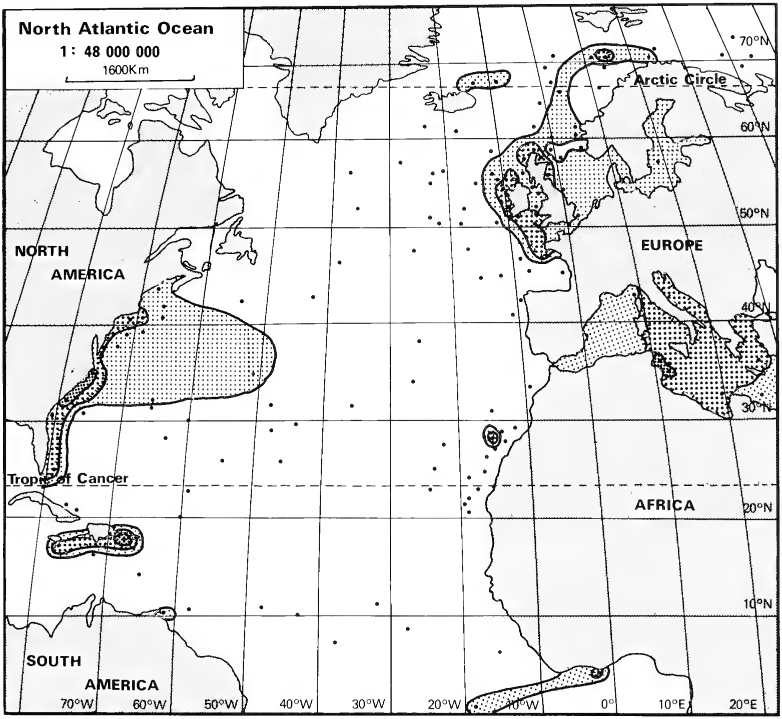
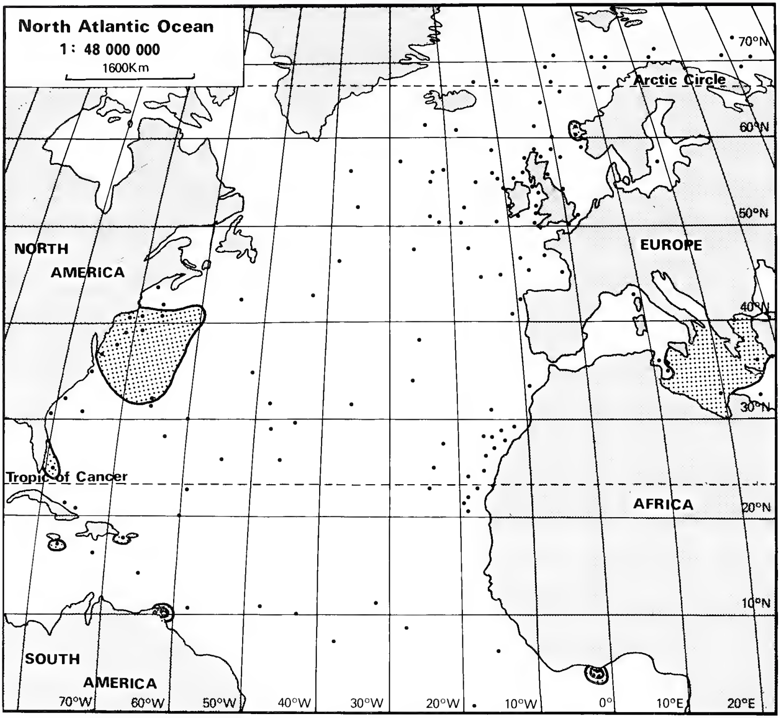
HARLAND, Recent dinoflagellates



TEXT-FIG. 14. Distribution of *Spiniferites mirabilis* (Rossignol) Sarjeant. Ornament as before.



TEXT-FIG. 15. Distribution of *Spiniferites ramosus* (Ehrenberg) Mantell. Ornament as before.



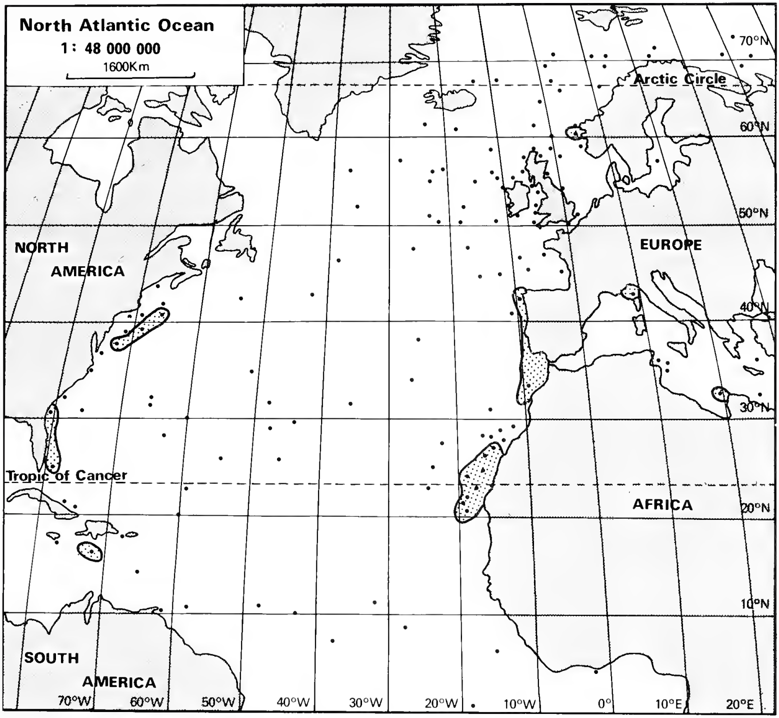
TEXT-FIG. 16. Distribution of *Spiniferites ramosus sensu* Wall. Ornament as before.

15 *Spiniferites ramosus sensu* Wall 1965

Text-fig. 16; Plate 45, fig. 8

Taxonomic Comments. This cyst of *Gonyaulax spinifera* (Claparède and Lachmann) Diesing has been confused with *S. ramosus* and *S. bulloideus*; see Harland (1977) for discussion.

Distribution. Restricted occurrences off the eastern seaboard of the United States and in the Mediterranean. Isolated occurrences are observed in the Caribbean, off Africa and off Norway. The latter may be a misidentification given the taxonomic uncertainty of the species, but certainly it has not been seen around the coasts of the British Isles, nor has it been seen in Quaternary sequences in marine offshore deposits near the United Kingdom.



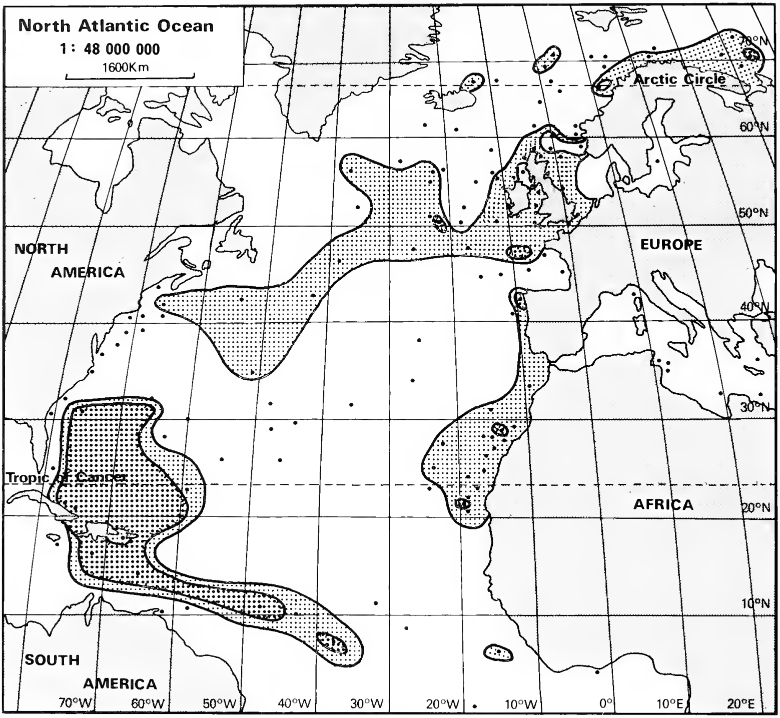
TEXT-FIG. 17. Distribution of *Spiniferites scabratus* Wall. Ornament as before.

16 *Spiniferites scabratus* Wall 1967

Text-fig. 17; Plate 45, fig. 7

Taxonomic Comments. S. scabratus is the cyst of an unknown *Gonyaulax* sp. and was first described by Wall (1967). It has, however, not been seen by me in my studies around the British Isles.

Distribution. Restricted occurrences off the eastern seaboard of the United States, Caribbean, Iberian peninsula, north-west Africa, and some isolated occurrences in the Mediterranean and Norway. The map certainly is suggestive that the cyst prefers neritic tropical to sub-tropical environments; its record off Norway is probably a misidentification or possibly a case of reworking. It has not been seen by me in offshore marine Quaternary sequences.



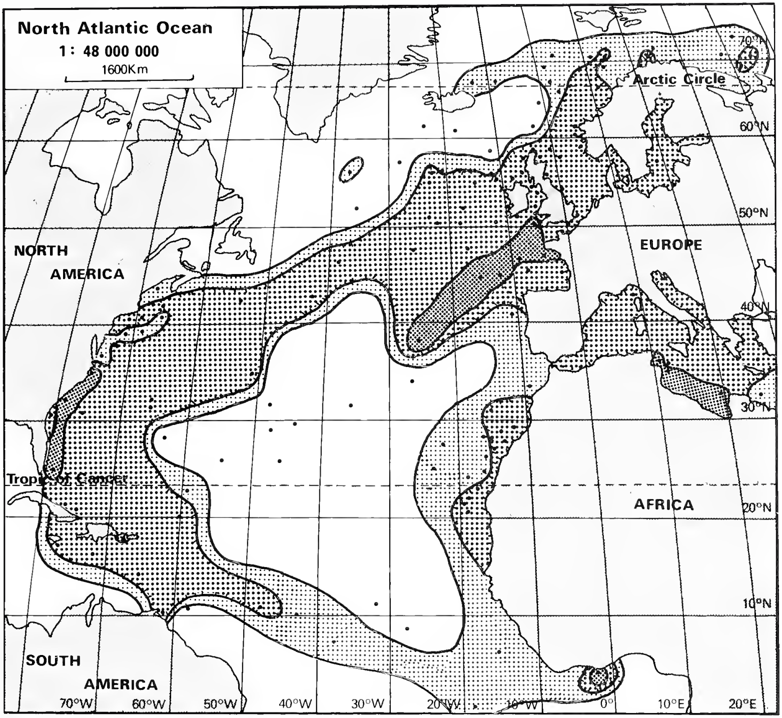
TEXT-FIG. 18. Distribution of *Spiniferites* spp. indet. Ornament as before.

17 *Spiniferites* spp. indet.

Text-fig. 18

Taxonomic Comments. This category combines all the records of *Spiniferites* cysts that have not been positively identified. Many may be badly orientated or broken whereas others may be new species not yet studied in detail.

Distribution. North Atlantic from the New England coast to the British Isles and into the Barents Sea, the Caribbean, and off the north-west coast of Africa. A major concentration in the Caribbean area is evident but further comment is not justified because of the nature of the record.

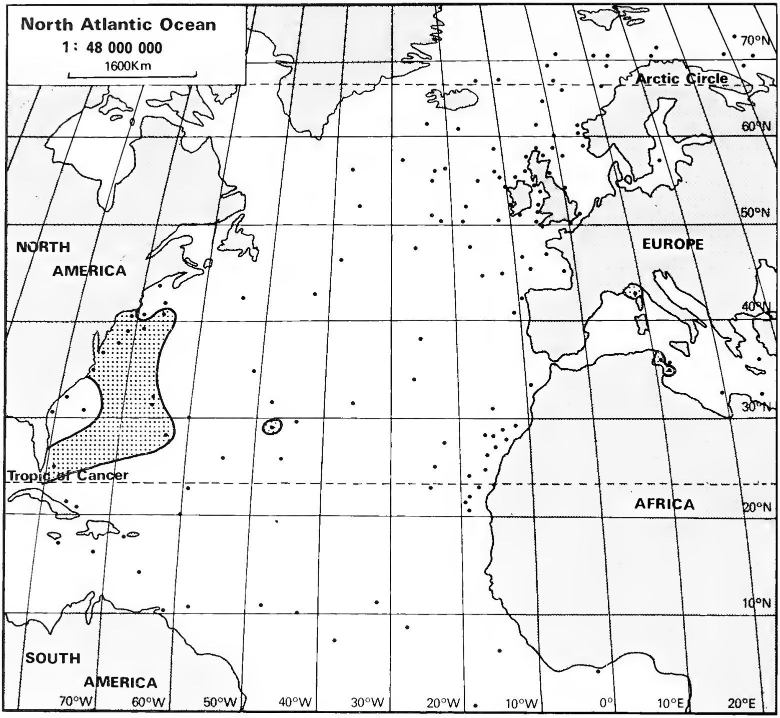


TEXT-FIG. 19. Distribution of total *Spiniferites* species. Ornament as before.

18 Total *Spiniferites* spp.

Text-fig. 19

General Comments. A widespread distribution with centres off the eastern seaboard of the United States, the eastern Atlantic, off the Iberian peninsular, the southern Mediterranean, and off the west coast of Africa. The pattern reflects the North Atlantic circulation pattern with the central Atlantic devoid of *Spiniferites* cysts. This may be accounted for in terms of distribution by current systems of a group of cysts that basically enjoy a neritic environment.



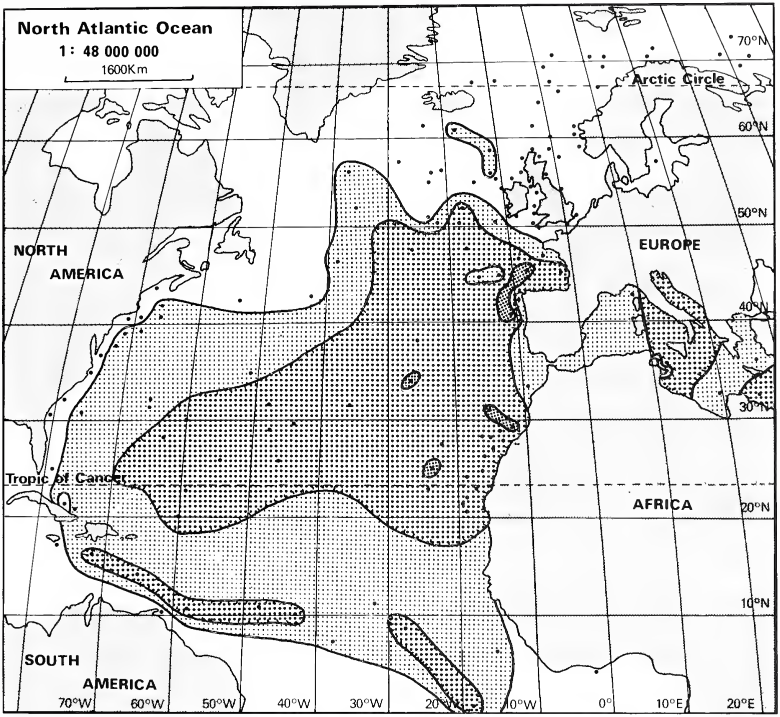
TEXT-FIG. 20. Distribution of *Tectatodinium pellitum* Wall. Ornament as before.

19 *Tectatodinium pellitum* Wall 1967

Text-fig. 20; Plate 45, fig. 9

Taxonomic Comments. T. pellitum is the cyst of an unidentified *Gonyaulax* species and is easily confused with *Bitectatodinium tepikiense* Wilson. It is distinguished by possession of a single paraplate precingular archeopyle. The distribution maps of *B. tepikiense* and *T. pellitum* are quite different.

Distribution. This cyst is known only from the south-eastern seaboard of the United States and from isolated occurrences in the Mediterranean. It is obviously a neritic cyst but is of especial interest in that it, like *Operculodinium israelianum* (Rossignol), makes up large percentages of early Pleistocene dinoflagellate cyst assemblages from southern England. This kind of occurrence in Pleistocene sequences is in marked contrast to its occurrence in Recent sediments and needs explanation, especially in relation to the 'cold' environment of the early Pleistocene in contrast to its present south-temperate to sub-tropical distribution.



TEXT-FIG. 21. Distribution of *Impagidinium aculeatum* (Wall) comb. nov. Ornament as before.

20 *Impagidinium aculeatum* (Wall) comb. nov.

Text-fig. 21; Plate 46, figs. 1–3

Taxonomic Comments. Stover and Evitt (1978) failed to transfer *Leptodinium aculeatum* Wall to their new genus *Impagidinium.* This is done here: *I. aculeatum* (Wall) comb. nov. = *L. aculeatum* Wall 1967, pp. 104–105, pl. 14, figs. 18, 19, text-figs. 3C, 3D. This form is a cyst type of one of the *Gonyaulax spinifera* group. It is a particularly characteristic morphotype characterized by the form of the parasutural membranes.

Distribution. Widespread in the central North Atlantic and Mediterranean with centres of concentration toward the eastern Atlantic particularly off the Iberian peninsula and north-west Africa. Its pattern of distribution is much more oceanic in aspect than any of those species previously discussed. Records of this species in Quaternary sediments are confined to very rare occurrences off the British Isles.

21 *Impagidinium paradoxum* (Wall) Stover and Evitt 1978

Text-fig. 22; Plate 46, figs. 4, 5

Taxonomic Comments. I. paradoxum is regarded as the cyst of a *Gonyaulax spinifera* group species. None of the *Impagidinium* cyst species have, however, been incubated to my knowledge. This species is somewhat like *I. aculeatum* but without the aculeate parasutural membranes and it does not possess an apical boss.

Distribution. Widespread in the central North Atlantic and also present in the Mediterranean with an isolated occurrence in the Norwegian Sea. As with *I. aculeatum* its pattern of distribution is oceanic. This species is also rarely seen in British offshore Quaternary deposits.

22 *Impagidinium patulum* (Wall) Stover and Evitt 1978

Text-fig. 23; Plate 46, figs. 6, 7

Taxonomic Comments. The cyst species *I. patulum* is yet another species that is attributable to the *G. spinifera* group. It is, however, characterized by its size and paratabulation particularly in the parasutural area.

Distribution. This species of *Impagidinium* is a little more restricted in its distribution than the previously described forms. It is present in the west-central part of the Atlantic off the eastern seaboard of the United States, off the north-west coast of Africa and in the Mediterranean Sea. It also occurs in isolated areas in the Norwegian Sea and in a strip slightly to the south and parallel to the 50°N. latitude line and in the southern part of the North Atlantic. Its major area of concentration is in the west-central part of the Atlantic. In spite of a more restricted occurrence it is still oceanic in aspect. It is rarely seen in Quaternary offshore sequences around the British Isles.

EXPLANATION OF PLATE 46

All photomicrographs were taken by Nomarski interference contrast and are illustrated at a magnification of × 500.

Figs. 1–3. *Impagidinium aculeatum* (Wall) comb. nov., Specimen MPK 3118. 1, dorsal view showing P archeopyle. 2, median view showing characteristic parasutural membranes and gonal processes. 3, ventral view showing broad sulcal area.

Figs. 4, 5. *I. paradoxum* (Wall) Stover and Evitt, Specimen MPK 3119. 4, dorsal view showing P archeopyle. 5, ventral view showing sulcus together with the triangular 6″ paraplate and small elongate 1″ paraplate.

Figs. 6, 7. *I. patulum* (Wall) Stover and Evitt, Specimen MPK 3120. 6, dorsal view showing P archeopyle and apical paraplates 2′ and 3′. 7, ventral view showing antapical part of sulcus with the posterior intercalary paraplate and posterior and median sulcal paraplates.

Figs. 8, 9. *I. sphaericum* (Wall) comb. nov., Specimen MPK 3121. 8, dorsal view showing the P archeopyle and apical paraplates 2′ and 3′. 9, ventral view showing the antapical part of the sulcus with the posterior intercalary paraplate and the posterior, right, left and right accessory sulcal paraplates.

Figs. 10–12. *I. strialatum* (Wall) Stover and Evitt, Specimen MPK 3122. 10, dorsal view showing the P archeopyle. 11, median view showing the parasutural membranes. 12, ventral view.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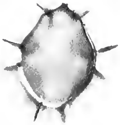
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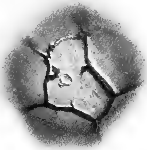
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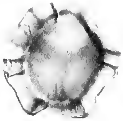
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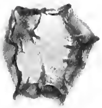
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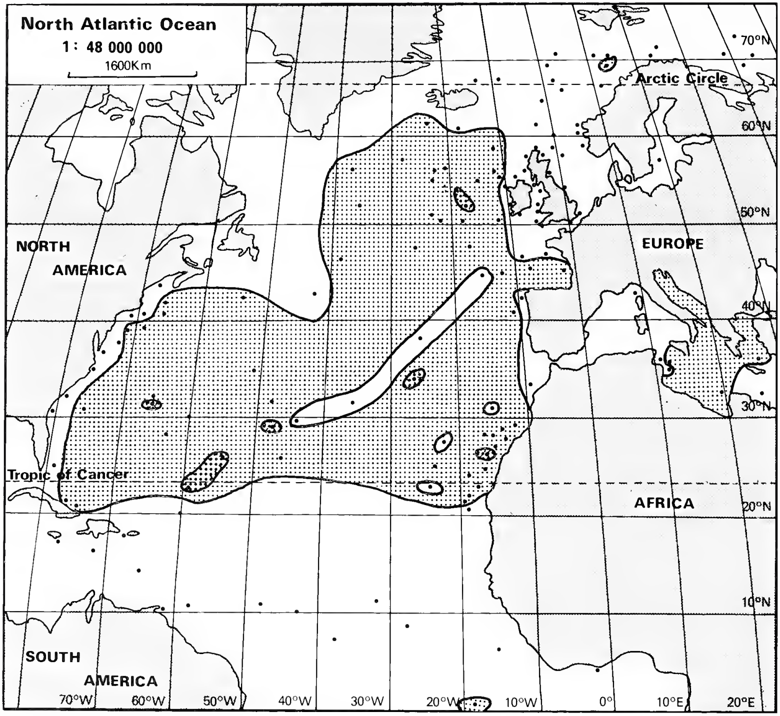
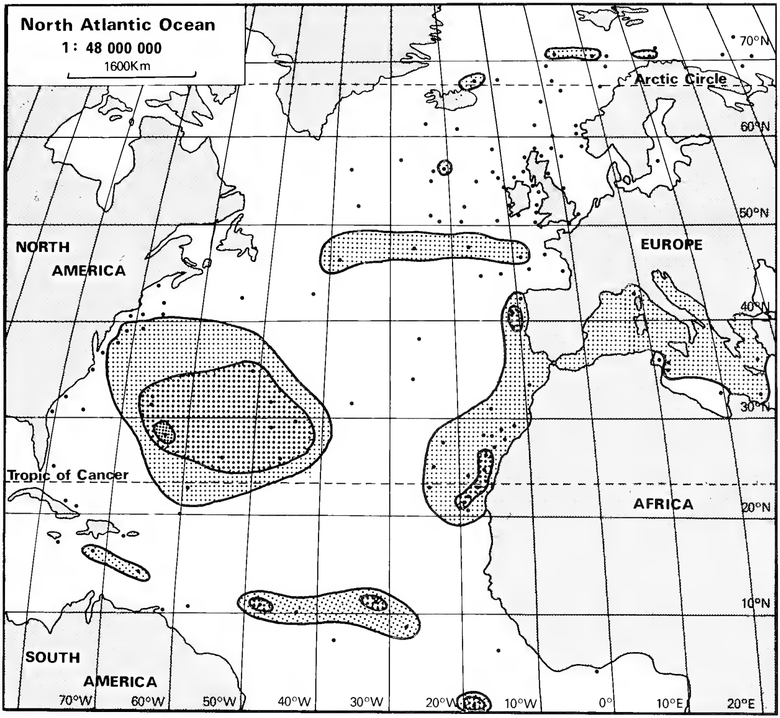
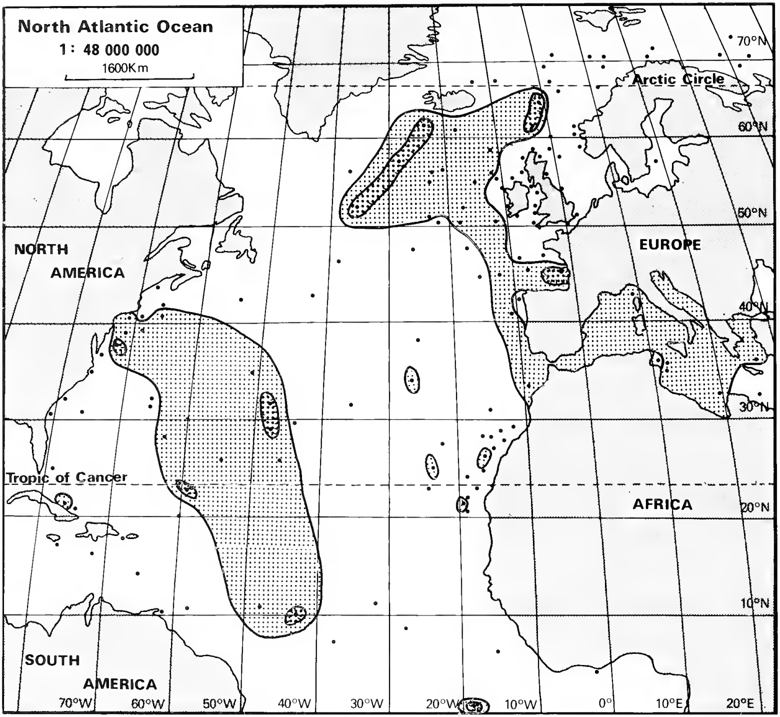
HARLAND, Recent dinoflagellates



TEXT-FIG. 22. Distribution of *Impagidinium paradoxum* (Wall) Stover and Evitt. Ornament as before.



TEXT-FIG. 23. Distribution of *Impagidinium patulum* (Wall) Stover and Evitt. Ornament as before.



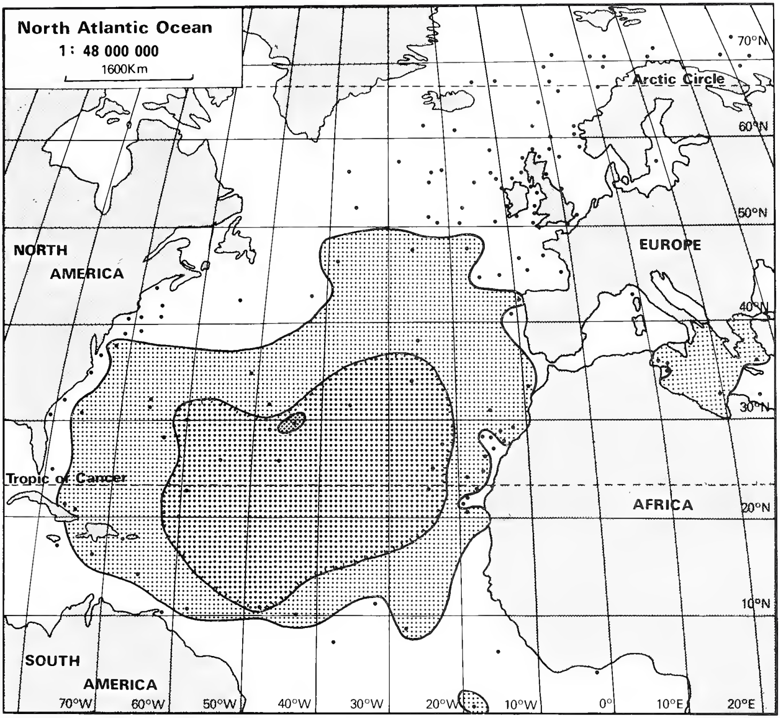
TEXT-FIG. 24. Distribution of *Impagidinium sphaericum* (Wall) comb. nov. Ornament as before.

23 *Impagidinium sphaericum* (Wall) comb. nov.

Text-fig. 24; Plate 46, figs. 8, 9

Taxonomic Comments. As with *I. aculeatum*, Stover and Evitt (1978) failed to transfer *L. sphaericum* Wall into the genus *Impagidinium*. It is therefore done here: *I. sphaericum* (Wall) comb. nov. = *Leptodinium sphaericum* Wall 1967, pp. 108, pl. 15, figs. 11–15, text-figs. 2A–C. This cyst form is also regarded as belonging to the *G. spinifera* group. It is characterized by its size, paratabulation details and apical boss.

Distribution. Its distribution, like that of *I. patulum*, centres off the eastern seaboard of the United States and north-west South America, also the Mediterranean and off the west coast of the British Isles and Iberian peninsula. There are some isolated occurrences off the north-west coast of Africa. This cyst, nevertheless, reveals an oceanic aspect in its distribution. It is very rarely seen in offshore Quaternary sequences in the British Isles area.



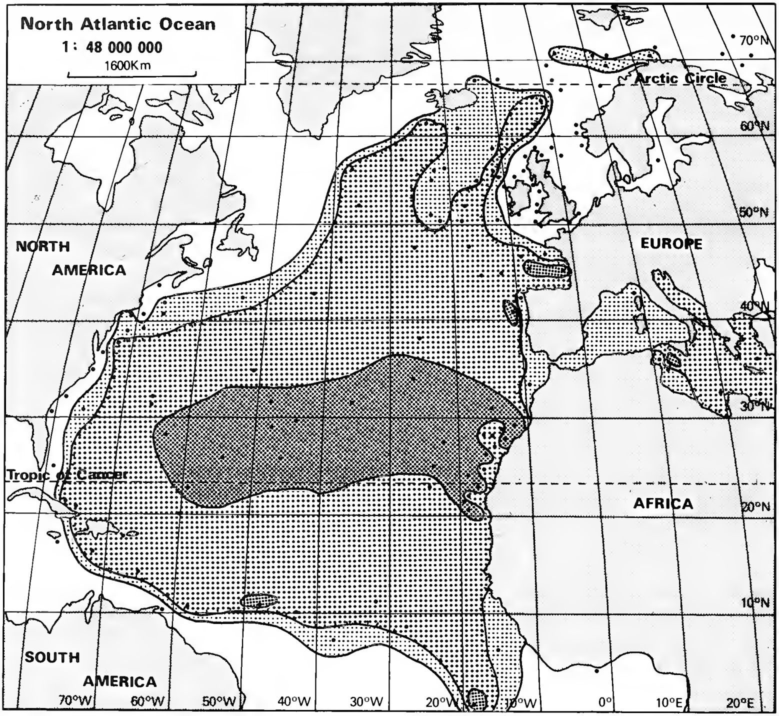
TEXT-FIG. 25. Distribution of *Impagidinium strialatum* (Wall) Stover and Evitt. Ornament as before.

24 *Impagidinium strialatum* (Wall) Stover and Evitt 1978

Text-fig. 25; Plate 46, figs. 10–12

Taxonomic Comments. Another cyst type related to the *G. spinifera* group. It is characterized by high parasutural membranes that are often striated, together with a distinctive parasulcal tabulation.

Distribution. It is distributed in the central North Atlantic but also in the Mediterranean with one isolated occurrence at the equator. This pattern is obviously oceanic, and the cyst is rarely seen in offshore Quaternary sequences around the British Isles.

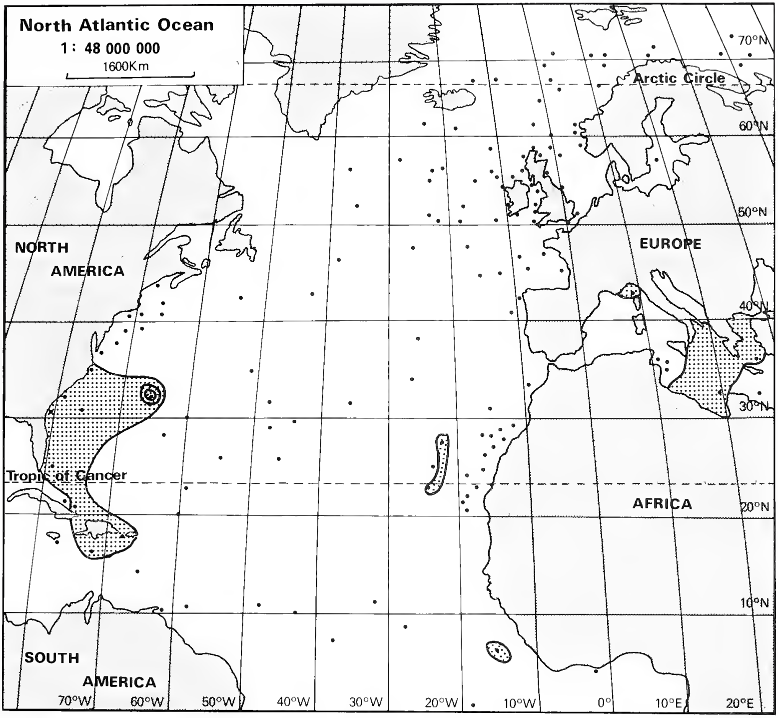


TEXT-FIG. 26. Distribution of total *Impagidinium* species. Ornament as before.

25 Total *Impagidinium* spp.

Text-fig. 26

General Comments. The total distribution pattern for *Impagidinium* species clearly shows a widespread North Atlantic distribution centred on the oceanic realm.



TEXT-FIG. 27. Distribution of *Polysphaeridium zoharyi* (Rossignol) Bujak *et al.* Ornament as before.

26 *Polysphaeridium zoharyi* (Rossignol) Bujak *et al.* 1980

Text-fig. 27; Plate 45, fig. 10

Taxonomic Comments. This morphospecies is the cyst of *Pyrodinium bahamense* Plate and is characterized by its large size and particularly its epicystal archeopyle. It is also better known as *Hemicystodinium zoharyi* (Rossignol) Wall but since the type species of *Polysphaeridium* has recently been discovered to have an epicystal archeopyle the genus *Hemicystodinium* Wall 1967 becomes a junior synonym of *Polysphaeridium*. Bujak *et al.* (1980) formally transferred *zoharyi* to *Polysphaeridium*.

Distribution. The occurrence of *P. zoharyi* appears restricted to the Caribbean, Bermuda and south-eastern seaboard of the United States, and to the Mediterranean with a couple of isolated occurrences off north-west Africa. A centre of concentration occurs at Bermuda. Its distribution points to a tropical–sub-tropical environmental preference. It has not been seen in marine offshore Quaternary deposits from the area of the British Isles. Occasional mentions in the literature from this area are without doubt the misidentification of *O. centrocarpum* (e.g. Harland 1968, Downie and Singh 1969).

Pyrophacacean Cysts

27 *Tuberculodinium vancampoae* (Rossignol) Wall 1967

Text-fig. 28; Plate 45, fig. 11

Taxonomic Comments. This large and distinctive species with an antapical archeopyle is the cyst of *Pyrophacus* Form B1 of Steidinger and Davis (1967).

Distribution. Restricted to the south-eastern seaboard of the United States, the Mediterranean and isolated occurrences including the west-central coast of Africa. As with *P. zoharyi* its restricted distribution pattern indicates a tropical–sub-tropical preference. It has not been seen in offshore Quaternary sediments in the British Isles area.

Peridiniacean Cysts

Following the recent review by Harland (1982), the names used in this section are those using the combined thecate and cyst taxonomies. Appendix I lists both the cyst names and the thecate names. No new cyst names are therefore proposed as the various species are all adequately covered by the combined approach of Harland (1982). Williams (1965, 1971) failed to distinguish the various species of *Protoperidinium* hence the record from his data may be somewhat incomplete.

28 *Protoperidinium* (*Protoperidinium* sect. *Asymmetropedinium*) *punctulatum* (Paulsen) Balech 1974

Plate 47, fig. 1

Taxonomic Comments. This spherical brown cyst of *P. punctulatum* is characterized by its asymmetrical archeopyle. However unless orientated advantageously it can be confused with other brown spherical *Protoperidinium* cysts. It has no palaeontological name but would be regarded as a new species of *Brigantedinium*.

Distribution. This species has not been unequivocally recognized in bottom sediments from the North Atlantic, hence the failure to publish a distribution map, but Wall and Dale (1968*b*) recorded these cysts from Woods Hole, U.S.A. It is, however, more than likely to have been included in counts of both *P. avellana* and total *Protoperidinium* spp.

EXPLANATION OF PLATE 47

All photomicrographs were taken by Nomarski interference contrast and are illustrated at a magnification of × 500.

Fig. 1. *Protoperidinium* (*Protoperidinium* sect. *Asymmetropedinium*) *punctulatum* (Paulsen) Balech, Specimen MPK 2953, showing the asymmetrical operculum.

Figs. 2, 3. *P.* (*Protoperidinium* sect. *Brigantedinium*) *conicoides* (Paulsen) Balech, Specimen MPK 1232. 1, dorsal view showing the archeopyle. 2, ventral view showing flagellar scars.

Fig. 4. *P.* (*Archaeperidinium* sect. *Fuscusasphaeridium*) *avellana* (Meunier) Balech, Specimen MPK 1236, showing symmetrical operculum in place at the archeopyle.

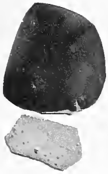
Fig. 5. *Protoperidinium* sp. indet., *Lejeunia paratenella* Benedek, Specimen MPK 1247, dorsal view showing attenuated hexa archeopyle with operculum in place.

Fig. 6. *P.* (*Archaeperidinium* sect. *Fuscusasphaeridium*) *denticulatum* (Gran and Braarud) Balech, photograph kindly supplied by D. Wall. Oblique dorsal view photographed in plain light.

Figs. 7, 8. *P.* (*Protoperidinium* sect. *Quinquecuspis*) *leonis* (Pavillard) Balech, Specimen MPK 1230. 7, dorsal view showing the archeopyle and operculum. 8, ventral view showing the deeply indented parasulcus.

Figs. 9, 10. *P.* (*Protoperidinium* sect. *Selenopemphix*) *conicum* (Gran) Balech. 9, Specimen MPK 2772. 10, Specimen MPK 2949. The two specimens show some of the range of variation in size.

Figs. 11, 12. *P.* (*Protoperidinium* sect. *Selenopemphix*) *subinerme* (Paulsen) Loeblich III, Specimen MPK 3151. 11, apical view showing offset archeopyle with the operculum in place. 12, antapical view.



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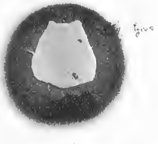

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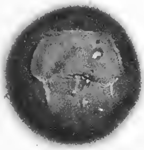

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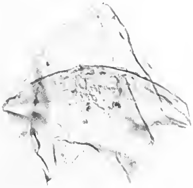

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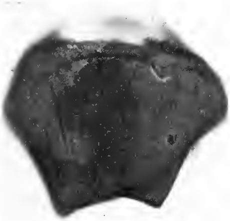

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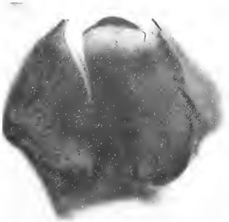

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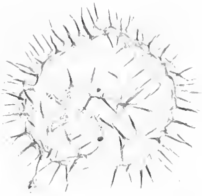

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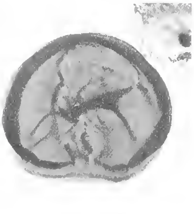

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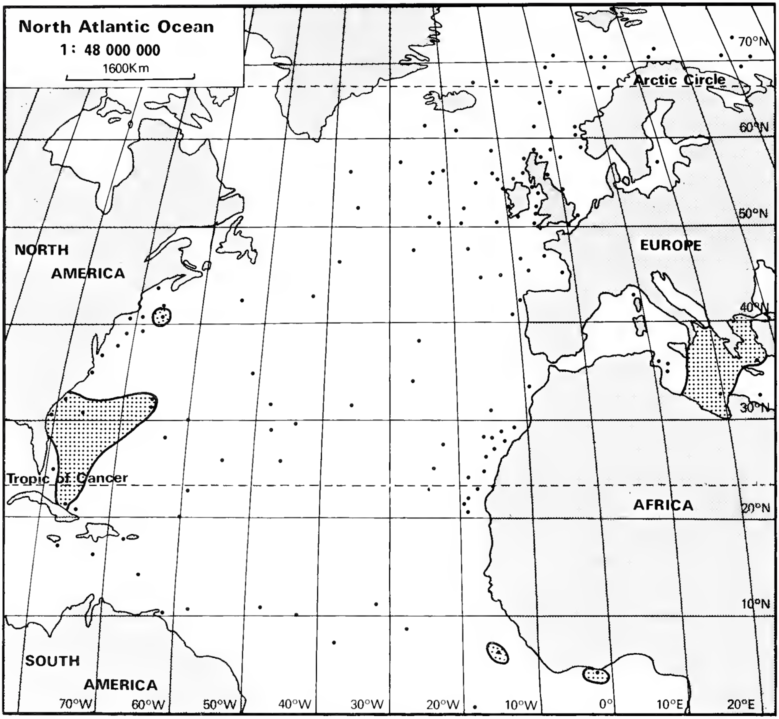
HARLAND, Recent dinoflagellates



TEXT-FIG. 28. Distribution of *Tuberculodinium vancampoae* (Rossignol) Wall. Ornament as before.

29 *Protoperidinium* (*Protoperidinium* sect. *Brigantedinium*) *conicoides* (Paulsen) Balech 1974

Text-fig. 29; Plate 47, figs. 2, 3

Taxonomic Comments. This is another brown spherical cyst but with a distinctive large intercalary archeopyle that may or may not be composed of one or two intercalary paraplates. It has been described under the palaeontological name of *B. simplex* (Wall) Reid.

Distribution. Only seen in nearshore sediments around parts of the British Isles particularly in the Irish Sea, Sea of the Hebrides, and Forth Approaches, although Wall and Dale (1968*b*) recorded it at Woods Hole, U.S.A., and Dale (1976) from Trondheimsfjord, Norway. The distribution is undoubtedly affected by identification difficulties if poorly orientated specimens are recovered. Some occurrences will have been included in the total *Protoperidinium* count.

30 *Protoperidinium* (*Archaeperidinium* sect. *Fuscusasphaeridium*) *avellana* (Meunier) Balech 1974

Plate 47, fig. 4

Taxonomic Comments. Yet another brown spheroidal cyst with a distinctive archeopyle which is laterally elongate but symmetrical. It has been described with the palaeontological name of *B. cariacoense* (Wall) Reid.

Distribution. Only recorded in bottom sediments in the Forth Approaches, sample number 29, but also seen by Wall and Dale (1968*b*) in the Woods Hole region and as a cf. by Dale (1976) in Trondheimsfjord, Norway. Again difficulties in identification of badly preserved or poorly orientated material may well have biased the record and many occurrences will have been included in the total *Protoperidinium* count.

31 *Protoperidinium* (*Archaeperidinium* sect. *Fuscusasphaeridium*) *denticulatum* (Gran and Braarud) Balech 1974

Plate 47, fig. 6

Taxonomic Comments. This cyst, another spheroidal brown species, is uniquely characterized by its laterally elongate symmetrical archeopyle (see Harland 1982, text-fig. 7). In palaeontological taxonomy it would perhaps be regarded as a new species of *Brigantedinium*. The photograph kindly supplied by D. Wall depicts a form more closely similar to *P. avellana* in terms of archeopyle than the drawing (Plate 3, fig. 30) published in Wall and Dale (1968*b*). Difficulties in positively identifying this cyst are immediately apparent.

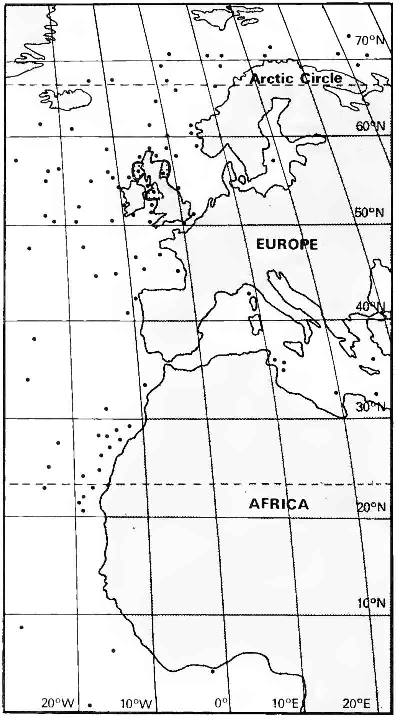
Distribution. Recorded from only one bottom sample, number 46, in the present study in the Irish Sea but Wall and Dale (1968*b*) have recorded it from the Woods Hole region, U.S.A. and Dale (1976) from Trondheimsfjord, Norway although both query the specific identification. Difficulties in identification suggest that this cyst may have been more commonly included in the total *Protoperidinium* counts.

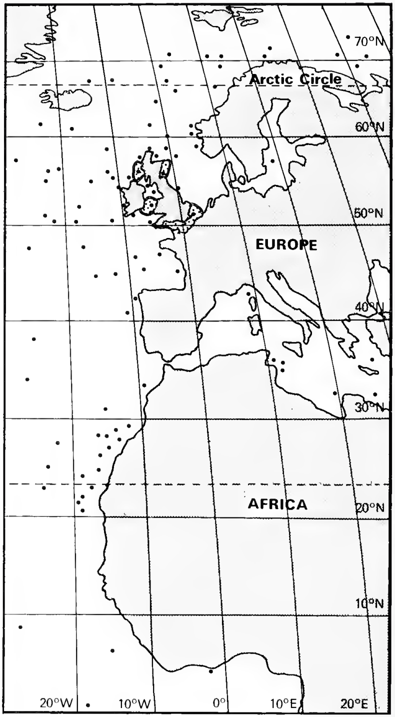
32 *Protoperidinium* sp. indet.

Text-fig. 30; Plate 47, fig. 5.

Taxonomic Comments. This cyst, undoubtedly of *Protoperidinium* affinity, is better known by its palaeontological species name *Lejeunia paratenella* Benedek. It is hoped that in the future living specimens of this species might be incubated to determine its specific affinity.

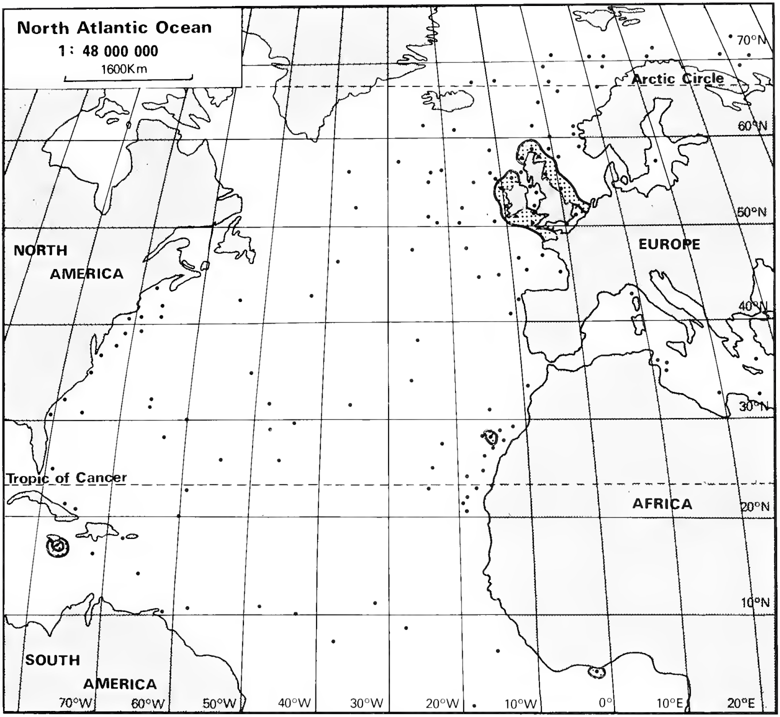
Distribution. Seen in nearshore sediments around the British Isles particularly in the Sea of the Hebrides, Cardigan Bay, English Channel, and Forth Approaches. It is thought to be indigenous to the assemblages although it and several related species occur in Tertiary marine sediments. It is on occasions prolific in certain assemblages e.g. Quaternary sequences in the Firth of Clyde (Harland 1973).





TEXT-FIG. 29 (*left*). Distribution of *Protoperidinium* (*Protoperidinium* sect. *Brigantedinium*) *conicoides* (Paulsen) Balech. Ornament as before.

TEXT-FIG. 30 (*right*). Distribution of *Protoperidinium* sp. indet. (*Lejeunia paratenella* Benedek). Ornament as before.



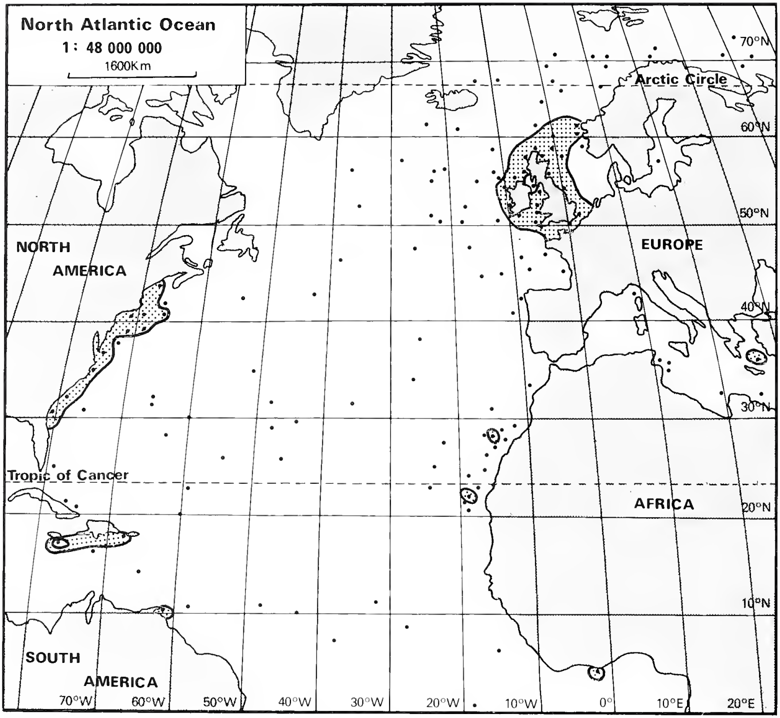
TEXT-FIG. 31. Distribution of *Protoperidinium* (*Protoperidinium* sect. *Quinquecuspis*) *leonis* (Pavillard) Balech. Ornament as before.

33 *Protoperidinium* (*Protoperidinium* sect. *Quinquecuspis*) *leonis* (Pavillard) Balech 1974

Text-fig. 31; Plate 47, figs. 7, 8

Taxonomic Comments. This brown peridinioid cyst has also been described under the palaeontological names *Trinovantedinium concretum* Reid and *Quinquecuspis concretum* (Reid) Harland. It is the cyst of *P. leonis* but there are some complications in the recognition of various 'species' having much the same morphology as this species (Harland 1982). Recognition of bona fide species within this group may lead to further precision in the understanding of the distribution of this and the other related species. Species not positively identified as *P. leonis* are included in the total *Protoperidinium* count.

Distribution. Restricted to the coastal areas around the British Isles and to some isolated occurrences in the Caribbean and off the west coast of Africa. This species has also been recorded by Wall and Dale (1968*b*) in the Woods Hole region of the U.S.A. It occasionally occurs in offshore marine Quaternary sequences.



TEXT-FIG. 32. Distribution of *Protoperidinium* (*Protoperidinium* sect. *Selenopemphix*) *conicum* (Gran) Balech. Ornament as before.

34 *Protoperidinium* (*Protoperidinium* sect. *Selenopemphix*) *conicum* (Gran) Balech 1974

Text-fig. 32; Plate 47, figs. 9, 10

Taxonomic Comments. This characteristic and well-known species is typically apically/antapically compressed, spinose and possesses an offset intercalary archeopyle. Variation in size has been noted (Bradford 1975) and this is illustrated in the photomicrographs presented here. In palaeontological literature it has been referred to as *Multispinula quanta* Bradford.

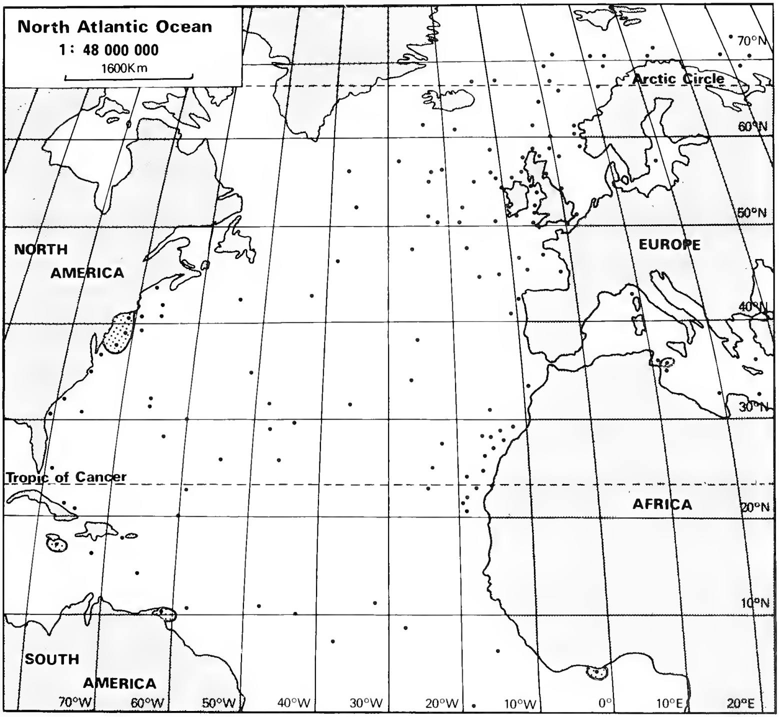
Distribution. Restricted to the coastal sediments around the British Isles and along the eastern seaboard of the United States. There appear to be some isolated occurrences in the Caribbean, off the north-east coast of South America, the Mediterranean, and off the west coast of Africa. This cyst is well known in Quaternary sequences from the offshore region of the British Isles, and may have the potential of identifying specific environmental conditions.

35 *Protoperidinium* (*Protoperidinium* sect. *Selenopemphix*) *nudum* (Meunier) Balech 1974

Plate 48, fig. 5

Taxonomic Comments. This cyst form is very similar to that of *P. conicum* but is smaller, and carries relatively longer spines. Some reservation is expressed in the assignation of these cysts (Wall and Dale 1968*b*) to the parental theca. In the present study difficulty was experienced in positively identifying this species given the intraspecific variability of *P. conicum* and the presence of other similar cysts such as *M. minuta* Harland and Reid and Cyst B of Harland (1977). Further work is clearly desirable on this group of species.

Distribution. Isolated occurrences in the North Sea, sample 53, and Barents Sea, sample 31, but has also been recorded by Wall and Dale (1968*b*) from the eastern seaboard of the United States. Other occurrences may be included, because of taxonomic and identification difficulties, in the maps for Cyst B of Harland (1977) or in the total *Protoperidinium* counts.



TEXT-FIG. 33. Distribution of *Protoperidinium* (*Protoperidinium* sect. *Selenopemphix*) *subinerme* (Paulsen) Loeblich III. Ornament as before.

36 *Protoperidinium* (*Protoperidinium* sect. *Selenopemphix*) *subinerme* (Paulsen) Loeblich III

Text-fig. 33; Plate 47, figs. 11, 12

Taxonomic Comments. An apically/antapically compressed cyst with an offset archeopyle but no spines. It has been described in the palaeontological literature as *Selenopemphix nephroides* Benedek.

Distribution. Isolated occurrences off the eastern seaboard of the United States, the Caribbean, the Mediterranean and off the west coast of Africa. It can be an important species in some Quaternary sequences especially in the Biscay area (work in preparation).

37 *Protoperidinium* (*Archaeperidinium* sect. *Stelladinium*) *compressum* (Abé) Balech 1974

Text-fig. 34; Plate 48, fig. 1

Taxonomic Comments. This cyst has a unique stellate morphology and a two paraplate intercalary archeopyle. It has been referred to as *Stelladinium stellatum* (Wall) Reid in the palaeontological literature.

Distribution. Restricted distribution in nearshore sediments of the British Isles particularly to the Irish Sea, and off the north-west and south-east coasts of Ireland. It has been noted in Quaternary sequences across the Pleistocene/Holocene boundary and it may signify some particular ecological condition. Wall and Dale (1968*b*) found it in local plankton around the Woods Hole region, U.S.A.

38 *Protoperidinium* (*Protoperidinium* sect. *Trinovantedinium*) *pentagonum* (Gran) Balech 1974

Text-fig. 35; Plate 48, figs. 2, 3

Taxonomic Comments. This cyst is characterized by its colourless wall, peridinioid shape and broad hexa archeopyle. In palaeontological literature it was known as *T. capitatum* Reid. The assignation of the cyst to the

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EXPLANATION OF PLATE 48

All photomicrographs were taken by Nomarski interference contrast unless otherwise stated and are illustrated at a magnification of × 500.

Fig. 1. *Protoperidinium* (*Archaeoperidinium* sect. *Stelladinium*) *compressum* (Abé) Balech, Specimen MPK 1256, showing the dorsal surface and 2 I symmetrical archeopyle.

Figs. 2, 3. *P.* (*Protoperidinium* sect. *Trinovantedinium*) *pentagonum* (Gran) Balech, Specimen 1240. 2, dorsal view showing archeopyle. 3, median view showing apical boss.

Fig. 4. *P.* (*Protoperidinium* sect. *Votadinium*) *claudicans* (Paulsen) Balech, photograph kindly supplied by D. Wall, dorsal view showing archeopyle. Photographed in plain light.

Fig. 5. *P.* (*Protoperidinium* sect. *Selenopemphix*) *nudum* (Meunier) Balech, photograph kindly supplied by D. Wall, dorsal view. Photographed in plain light.

Figs. 6, 7. *P.* (*Protoperidinium* sect. *Votadinium*) *oblongum* (Aurivillius) Balech, Specimen MPK 2778. 6, dorsal view showing the archeopyle. 7, ventral view.

Fig. 8. *Protoperidinium* sp. indet., *Xandarodinium xanthum* Reid, Specimen MPK 2773.

Fig. 9. *Protoperidinium* sp. indet., Cyst-type B of Harland (1977), Specimen MPK 1251.

Figs. 10–12. *Polykrikos schwartzii* Bütschli, Specimens MPK 2600 and 2605.


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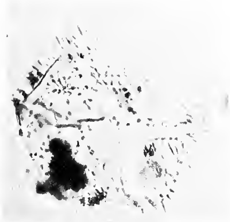
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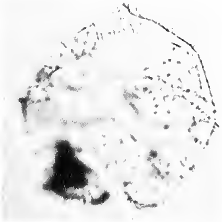
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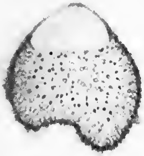
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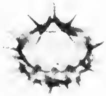
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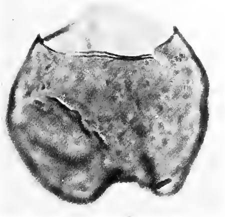
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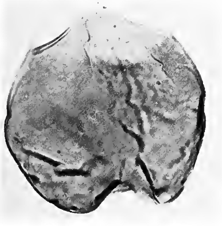
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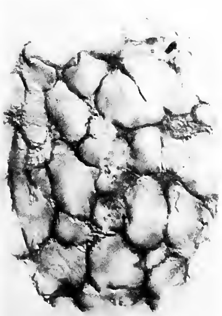
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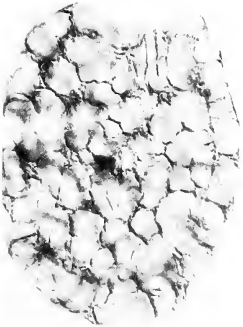
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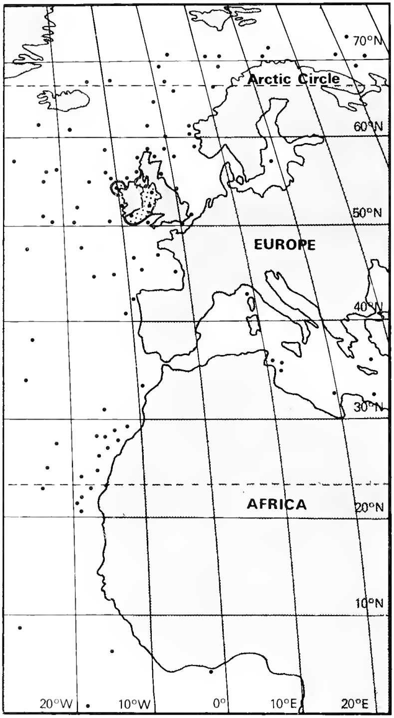
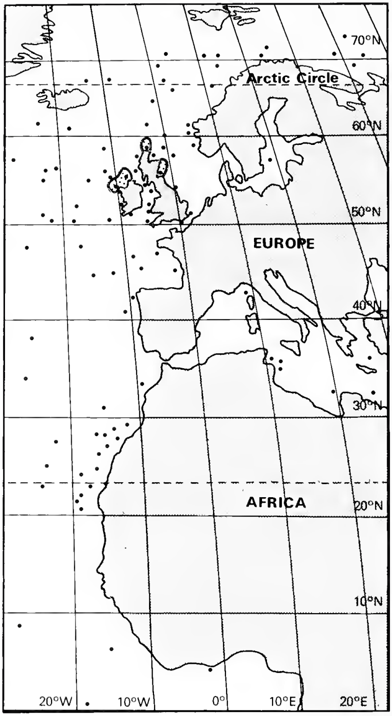
HARLAND, Recent dinoflagellates



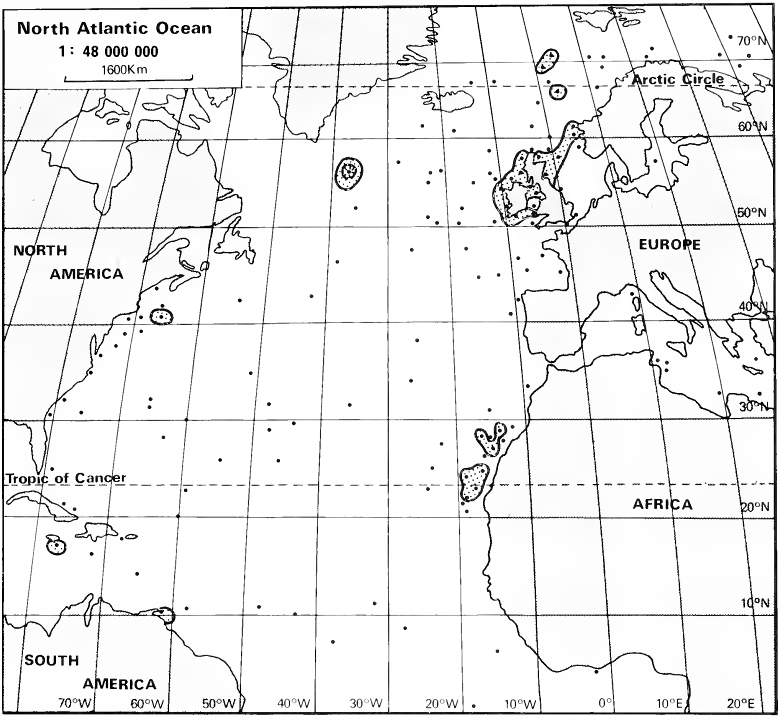


TEXT-FIG. 34 (*left*). Distribution of *Protoperidinium* (*Archaeoperidinium* sect. *Stelladinium*) *compressum* (Abé) Balech. Ornament as before.

TEXT-FIG. 35 (*right*). Distribution of *Protoperidinium* (*Protoperidinium* sect. *Trinovantedinium*) *pentagonum* (Gran.) Balech. Ornament as before.

parent theca is known (Wall and Dale 1968*b*), but similar cysts have produced thecae with minor differences such that several species or varieties may be involved.

Distribution. Around the coast of the British Isles, the North Sea, off the north-west coast of Africa and some isolated occurrences in the Norwegian Sea, Atlantic, off the eastern seaboard of the United States and the Caribbean. It is occasionally found in marine offshore Quaternary sequences. Its occurrence may have some particular environmental significance.



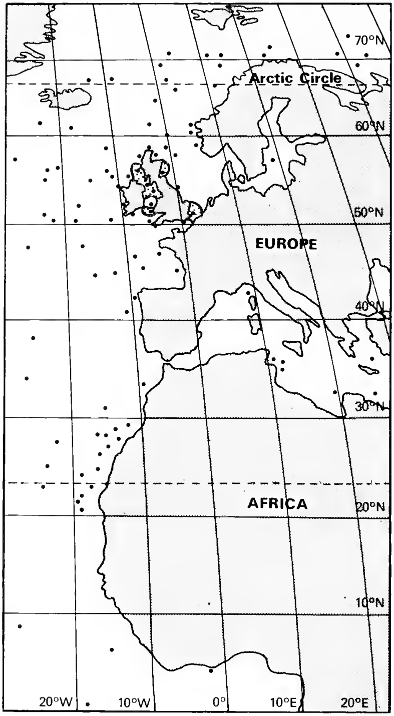
TEXT-FIG. 36. Distribution of *Protoperidinium* (*Protoperidinium* sect. *Votadinium*) *claudicans* (Paulsen) Balech. Ornament as before.

39 *Protoperidinium* (*Protoperidinium* sect. *Votadinium*) *claudicans* (Paulsen) Balech 1974

Text-fig. 36; Plate 48, fig. 4

Taxonomic Comments. This cyst is characterized by its chordate shape and archeopyle that truncates the apex. It has, in the past, been referred to as *Votadinium spinosum* Reid in palaeontological literature.

Distribution. Restricted to the nearshore sediments around the British Isles in particular off northern Scotland and Ireland and in the Forth Approaches. Wall and Dale (1968*b*) also recorded it from Bermuda and from local plankton in the Woods Hole region of the U.S.A. It is a cyst that I have never seen in offshore Quaternary sequences, and only rarely in Recent bottom sediments.



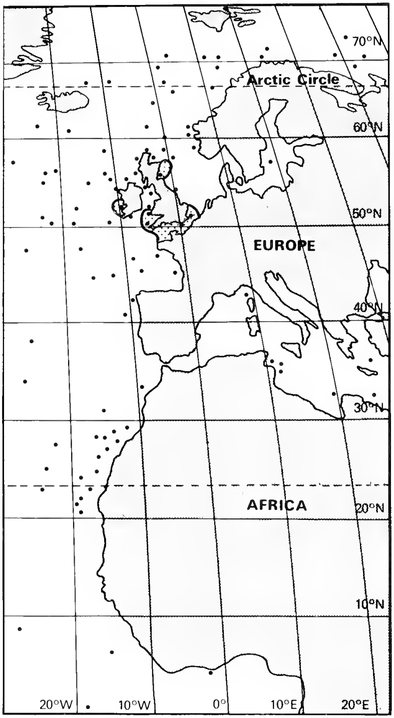
TEXT-FIG. 37. Distribution of *Protoperidinium* (*Protoperidinium* sect. *Votadinium*) *oblongum* (Aurivillius) Balech. Ornament as before.

40 *Protoperidinium* (*Protoperidinium* sect. *Votadinium*) *oblongum* (Aurivillius) Balech 1974

Text-fig. 37; Plate 48, figs. 6, 7

Taxonomic Comments. Like *P. claudicans* this cyst is characterized by its chordate shape and characteristic archeopyle but it is brown and does not possess spines. Reid (1977) referred to this cyst as *Votadinium calvum* Reid.

Distribution. Restricted to nearshore sediments around the British Isles particularly the Irish Sea, Sea of the Hebrides, Forth Approaches, and eastern English Channel. It has also been noted in the local plankton at Woods Hole, U.S.A. (Wall and Dale 1968*b*). It is very rarely seen in offshore Quaternary sequences.



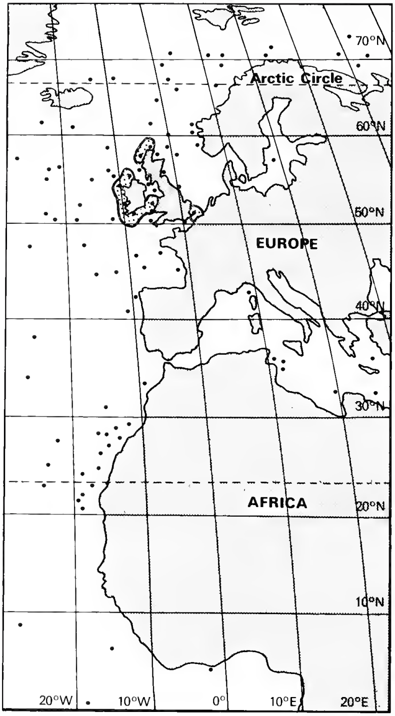
TEXT-FIG. 38. Distribution of *Protoperidinium* sp. indet. (*Xandarodinium xanthum* Reid). Ornament as before.

41 ?*Protoperidinium* sp. indet.

Text-fig. 38; Plate 48, fig. 8

Taxonomic Comments. This cyst, known as *Xandarodinium xanthum* Reid in palaeontological literature is thought to be a cyst of a *Protoperidinium* sp. but to date no incubation experiments have confirmed or denied this hypothesis. The cyst has a unique morphology with hollow processes carrying distal furcate and bifid solid tips and an often reniform ambitus suggestive of an apical/antapical compression. It is a cyst type in need of further study.

Distribution. Restricted to the southern and south-western coast of England, the Forth Approaches, and off the west coast of Ireland. It is extremely rare in offshore Quaternary sequences.



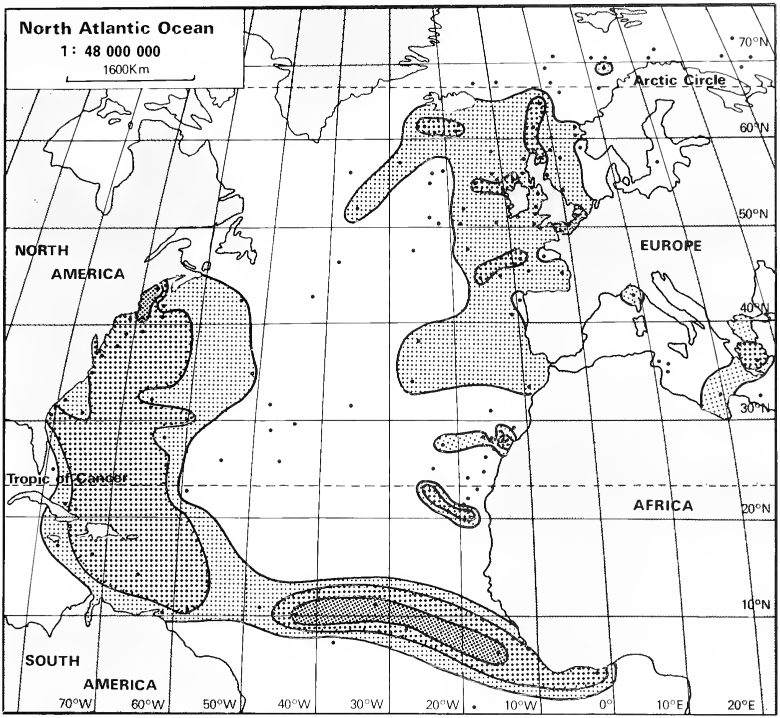
TEXT-FIG. 39. Distribution of ?*Protoperidinium* sp. indet. (Cyst type B of Harland 1977). Ornament as before.

42 Cyst-type B of Harland (1977)

Text-fig. 39; Plate 48, fig. 9

Taxonomic Comments. A spheroidal cyst that carries numerous processes up to $\frac{1}{6}$th the cyst diameter in length. Each process has a number of small backward facing distal spinules. The affinities of this cyst are not known as no paratabulation or archeopyle have been observed. It is possibly a *Protoperidinium* cyst or a cyst of a gymnodinialean dinoflagellate.

Distribution. Restricted around the coast of the British Isles particularly off north-west Scotland, south and west coasts of Ireland, Cardigan Bay, and the eastern English Channel. It is rarely seen in offshore Quaternary sequences but may have been confused with *Multispinula minuta* Harland and Reid which differs in having aciculate processes.



TEXT-FIG. 40. Distribution of *Protoperidinium* spp. indet. Ornament as before.

43 *Protoperidinium* spp. indet.

Text-fig. 40

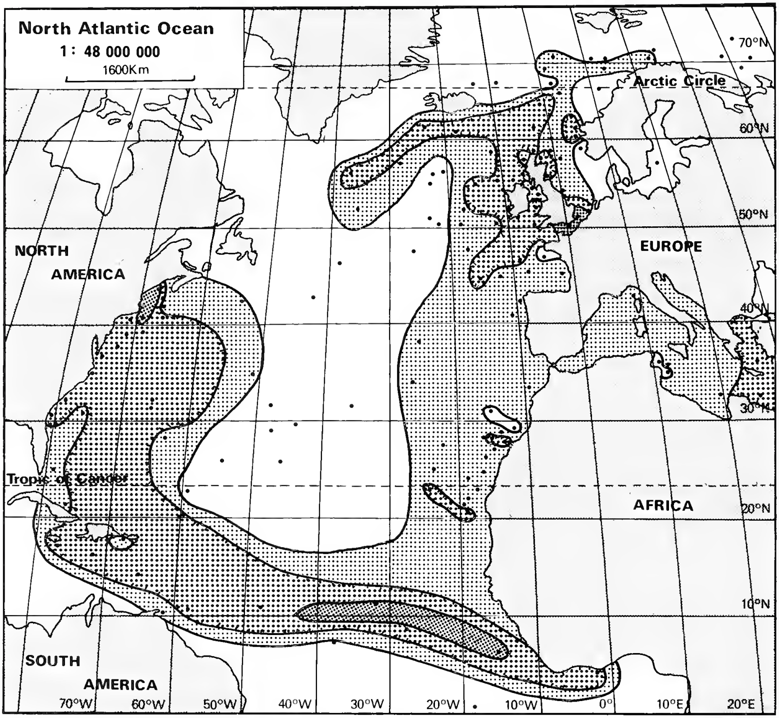
Taxonomic Comments. This category puts together all the cysts thought to belong to the genus *Protoperidinium*. A large proportion of these cysts consists of unidentified brown spheroidal forms not orientated to allow positive identification or badly preserved.

Distribution. Widespread in the north-eastern Atlantic around the British Isles and Iberian peninsula and also off the eastern seaboard of the United States, into the Caribbean and along latitude 10°N. to the west coast of Africa. Also present off the north-west coast of Africa and in the Mediterranean. Major areas of concentration occur off the eastern seaboard of the United States and along latitude 10°N. Unidentifiable *Protoperidinium* cysts are nearly always present in offshore marine Quaternary sequences.

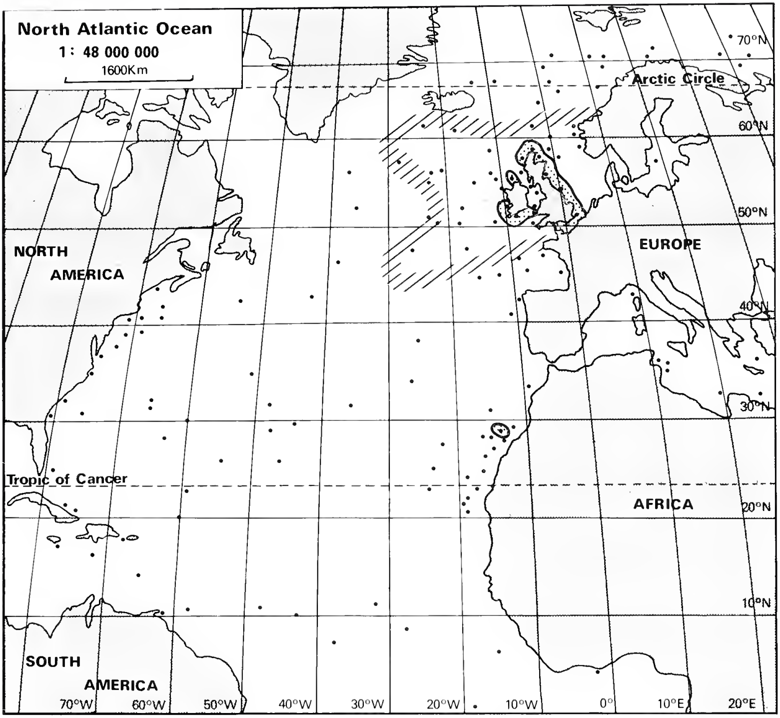
44 Total *Protoperidinium* spp.

Text-fig. 41

General Comments. The distribution map for total *Protoperidinium* is extremely like that presented for the unidentified *Protoperidinium* cysts and in essence outlines the fact that much of the peridiniacean assemblage is not identified to specific level. The scope for future research in this area is therefore great and no doubt much more is to be learned from more precise identifications of peridiniacean material. Areas of major concentrations of *Protoperidinium* cysts are close to the Bay of Fundy area off the eastern seaboard of North America, along 10°N. latitude between longitude 40°W. and 15°W. and also in the English Channel. *Protoperidinium* cysts are often seen in offshore marine Quaternary sequences sometimes in great profusion.



TEXT-FIG. 41. Distribution of the total *Protoperidinium* spp. Ornament as before.



TEXT-FIG. 42. Distribution of *Polykrikos schwartzii* Bütschli. Ornament as before. Hachured boundary indicates approximate distribution as given in Harland (1981).

Polykrikacacean Cysts

45 *Polykrikos schwartzii* Bütschli 1873

Text-fig. 42; Plate 48, figs. 10–12

Taxonomic Comments. These cysts are morphologically unique and have recently been described in detail (Harland 1981). Particularly interesting is the wide range of variation seen within this one species.

Distribution. The distribution portrayed in text-fig. 42 is somewhat misleading in that it appears to be restricted along the coasts of the British Isles particularly the north-eastern coast of Scotland and the southern coast of England, and off the northern, southern and south-western coasts of Ireland. Harland (1981) collated additional data from Reid (1978), Dale (1976) and from Professor John Dodge (pers. comm.) to show a much broader distribution in the eastern Atlantic and this is indicated by the hachured boundary. These cysts are occasionally present in offshore Quaternary sequences.

RESULTS

Constraints

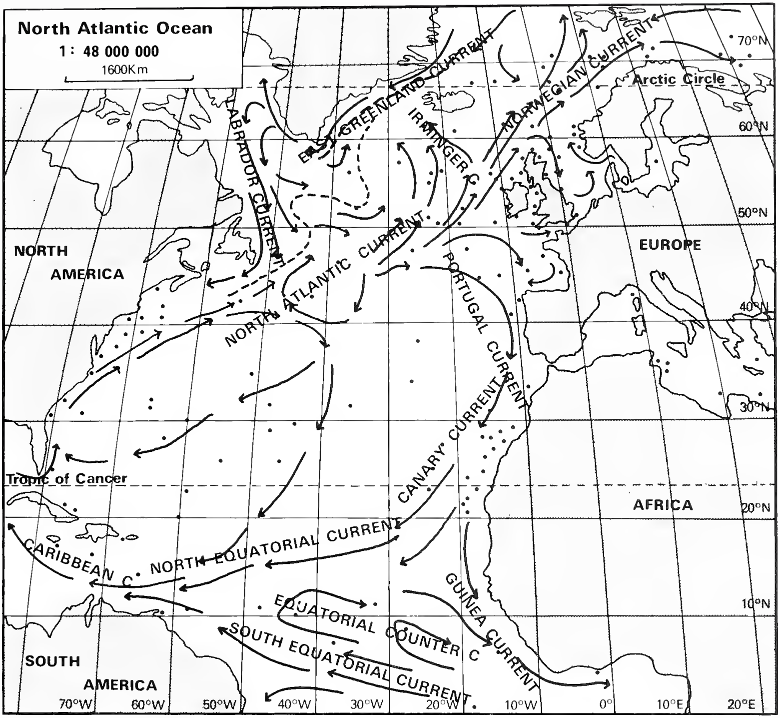
It is necessary, before discussing the results, to mention the constraints that must be taken into account with work of this kind. It is too easy and attractive to make broad generalizations without bearing in mind a number of factors that affect the results.

The first and most obvious constraint is that the assemblages examined are thanatocoenoses and therefore may be somewhat removed from the real dinoflagellate cyst biocoenosis. All the assemblages will have contained unknown proportions of living and dead dinocysts. In addition the dinoflagellate cyst assemblages, whether alive or dead, are also removed again from the living thecate dinoflagellate populations of the area. Indeed Dale (1976) has pointed out that only a very small proportion of the total living dinoflagellate population in a given area will produce cysts and indeed only some of these will be preserved as fossils and survive the palynological processing techniques. It is now realized that not all dinoflagellate cysts have the same inherent structural potential for being fossilized, a vital factor in surviving palynological processing techniques. It is therefore difficult, if not almost impossible, to give any conclusions concerning the total living dinoflagellate population. It is also difficult to determine whether, given the knowledge from incubation experiments that a cyst and thecate stage are related, the motile/thecate dinoflagellate was living in the overlying waters. In this respect transport along current systems (text-fig. 43), and sorting according to particle size and specific density will affect the thanatocoenosis and remove it, to a greater or lesser degree, from the biocoenosis. Dinoflagellate cysts act as sedimentary particles of variously clay or fine silt size and this may affect concentrations of cysts in particular areas. Indeed a comparison of many of the distribution charts with the surface current patterns will often show a close correspondence.

A second factor involves the integration of the record in bottom sediments. The samples used were taken using grab samples, vibrocorers, piston corers, and dredgers. This taken together with the knowledge that bottom sediments are generally extensively bioturbated, even in oceanic bottom sediments means that the samples used in this study are probably integrating many hundreds of years of deposition and possibly several thousands. It is probably more accurate to refer them to the late Flandrian, than to call them modern or Recent. In addition it is probable that shelf sediments are an integration of hundreds of years whilst those in the deep ocean integrate thousands of years because of major differences in sedimentation rates. The distinction between shelf and oceanic dinoflagellate cyst assemblages will be accentuated by this factor. These factors should be considered in any study of fossil dinoflagellate cyst assemblages when similar aged samples from differing geographical localities are being compared.

A third important factor that seriously affects the interpretation of this study and indeed any quantitative work on Quaternary or older sequences is the overrepresentation of some species. It has been reported (Dale 1976) that in plankton counts at Woods Hole, the ratio of cysts to thecae for *Gonyaulax grindleyi* was about 1:2 whereas for *Protoperidinium oblongum* is was 1 : 120 and for *G. digitalis* 1 : 500. In terms of the record here and in the analysis of Quaternary sequences small changes in the living plankton population would give large changes in the resultant cyst assemblages.

Other factors include the danger of including material reworked from older sediments, a possibility that experience can go some way to eliminating especially in the case of Tertiary or older sediments. Whereas the spectre of reworking from older Quaternary sediments is one that cannot be eliminated, it is hoped that it is negligible in the present study. It is also possible that some of the bottom sediments are considerably older because of scour effects etc., and contain dinoflagellate cyst assemblages not in ecological equilibrium with the present oceanographical conditions. This factor is especially important if on comparison of these results with those taken from living cyst populations discrepancies are noticed. This work assumes that, given the integration effect, these assemblages are in ecological equilibrium until proved otherwise.



TEXT-FIG. 43. North Atlantic surface currents (compiled from various sources).

The data is mapped as percentage counts and therefore in interpreting the maps it must be realized that any change of one species will obviously alter the proportions of all the other species. Equal emphasis should be placed upon those species that only appear as a tiny proportion of the cyst assemblage, but may indeed reveal interesting information concerning the environment.

The present data set is naturally subject to the particular biases of the various authors that have contributed data, including myself. This is manifest in the different processing techniques that were undoubtedly used, in the identification procedures, and the state of taxonomy at the time the work was done. D. B. Williams (1965, 1971), for instance, recognized very few *Protoperidinium* spp. but saw plenty of brown spherical objects, totalled with the *Protoperidinium* spp. indet. category here, and only a few people have consistently recognized the various *Spiniferites* species erected by Reid (1974).

Finally, this study is based upon a limited number of samples and further work should be done to improve the coverage. Of particular interest are the areas of the Labrador Sea (see Mudie 1981*a* and *b*), the region between latitudes 10°N. and 20°N. and better coverage in the Mediterranean.

Results

The maps show that the distribution of many species is closely linked with the patterns of currents in the North Atlantic and that many areas of concentration occur associated with areas of convergence and/or divergence, e.g. *B. tepikiense* (text-fig. 3) on the Iceland-Faroes Ridge, *S. mirabilis* (text-fig. 14) in the Portugal Current, i.e. East Atlantic gyre. This agrees well with the earlier findings of Williams (1971) and subsequent workers.

The species concerned can now, however, be categorized using these maps into a broad ecological classification similar to that compiled by Wall *et al.* (1977). This classification is presented in Table 1 and is a broader based scheme than that of Wall *et al.* (1977). It may, however, be a better basis because of this for the interpretation of Quaternary sequences as no doubt the constraints discussed earlier are directly at work here in smudging some of these rather arbitrary ecological divisions. It should be possible to place any Quaternary assemblage into this scheme by virtue of its contained species, but there is an obvious need to refine and subdivide each of the areas depicted here, especially in the light of comments made concerning the identifications of particular species. The addition of data from living cyst work will no doubt improve this kind of classification and identify areas where the smudging is great and can be discounted.

Also apparent is the correspondence between the diversity, i.e. number of species/assemblage, and distribution, as depicted in text-fig. 44 and Table 1. The greatest species diversity occurs in the temperate neritic realm followed by the tropical neritic and arctic neritic.

The separation of the neritic and oceanic realms is also clearly demonstrable (compare the distribution maps of the *Impagidinium* and *Spiniferites/Protoperidinium* spp.) in the present study. This factor was discussed by Wall *et al.* (1977) and earlier by Williams (1971) but there does seem to be a fundamental division in terms of the cyst thanatocoenosis even given all our constraints especially those of the problems of the integration of the record. Recent work (Dale in prep.) confirms this but also reveals significant differences between the flux of dinoflagellates into deep ocean sediment and assemblages similar to those described here. There is much to be learnt in terms of thanatocoenosis vs. biocoenosis but it may nevertheless be speculated that oceanic dinoflagellates have a somewhat different life cycle to those living in neritic waters and do not have benthonic cysts but ones that adopt a planktonic life style only dropping into bottom sediments after their function is complete.

A final result that comes out of this work substantiates remarks made by Reid and Harland (1977) on the separate distributions of various cysts all attributed to a single thecate species. In this respect it is worth comparing the distributions of *Bitectatodinium tepikiense* (text-fig. 3), *Nematosphaeropsis labyrinthea* (text-fig. 5), *Spiniferites elongatus* (text-fig. 11), *S. membranaceus* (text-fig. 13), *S. mirabilis* (text-fig. 14), and *S. ramosus* (text-fig. 15) all of which have been incubated to produce thecae attributable to *G. spinifera* and the *Impagidinium* spp. which are supposed, because of reasons based upon their paratabulation to also be referable to the *G. spinifera* group. This disparity in the geographical ranges of the various *Gonyaulax spinifera* cysts may indicate either different ecophenotypes expressed in the cyst morphology or the presence of a number of related species that are difficult to separate using the criteria currently employed. A further study of *G. spinifera* and its several cyst types is obviously required.

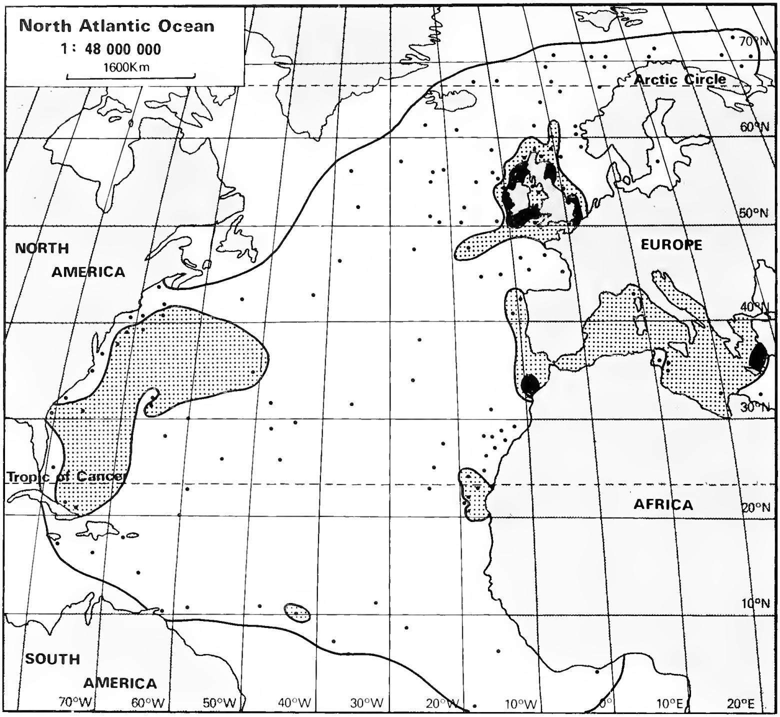
DISCUSSION

The main purpose of this study was to provide a series of maps showing the distribution of various dinoflagellate cyst species in bottom sediments throughout the North Atlantic area. The data were culled from various sources and some of the constraints and results have already been commented upon. The information is limited and should not be over-interpreted, if for no other reason than that we are not dealing with living material. It is, however, probably worthwhile to make some comparisons with the work of Wall *et al.* (1977) which is the most up to date account of dinoflagellate cyst distributions, and the factors that control the distributions.

Wall *et al.* (1977) set out to provide an environmental-climatic analysis of extant cyst-based

TABLE 1. An ecological classification of extant dinoflagellate cysts

	Inner Neritic		Outer Neritic		Oceanic	
Arctic	*O. centrocarpum*		*B. tepikiense*	*S. lazus*	*B. tepikiense*	*I. patulum*
	S. elongatus		*N. labyrinthea*	*S. mirabilis*	*N. labyrinthea*	
			O. centrocarpum	*S. ramosus*	*O. centrocarpum*	
			S. elongatus		*S. elongatus*	
Temperate	*L. machaerophorum*	*T. vancampoae*	*A. andalousiense*	*S. scabratus*	*B. tepikiense*	
	O. centrocarpum	*P. conicoides*	*B. tepikiense*	*T. pellitum*	*L. machaerophorum*	
	O. israelianum	*P. avellana*	*L. machaerophorum*	*I. aculeatum*	*N. labyrinthea*	
	S. belerius	*P. denticulatum*	*N. labyrinthea*	*I. paradoxum*	*O. centrocarpum*	
	S. bentori	*L. paratenella*	*O. centrocarpum*	*I. patulum*	*S. elongatus*	
	S. delicatus	*P. leonis*	*O. israelianum*	*I. sphaericum*	*S. mirabilis*	
	S. elongatus	*P. conicum*	*S. belerius*	*I. strialatum*	*I. aculeatum*	
	S. lazus	*P. subinerme*	*S. bentori*	*P. zoharyi*	*I. paradoxum*	
	S. membranaceus	*P. compressum*	*S. delicatus*	*T. vancampoae*	*I. patulum*	
	S. mirabilis	*P. pentagonum*	*S. elongatus*	*P. leonis*	*I. sphaericum*	
	S. ramosus	*P. claudicans*	*S. lazus*	*P. conicum*	*I. strialatum*	
	S. ramosus s. Wall	*P. oblongum*	*S. membranaceus*	*P. pentagonum*		
	S. scabratus	*X. xanthum*	*S. mirabilis*	*P. schwartzii*		
	T. pellitum	*P. schwartzii*	*S. ramosus*			
	P. zoharyi		*S. ramosus s. Wall*			
Tropical	*L. machaerophorum*	*P. conicum*	*B. tepikiense*	*I. strialatum*	*B. tepikiense*	
	O. centrocarpum		*L. machaerophorum*	*P. zoharyi*	*L. machaerophorum*	
	O. israelianum		*N. labyrinthea*	*T. vancampoae*	*N. labyrinthea*	
	S. ramosus		*O. centrocarpum*	*P. leonis*	*O. centrocarpum*	
	S. ramosus s. Wall		*O. israelianum*	*P. conicum*	*I. aculeatum*	
	P. zoharyi		*S. ramosus*		*I. patulum*	
	T. vancampoae		*I. aculeatum*		*I. sphaericum*	
	P. leonis		*I. sphaericum*		*I. strialatum*	



TEXT-FIG. 44. North Atlantic showing the areas of different species diversity; blank areas 1–10 species, stippled areas 11–15 species, black areas 16–20 species.

dinoflagellate species, to develop an ecological/environmental classification, to determine the factors that influence distributions and to put forward a theoretical model to explain dinoflagellate cyst distributions. There are no great discrepancies between that and the present study and both the climatic and environmental trends are clearly visible in the maps herein and are summarized in Table 1, and this is also true for the inshore-offshore trend. Some differences are apparent in the species diversity distributions and unlike the study of Wall *et al.* (1977) this work does not show a consistent increase in diversity seaward but shows, for instance (text-fig. 44) an increase offshore in the eastern seaboard of North America but an increase towards the shore around the British Isles. This no doubt reflects the greater number of known cyst species around the British Isles due to the detailed work of Reid (1974, 1977).

The notion of specific species-water type relationships also appears to be borne out by the maps produced here as some close similarities are apparent between current patterns and cyst distributions.

High concentrations of particular cyst species also seem related to hydrographical effects, although particular cause-effect relationships are not dealt with here. There is then an intimate relationship between individual and grouped cyst species, water types, and hydrography. Further studies using cluster analysis and multidimensional scaling techniques are under way. Preliminary results show that reasonably sensible groups do occur and that they are linked to the hydrography of the area. The possibility of understanding the individual effects of latitude and hydrography upon the cyst distributions is real.

The comparison between the present work and that of Wall *et al.* (1977) can also be carried out on an individual species basis. This is done here for species where discrepancies are worth noting and where the data are particularly useful in interpreting the Quaternary dinoflagellate record.

(a) *Bitectatodinium tepikiense* Wilson—this species is categorized as an estuarine temperate species by Wall *et al.* (1977) based upon its occurrence in their samples but only to a maximum of 11% in one of their assemblages. The map published herein indicates maximum concentrations of over 50% in the area between Iceland and Scotland suggesting that it is more properly associated with a north-temperate oceanic to outer neritic environment. This also better compares with its rich occurrences in offshore Quaternary marine sediments.

(b) *Lingulodinium machaerophorum* (Deflandre and Cookson) Wall—the map presented here suggests a wider environmental niche than the cosmopolitan estuarine of Wall *et al.* (1977). It is probably a species that is tolerant of wide environmental fluctuations and can withstand both reductions and increases in salinity better than most. Alternatively its great specific variability *in toto* suggests the distinct possibility that several morphotypes, with ?differing ecological requirements, may be encompassed within the present diagnosis of the species.

(c) *Nematosphaeropsis labyrinthea* (Ostenfeld) Reid—the map herein largely supports the ecological grouping as given in Wall *et al.* (1977) but does highlight a major concentration of the cysts in the mid-Atlantic off Ireland, possibly associated with the eastern Atlantic gyre or the submarine topography of the area.

(d) *Operculodinium centrocarpum* (Deflandre and Cookson) Wall—the association with the North Atlantic Current is obvious together with the general cosmopolitanism of this cyst species. The high concentrations in arctic waters may be somewhat false in that it is probably an artificial effect due to the general reduction of other cyst species or alternatively it may indicate a possible real ecological preference for that habitat.

(e) *O. israelianum* (Rossignol) Wall—the map produced supports the tropical-subtropical estuarine or nearshore categorization of this cyst type (Wall *et al.* 1977) but its occurrence off the Iberian peninsula may be significant in relation to its presence in early Pleistocene assemblages in East Anglia and in offshore areas.

(f) *Spiniferites* spp.—although the *Spiniferites* group shows a preference for a cosmopolitan neritic environment many individual species appear linked to specific conditions, e.g. *S. bentori* (Rossignol) Wall and Dale, *S. lazus* Reid and *S. membranaceus* (Rossignol) Sarjeant. In contrast *S. elongatus* Reid appears to be a mainly north-temperate to arctic neritic to oceanic species whose potential for the interpretation of Quaternary sequences is good, and *S. mirabilis* (Rossignol) Sarjeant shows a centre of concentration in the eastern Atlantic with potential for the interpretation of Quaternary sequences from that area. Unfortunately the nature of the detailed ecological requirements of these species is still not known.

(g) *Tectatodinium pellitum* Wall—the map herein tends to show a rather more restricted distribution than the ecological classification of Wall *et al.* (1977) suggests. Its widespread occurrence in early Pleistocene sediments in East Anglia and offshore the British Isles at times of interpreted climatic deterioration (Wall and Dale 1968*a*) certainly needs some explanation.

(h) *Impagidinium* spp.—these species identify as tropical to temperate oceanic forms. However, their individual distributions show differences that are probably most significant and certainly in some Quaternary sequences the high percentages of particular species points to specific environmental conditions.

(i) *Polysphaeridium zoharyi* (Rossignol) Bujak *et al.*—the ecological classification of this species (Wall *et al.* 1977) is supported by the map published herein.

(j) *Tuberculodinium vancampoae* (Rossignol)—the map published herein supports the position of this species in terms of the ecological classification of Wall *et al.* (1977).

(k) *Protoperidinium* spp.—these species generally show a fairly cosmopolitan temperate to tropical, coastal to outer neritic/oceanic distribution. There is, however, much to be learned about individual species as this group is often not well speciated. In particular knowledge of the ecological requirements of *P. compressum* (Abé) Balech, *P. conicum* (Gran) Balech, and *P. subinerme* (Paulsen) Loeblich III would be most useful as these species regularly turn up in many offshore Quaternary sequences. Indeed many of the currently recognized species may in fact encompass several varieties or species and this is also an area in need of more investigation.

CONCLUSIONS

The series of maps produced have shown the distributions of forty-two extant dinoflagellate cyst species in the North Atlantic area based upon both published and unpublished data. The maps clearly show both the latitudinal–climatic and onshore–offshore trends already identified by Wall *et al.* (1977) and Reid and Harland (1977) and the influence of the oceanic current systems. It is obvious that much more is to be learnt concerning the ecological requirements of species but it is hoped that these maps may constitute some sort of basis to which other pieces of information can be added. Particular emphasis has been placed upon these species that turn up with some frequency in offshore marine Quaternary sequences as the potential in their use in interpreting the Quaternary history of climate and oceanography is great. Finally it must be stressed that the need to understand the living dinoflagellate in its natural habitat is paramount in understanding both the implications of this kind of work and in utilizing all the potential of this group in understanding past oceanographic realms.

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REFERENCES

ANDERSON, D. M. and WALL, D. 1978. Potential importance of benthic cysts of *Gonyaulax tamarensis* and *G. excavata* in initiating toxic dinoflagellate blooms. *J. Phycol.* **14,** 224–234.

BINNS, P. E., HARLAND, R. and HUGHES, M. J. 1974. Glacial and postglacial sedimentation in the Sea of the Hebrides. *Nature*, **248,** 751–754.

BRADFORD, M. R. 1975. New dinoflagellate cyst genera from the Recent sediments of the Persian Gulf. *Can. J. Bot.* **53,** 3064–3074.

BUJAK, J. P., DOWNIE, C., EATON, G. L. and WILLIAMS, G. L. 1980. Dinoflagellate cysts and acritarchs from the Eocene of southern England. *Palaeontology, Spec. Papers.* **24,** 1–100.

DALE, B. 1976. Cyst formation, sedimentation, and preservation: factors affecting dinoflagellate assemblages in Recent sediments from Trondheimsfjord, Norway. *Rev. Palaeobot. Palynol.* **22,** 39–60.

—— 1977. New observations on *Peridinium faeroense* Paulsen (1905), and classification of small orthoperidinioid dinoflagellates. *Br. phycol. J.* **12,** 241–253.

—— 1978. Acritarchous cysts of *Peridinium faeroense* Paulsen: implications for dinoflagellate systematics. *Palynology*, **2,** 187–193.

DODGE, J. D. 1977. The early summer bloom of dinoflagellates in the North Sea, with special reference to 1971. *Marine Biology*, **40,** 327–336.

——and HART-JONES, B. 1974. The vertical and seasonal distribution of dinoflagellates in the North Sea. *Botanica Marina*, **17,** 113–117.

—— —— 1977. The vertical and seasonal distribution of dinoflagellates in the North Sea. II. Blyth 1973–1974 and Whitby 1975. *Botanica Marina*, **20,** 307–311.

DOWNIE, C. and SINGH, G. 1969. Dinoflagellate cysts from estuarine and raised beach deposits at Woodgrange, Co. Down, N. Ireland. *Grana palynol.* **9,** 124–132.

GRAHAM, H. W. and BRONIKOWSKY, N. 1944. The genus *Ceratium* in the Pacific and North Atlantic Oceans. *Publs. Carnegie Inst., Washington*, **565,** 1–209.

GREGORY, D. and HARLAND, R. 1978. The late Quaternary climatostratigraphy of IGS Borehole SLN 75/33 and its application to the palaeoceanography of the north-central North Sea. *Scott. J. Geol.* **14,** 147–155.

—— —— and WILKINSON, I. P. 1978. Palaeontology of a series of boreholes through the drift of the Firth of Forth and the Forth Approaches. *In* THOMSON, M. E. IGS studies of the geology of the Firth of Forth and its Approaches. *Rep. Inst. Geol. Sci.* **77/17,** 41–48.

HARLAND, R. 1968. A microplankton assemblage from the post-Pleistocene of Wales. *Grana palynol.* **8,** 536–554.

—— 1973. Microplankton from boreholes in the lower reaches of the Firth of Clyde. *In* DEEGAN, C. E., KIRBY, R., RAE, I. and FLOYD, R. The superficial deposits of the Firth of Clyde and its sea lochs. *Rep. Inst. Geol. Sci.* **73/9,** 36–39.

—— 1974. Quaternary organic-walled microplankton from Boreholes 71/9 and 71/10. *In* BINNS, P. E., MCQUILLIN, R. and KENOLTY, N. The geology of the Sea of the Hebrides. *Rep. Inst. Geol. Sci.* **73/14,** 37–39.

—— 1977. Recent and late Quaternary (Flandrian and Devensian) dinoflagellate cysts from marine continental shelf sediments around the British Isles. *Palaeontographica Abt.B.* **164,** 87–126.

—— 1978. Modern and Quaternary organic-walled microplankton from the north-east Irish Sea. *In* PANTIN, H. M. Quaternary sediments from the north-east Irish Sea: Isle of Man to Cumbria. *Bull. Geol. Surv. G.B.* **64,** 41–43.

—— 1981. Cysts of the colonial dinoflagellate *Polykrikos schwartzii* Bütschli 1873, (Gymnodiniales), from Recent sediments, Firth of Forth, Scotland. *Palynology*, **5,** 65–79.

—— 1982*a*. A review of Recent and Quaternary organic-walled dinoflagellate cysts of the genus *Protoperidinium*. *Palaeontology*, **25,** 369–397.

—— 1982*b*. Recent dinoflagellate cyst assemblages from the southern Barents Sea. *Palynology*, **6,** 9–18.

——and DOWNIE, C. 1969. The dinoflagellates of the interglacial deposits at Kirmington, Lincolnshire. *Proc. Yorks. geol. Soc.* **37,** 231–237.

—— GREGORY, D. M., HUGHES, M. J. and WILKINSON, I. P. 1978. A late Quaternary bio- and climatostratigraphy for marine sediments in the north-central part of the North Sea. *Boreas*, **7,** 91–96.

—— REID, P. C., DOBELL, P. and NORRIS, G. 1980. Recent and sub-Recent dinoflagellate cysts from the Beaufort Sea, Canadian Arctic. *Grana*, **19,** 211–225.

HOLLIGAN, P. M. 1979. Dinoflagellate blooms associated with tidal fronts around the British Isles. Pp. 249–256. *In* TAYLOR, F. J. R. and SELIGER, H. (eds). *Toxic dinoflagellate blooms*. Elsevier North Holland, Amsterdam.

—— 1981. Biological implications of fronts on the northwest European continental shelf. *Phil. Trans. R. Soc. Lond.* A **302,** 547–562.

—— MADDOCK, L. and DODGE, J. D. 1980. The distribution of dinoflagellates around the British Isles in July 1977: a multivariate analysis. *J. mar. biol. Ass. U.K.* **60,** 851–867.

HUGHES, M. J., GREGORY, D. M., HARLAND, R. and WILKINSON, I. P. 1977. Late Quaternary foraminifera and dinoflagellate cysts from boreholes in the UK sector of the North Sea between 56° N and 58° N. *In* HOLMES, R. Quaternary deposits of the central North Sea 5. The Quaternary geology of the UK sector of the North Sea between 56° and 58° N. *Rep. Inst. Geol. Sci.* **77/14,** 36–46.

JAN DU CHÊNE, R. 1977. Étude palynologique du Miocene Superieur Andalou (Espagne). *Rev. Espanola Micropal.* **9,** 97–114.

MORZADEC-KERFOURN, M.-T. 1977. Les kystes de dinoflagellés dans les sédiments Récents le long des Côtes Bretonnes. *Rev. Micropaléont.* **20,** 157–166.

—— 1979. Les kystes de dinoflagellés. In: *Géologie Méditerranéenne, La Mer Pélagienne*, **6,** 221–246.

MUDIE, P. 1981*a*. Dinoflagellate cysts in Holocene sediments, eastern Canadian Arctic (Abs.). *Amer. Ass. Strat. Palynol., Program and Abstracts. New Orleans Meeting*, 36.

—— 1981*b*. Dinoflagellate cysts in Quaternary sediments around the Grand Banks, Canada (Abs.) *Amer. Ass. Strat. Palynol., Program and Abstracts. New Orleans Meeting*, 36–37.

PANTIN, H. M. 1978. Quaternary sediments from the north-east Irish Sea: Isle of Man to Cumbria. *Bull. Geol. Surv. G.B.* **64,** 1–43.

REID, P. C., 1972*a*. The distribution of dinoflagellate cysts, pollen and spores in Recent marine sediments from the coast of the British Isles. *Unpubl. Ph.D. thesis, Univ. of Sheffield*, 1–273.

—— 1972*b*. Dinoflagellate cyst distribution around the British Isles. *J. mar. biol. Ass. U.K.* **52,** 939–944.

—— 1974. Gonyaulacacean dinoflagellate cysts from the British Isles. *Nova Hedwigia*, **25,** 579–637.

—— 1975. A regional sub-division of dinoflagellate cysts around the British Isles. *New Phytol.* **75,** 589–603.

—— 1977. Peridiniacean and glenodiniacean dinoflagellate cysts from the British Isles. *Nova Hedwigia*, **29,** 429–463.

—— 1978. Dinoflagellate cysts in the plankton. *New Phytol.* **80,** 219–229.

—— and HARLAND, R. 1977. Studies of Quaternary dinoflagellate cysts from the North Atlantic. *Amer. Assoc. Strat. Palynol., Contr. Ser.* **5A,** 147–169.

ROSSIGNOL, M. 1964. Hystrichosphères du Quaternaire en Méditerranée orientale, dans les sédiments Pléistocènes et les boues marines actuelles. *Rev. Micropaléont.* **7,** 83–99.

STEIDINGER, K. A. and DAVIS, J. T. 1967. The genus *Pyrophacus*, with a description of a new form. *Fla. Bd. Conserv. Mar. Lab. Leaflet Ser.* **1,** 1–8.

STOVER, L. E. and EVITT, W. R. 1978. Analyses of pre-Pleistocene organic-walled dinoflagellates. *Stanford Univ. Publ., Geol. Sci.* **15,** 1–298.

TURON, J.-L. 1980. Dinoflagellés et environnement climatique. Les kystes de dinoflagellés dans les sédiments Récents de l'Atlantique nord-oriental et leurs relations avec l'environnement océanique. Application aux dépôts Holocènes du Chenal de Rockall. *Mem. Mus. Hist. Nat.* **B 27,** 269–282.

WALL, D. 1967. Fossil microplankton in deep-sea cores from the Caribbean Sea. *Palaeontology*, **10,** 95–123.

—— and DALE, B. 1968*a*. Early Pleistocene dinoflagellates from the Royal Society Borehole at Ludham, Norfolk. *New Phytol.* **67,** 315–326.

—— —— 1968*b*. Modern dinoflagellate cysts and evolution of the Peridiniales. *Micropaleontology* **14,** 265–304.

—— —— LOHMANN, G. P. and SMITH, W. K. 1977. The environmental and climatic distribution of dinoflagellate cysts in Modern marine sediments from regions in the North and South Atlantic Oceans and adjacent seas. *Mar. Micropaleontol.* **2,** 121–200.

WILLIAMS, D. B. 1965. The distribution and palaeontology of microplankton in Recent marine sediments. *Unpubl. Ph.D. thesis, Univ. of Reading*, 1–289.

—— 1971. The occurrence of dinoflagellates in marine sediments. Pp. 231–243. *In* FUNNELL, B. M. and RIEDEL, W. R. (eds.). *Micropalaeontology of Oceans*, Cambridge University Press.

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APPENDICES

I SAMPLE LOCALITY DATA

The samples studied, their localities, sources of data, and the authors responsible for the original percentage counts of the contained dinoflagellate cyst assemblages are listed below. The Institute of Geological Sciences registered numbers and the British Museum (Natural History) catalogue numbers are also included where applicable. Latitude and longitude are quoted to the nearest minute.

Sample No.	*Locality*	*Author*	*IGS Reg. No.*	*B.M.(N.H.) Cat. No.*
1	44°01′N.; 68°30′W.	Wall *et al.* (1977)	—	—
2	40°18′N.; 67°00′W.	,, ,,	—	—
3	40°28′N.; 69°31′W.	,, ,,	—	—
4	39°08′N.; 69°28′W.	,, ,,	—	—
5	40°54′N.; 70°45′W.	,, ,,	—	—
6	38°59′N.; 70°29′W.	,, ,,	—	—
7	38°14′N.; 72°16′W.	,, ,,	—	—
8	37°02′N.; 75°54′W.	,, ,,	—	—

Sample No.	*Locality*	*Author*	*IGS Reg. No.*	*B.M. (N.H.) Cat. No.*
9	35°24′N.; 75°42′W.	Wall *et al.* (1977)	—	—
10	33°02′N.; 79°33′W.	,, ,,	—	—
11	31°14′N.; 81°14′W.	,, ,,	—	—
12	32°15′N.; 64°50′W.	,, ,,	—	—
13	24°13′N.; 78°09′W.	,, ,,	—	—
14	17°57′N.; 76°44′W.	,, ,,	—	—
15	18°01′N.; 67°12′W.	,, ,,	—	—
16	10°21′N.; 61°48′W.	,, ,,	—	—
17	62°10′N.; 05°59′E.	,, ,,	—	—
18	60°11′N.; 05°13′E.	,, ,,	—	—
19	57°04′N.; 17°37′E.	,, ,,	—	—
20	42°16′N.; 07°11′E.	,, ,,	—	—
21	33°56′N.; 19°39′E.	,, ,,	—	—
22	32°33′N.; 25°15′E.	,, ,,	—	—
23	35°45′N.; 25°15′E.	,, ,,	—	—
24	34°47′N.; 13°09′E.	,, ,,	—	—
25	29°00′N.; 47°28′W.	,, ,,	—	—
26	28°09′N.; 15°25′E.	,, ,,	—	—
27	01°29′N.; 19°43′W.	,, ,,	—	—
28	05°00′N.; 03°34′W.	,, ,,	—	—
29	56°03′N.; 03°30′W.	Harland (1981)	CSB 2066–2085 2266–2285	—
30	73°20′N.; 25°29′E.	,, (1982*b*)	2305	1957, 328(3)
31	71°15′N.; 27°54′E.	,, ,,	2306	1957, 328(6)
32	71°28′N.; 38°20′E.	,, ,,	2308	1957, 328(16)
33	73°28′N.; 41°19′E.	,, ,,	2310	1957, 328(23)
34	69°28′N.; 41°27′E.	,, ,,	2311	1957, 328(30)
35	70°28′N.; 43°28′E.	,, ,,	2312	1957, 328(31)
36	70°31′N.; 10°46′E.	,, (unpubl.)	2314	1957, 328(52)
37	70°29′N.; 04°30′E.	,, ,,	2315	1957, 328(54)
38	69°30′N.; 01°18′E.	,, ,,	2316	1957, 328(56)
39	69°29′N.; 01°24′E.	,, ,,	2317	1957, 328(57)
40	66°31′N.; 03°28′E.	,, ,,	2318	1957, 328(58)
41	66°30′N.; 11°00′E.	,, ,,	2319	1957, 328(72)
42	69°29′N.; 13°12′E.	,, ,,	2320	1957, 328(81)
43	71°28′N.; 13°37′E.	,, ,,	2321	1957, 328(90)
44	67°36′N.; 10°33′W.	,, ,,	2322	1962, 160(10)
45	67°19′N.; 13°25′W.	,, ,,	2323	1962, 160(13)
46	54°00′N.; 04°00′W.	,, (1977)	CSA 96–150	—
47	57°00′N.; 07°00′W.	,, ,,	composite	—
48	59°23′N.; 03°29′E.	,, (unpubl.)	CSA 1332, 1292	—
49	55°22′N.; 05°30′W.	,, (1977)	composite	—
50	58°04′N.; 00°34′E.	,, ,,	CSA 1533	—
51	Sample of reworked older material; removed from data			—
52	58°30′N.; 00°20′E.	Harland (unpubl.)	composite	—
53	60°00′N.; 00°00′E.	,, ,,	composite	—
54	58°07′N.; 03°40′W.	Reid (1972*b*, 1974, 1975, 1977)	—	—
55	54°17′N.; 00°24′W.	,, ,,	—	—
56	51°20′N.; 01°25′E.	,, ,,	—	—
57	50°47′N.; 00°03′E.	,, ,,	—	—
58	50°10′N.; 05°20′W.	,, ,,	—	—
59	51°42′N.; 04°56′W.	,, ,,	—	—
60	52°43′N.; 04°03′W.	,, ,,	—	—
61	51°55′N.; 08°16′W.	,, ,,	—	—
62	52°35′N.; 09°30′W.	,, ,,	—	—
63	54°20′N.; 09°35′W.	,, ,,	—	—

Sample No.	*Locality*	*Author*	*IGS Reg. No.*	*B.M. (N.H.) Cat. No.*
64	55° 12′ N.; 07° 52′ W.	Reid (1972*b*, 1974, 1975, 1977)	—	—
65	57° 40′ N.; 06° 50′ W.	,, ,,	—	—
66	58° 25′ N.; 04° 30′ W.	,, ,,	—	—
67	16° 19′ N.; 70° 29′ W.	Williams (1965)	—	D9.38
68	32° 06′ N.; 64° 30′ W.	,, ,,	—	D15.4
69	06° 03′ N.; 15° 08′ W.	,, ,,	—	D21.12
70	30° 00′ N.; 59° 58′ W.	,, ,,	—	D23.16
71	20° 00′ N.; 60° 02′ W.	,, ,,	—	D23.22
72	Data not available: position taken from thesis figure	,, ,,	—	M25
73	″ ″ ″	,, ,,	—	M69
74	09° 29′ N.; 27° 59′ W.	,, ,,	—	M4630
75	20° 14′ N.; 19° 22′ W.	,, ,,	—	M4751
76	10° 18′ N.; 30° 19′ W.	,, ,,	—	M4632
77	31° 15′ N.; 75° 08′ W.	,, ,,	—	M7380
78	38° 53′ N.; 25° 09′ W.	,, ,,	—	M9036
79	21° 00′ N.; 75° 05′ W.	,, ,,	—	M9070
80	21° 05′ N.; 74° 56′ W.	,, ,,	—	M9071
81	43° 21′ N.; 52° 24′ W.	,, ,,	—	M9110
82	42° 56′ N.; 40° 19′ W.	,, ,,	—	M9113
83	45° 53′ N.; 39° 26′ W.	,, ,,	—	M9114
84	45° 26′ N.; 09° 20′ W.	,, ,,	—	M9711
85	28° 08′ N.; 13° 35′ W.	,, ,,	—	M9722
86	31° 20′ N.; 35° 07′ W.	,, ,,	—	M9728
87	47° 32′ N.; 16° 38′ W.	,, ,,	—	M9737
88	Data not available: position taken from thesis figure	,, ,,	—	SM 231
89	40° 07′ N.; 25° 22′ W.	,, ,,	—	SM 876
90	14° 01′ N.; 64° 31′ W.	,, ,,	—	1938, 1290(5)
91	47° 44′ N.; 25° 26′ W.	,, ,,	—	1954, 40(6)
92	41° 49′ N.; 09° 34′ W.	,, ,,	—	1956, 389(22)
93	33° 27′ N.; 09° 21′ W.	,, ,,	—	1957, 648(57)
94	30° 30′ N.; 14° 11′ W.	,, ,,	—	1957, 648(63)
95	30° 03′ N.; 42° 16′ W.	,, ,,	—	1962, 333
96	10° 07′ N.; 58° 32′ W.	,, ,,	—	1962, 338
97	10° 00′ N.; 46° 53′ W.	,, ,,	—	1962, 345
98	09° 58′ N.; 42° 50′ W.	,, ,,	—	1962, 346
99	07° 58′ N.; 36° 19′ W.	,, ,,	—	1962, 347
100	52° 42′ N.; 36° 05′ W.	Turon (1980)	—	—
101	57° 56′ N.; 29° 08′ W.	,, ,,	—	—
102	62° 01′ N.; 24° 29′ W.	,, ,,	—	—
103	61° 20′ N.; 18° 26′ W.	,, ,,	—	—
104	63° 01′ N.; 01° 59′ W.	,, ,,	—	—
105	61° 59′ N.; 02° 30′ W.	,, ,,	—	—
106	58° 05′ N.; 10° 43′ W.	,, ,,	—	—
107	56° 19′ N.; 11° 33′ W.	,, ,,	—	—
108	55° 36′ N.; 14° 29′ W.	,, ,,	—	—
109	51° 28′ N.; 17° 41′ W.	,, ,,	—	—
110	50° 09′ N.; 17° 22′ W.	,, ,,	—	—
111	46° 46′ N.; 08° 41′ W.	,, ,,	—	—
112	45° 05′ N.; 02° 57′ W.	,, ,,	—	—
113	45° 28′ N.; 13° 31′ W.	,, ,,	—	—
114	40° 55′ N.; 10° 35′ W.	,, ,,	—	—
115	34° 49′ N.; 26° 12′ W.	,, ,,	—	—

Sample No.	*Locality*	*Author*	*IGS Reg. No.*	*B.M. (N.H.) Cat. No.*
116	27°29′ N.; 64°59′ W.	Harland (unpubl.)	CSB 3267	M49
117	35°35′ N.; 50°27′ W.	,, ,,	CSB 3268	M86
118	28°17′ N.; 15°06′ W.	,, ,,	CSB 3269	M3608
119	28°25′ N.; 14°46′ W.	,, ,,	CSB 3270	M3609
120	20°20′ N.; 19°35′ W.	,, ,,	CSB 3271	M4752
121	21°07′ N.; 18°49′ W.	,, ,,	CSB 3272	M4756
122	22°38′ N.; 18°30′ W.	,, ,,	CSB 3273	M4762
123	23°46′ N.; 18°09′ W.	,, ,,	CSB 3274	M4766
124	25°10′ N.; 16°58′ W.	,, ,,	CSB 3275	M4770
125	26°11′ N.; 16°25′ W.	,, ,,	CSB 3276	M4777
126	26°27′ N.; 15°15′ W.	,, ,,	CSB 3277	M4782
127	25°31′ N.; 54°40′ W.	,, ,,	CSB 3279	M7337
128	26°32′ N.; 56°45′ W.	,, ,,	CSB 3280	M7338
129	32°43′ N.; 47°30′ W.	,, ,,	CSB 3281	M7393
130	24°56′ N.; 24°46′ W.	,, ,,	CSB 3282	M7397
131	56°11′ N.; 37°41′ W.	,, ,,	CSB 3283	M8777
132	28°08′ N.; 13°35′ W.	,, ,,	CSB 3284	M9722
133	50°22′ N.; 11°44′ W.	,, ,,	CSB 3285	M9739
134	23°20′ N.; 59°58′ W.	,, ,,	CSB 3286	D23.20
135	51°55′ N.; 23°03′ W.	,, ,,	CSB 3288	1953, 164(6)
136	55°03′ N.; 23°59′ W.	,, ,,	CSB 3289	1953, 164(7)
137	55°13′ N.; 22°37′ W.	,, ,,	CSB 3290	1954, 40(5)
138	55°19′ N.; 11°02′ W.	,, ,,	CSB 3291	1954, 41(3)
139	56°24′ N.; 20°07′ W.	,, ,,	CSB 3292	1954, 41(4)
140	50°06′ N.; 21°54′ W.	,, ,,	CSB 3293	1954, 41(8)
141	47°43′ N.; 04°55′ W.	Morzadec-Kerfourn (1977)	—	—
142	35°59′ N.; 11°51′ E.	,, ,, (1979)	—	—
143	34°45′ N.; 13°04′ E.	,, ,, ,,	—	—

II DINOFLAGELLATE TAXA

The dinoflagellate taxa included in this study, their thecal equivalence and the relevant plate and figures in this publication are listed below.

DIVISION Pyrrhophyta Pascher 1914
CLASS Dinophyceae Fritsch 1929
ORDER Peridiniales Haeckel 1894

Family Gonyaulacaceae Lindemann 1928

Reference No	Cyst Name	Thecate Name	Figure
1	*Achomosphaera andalousiense* Jan du Chêne	?*Gonyaulax* sp. indet.	Pl. 43, figs. 1, 2
2	*Bitectatodinium tepikiense* Wilson	*G. spinifera* (Claparède & Lachmann) Diesing	Pl. 43, figs. 3, 4
3	*Lingulodinium machaerophorum* (Deflandre and Cookson) Wall	*G. polyedra* Stein	Pl. 43, figs. 5, 6
4	*Nematosphaeropsis labyrinthea* (Ostenfeld) Reid	*G. spinifera* (Claparède and Lachmann) Diesing	Pl. 43, figs. 7, 8
5	*Operculodinium centrocarpum* (Deflandre and Cookson) Wall	*G. grindleyi* (Reinecke) Von Stosch	Pl. 43, figs. 9, 10
6	*O. israelianum* (Rossignol) Wall	*G.* sp. indet? *grindleyi* (Reinecke) Von Stosch	Pl. 43, figs. 11, 12
7	*Spiniferites belerius* Reid	?*G. scrippsae* Kofoid	Pl. 44, figs. 1, 2
8	*S. bentori* (Rossignol) Wall and Dale	*G. digitalis* (Pouchet) Kofoid	Pl. 44, figs. 3, 4
9	*S. delicatus* Reid	*Gonyaulax* sp. indet.	Pl. 44, figs. 5, 6
10	*S. elongatus* Reid [incl. *S. frigidus* Harland and Reid]	*G. spinifera* (Claparède and Lachmann) Diesing	Pl. 44, figs. 7–10
11	*S. lazus*	*Gonyaulax* sp. indet.	Pl. 44, figs. 11, 12
12	*S. membranaceus* (Rossignol) Sarjeant	*G. spinifera* (Claparède and Lachmann) Diesing	Pl. 45, figs. 3, 4
13	*S. mirabilis* (Rossignol) Sarjeant	*G. spinifera* (Claparède and Lachmann) Diesing	Pl. 45, figs. 1, 2
14	*S. ramosus* (Ehrenberg) Mantell	*G. scrippsae* Kofoid	Pl. 45, figs. 5, 6
15	*S. ramosus* (Ehrenberg) Mantell *sensu* Wall	*G. spinifera* (Claparède and Lachmann) Diesing	Pl. 45, fig. 8
16	*S. scabratus* Wall	*Gonyaulax* sp. indet.	Pl. 45, fig. 7
17	*Spiniferites* spp. indet.	*Gonyaulax* spp. indet.	
19	*Tectatodinium pellitum*	*Gonyaulax* sp. indet.	Pl. 45, fig. 9
20	*Impagidinium aculeatum* (Wall) comb. nov.	*Gonyaulax* sp. indet.	Pl. 46, figs. 1–3
21	*I. paradoxum* (Wall) Stover and Evitt	*Gonyaulax* sp. indet.	Pl. 46, figs. 4, 5
22	*I. patulum* (Wall) Stover and Evitt	*Gonyaulax* sp. indet.	Pl. 46, figs. 6, 7
23	*I. sphaericum* (Wall) comb. nov.	*Gonyaulax* sp. indet.	Pl. 46, figs. 8, 9
24	*I. strialatum* (Wall) Stover and Evitt	*Gonyaulax* sp. indet.	Pl. 46, figs. 10–12
26	*Polysphaeridium zoharyi* (Rossignol) Bujak *et al.*	*Pyrodinium bahamense* Plate	Pl. 46, fig. 10

	Family Pyrophacaceae Lindemann 1928		
27	*Tuberculodinium vancampoae* (Rossignol) Wall	*Pyrophacus* Form B1, Steidinger and Davis	Pl. 45, fig. 11
	Family Peridiniaceae Ehrenberg 1832		
28	*Brigantedinium* sp. nov.	*Protoperidinium* (*Protoperidinium*) *punctulatum* (Paulsen) Balech	Pl. 47, fig. 1
29	*B. simplex* (Wall) Reid	*P.* (*Protoperidinium*) *conicoides* (Paulsen) Balech	Pl. 47, figs. 2, 3
30	*B. cariacoense* (Wall) Reid	*P.* (*Archaeperidinium*) *avellana* (Meunier) Balech	Pl. 47, fig. 4
31	*Brigantedinium* sp. nov.	*P.* (*Archaeperidinium*) *denticulatum* (Gran and Braarud) Balech	Pl. 47, fig. 6
32	*Lejeunia paratenella* Benedek	*Protoperidinium* sp. indet.	Pl. 47, fig. 5
33	*Quinquecuspis concretum* (Reid) Harland	*P.* (*Protoperidinium*) *leonis* (Pavillard) Balech	Pl. 47, figs. 7, 8
34	*Selenopemphix quanta* (Bradford) comb. nov.	*P.* (*Protoperidinium*) *conicum* (Gran) Balech	Pl. 47, figs. 9, 10
35	*Selenopemphix* sp. nov.	*P.* (*Protoperidinium*) *nudum* (Meunier) Balech	Pl. 48, fig. 5
36	*S. nephroides* Benedek	*P.* (*Protoperidinium*) *subinerme* (Paulsen) Loeblich III	Pl. 48, fig. 11, 12
37	*Stelladinium stellatum* (Wall) Reid	*P.* (*Archaeperidinium*) *compressum* (Abé) Balech	Pl. 48, fig. 1
38	*Trinovantedinium capitatum* Reid	*P.* (*Protoperidinium*) *pentagonum* (Gran) Balech	Pl. 48, figs. 2, 3
39	*Votadinium spinosum* Reid	*P.* (*Protoperidinium*) *claudicans* (Paulsen) Balech	Pl. 48, fig. 4
40	*Votadinium calvum* Reid	*P.* (*Protoperidinium*) *oblongum* (Aurivillius) Balech	Pl. 48, figs. 6, 7
41	*Xandarodinium xanthum* Reid	?*Protoperidinium* sp. indet.	Pl. 48, fig. 8
42	Cyst-type B of Harland	*Protoperidinium* sp. indet.	Pl. 48, fig. 9
	ORDER Gymnodiniales Lemmermann 1910		
	Family Polykrikaceae Kofoid and Swezy 1921		
45	Cyst nov.	*Polykrikos schwartzii* Bütschli	Pl. 48, figs. 10–12

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5	*Operculodinium centrocarpum* (Deflandre and Cookson) Wall	*G. grindleyi* (Reinecke) Von Stosch	Pl. 43, figs 9, 10
6	*O. israelianum* (Rossignol) Wall	*G.* sp. indet? *grindleyi* (Reinecke) Von Stosch	Pl. 43, figs 11, 12
7	*Spiniferites belerius* Reid	?*G. scrippsae* Kofoid	Pl. 44 figs 1, 2
8	*S. bentori* (Rossignol) Wall and Dale	*G. digitalis* (Pouchet) Kofoid	Pl. 44, figs. 3, 4
9	*S. delicatus* Reid	*Gonyaulax* sp. indet	Pl. 44, figs 5, 6
10	*S. elongatus* Reid [incl. *S. frigidus* Harland and Reid]	*G. spinifera* (Claparede and Lachmann) Diesing	Pl. 44, figs. 7-10
11	*S. lazus*	*Gonyaulax* sp. indet.	Pl. 44, figs 11, 12
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16	*S. scabratus* Wall	*Gonyaulax* sp. indet	Pl. 45, fig. 7
17	*Spiniferites* spp. indet	*Gonyaulax* spp. indet.	
19	*Tectatodinium pellitum*	*Gonyaulax* sp. indet.	Pl. 45, fig 9
20	*Impagidinium aculeatum* (Wall) comb. nov	*Gonyaulax* sp. indet.	Pl. 46, figs. 1-3
21	*I. paradoxum* (Wall) Stover and Evitt	*Gonyaulax* sp. indet.	Pl. 46, figs. 4, 5
22	*I. patulum* (Wall) Stover and Evitt	*Gonyaulax* sp. indet	Pl. 46, figs 6, 7
23	*I. sphaericum* (Wall) comb. nov	*Gonyaulax* sp. indet.	Pl. 46, figs 8, 9
24	*I. strialatum* (Wall) Stover and Evitt	*Gonyaulax* sp. indet.	Pl. 46, figs. 10-12
26	*Polysphaeridium zoharyi* (Rossignol) Bujak *et al*	*Pyrodinium bahamense* Plate	Pl. 46, fig. 10

Family Pyrophacaceae Lindemann 1928

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29	*B. simplex* (Wall) Reid	*P.* (*Protoperidinium*) *conicoides* (Paulsen) Balech	Pl. 47, figs 2, 3
30	*B. cariacoense* (Wall) Reid	*P.* (*Archaeperidinium*) *avellana* (Meunier) Balech	Pl. 47, fig. 4
31	*Brigantedinium* sp. nov	*P.* (*Archaeperidinium*) *denticulatum* (Gran and Braarud) Balech	Pl. 47, fig. 6
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35	*Selenopemphix* sp. nov.	*P.* (*Protoperidinium*) *nudum* (Meunier) Balech	Pl. 48, fig. 5
36	*S. nephroides* Benedek	*P.* (*Protoperidinium*) *subinerme* (Paulsen) Loeblich III	Pl. 48, fig. 11, 12
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ORDER Gymnodiniales Lemmermann 1910
Family Polykrikaceae Kofoid and Swezy 1921

45	Cyst nov	*Polykrikos schwartzii* Bütschli	Pl. 48, figs. 10-12

A NEW GENUS OF TRIASSIC DICYNODONT FROM EAST AFRICA AND ITS CLASSIFICATION

by C. BARRY COX *and* LI, JIN-LING

ABSTRACT. A new Triassic dicynodont *Angonisaurus cruikshanki* gen. et sp. nov. from the Manda Formation of Tanzania is described. The specimen is considered to be closely related to *Tetragonias* from the same Formation and belongs to the same family, the Shansiodontidae. The classification of Triassic dicynodonts is reviewed. Using the characteristics of snout shape and length, proportion of preorbital and postorbital region, and degree of obliquity of occiput, most genera are put into the three families Kannemeyeriidae, Stahleckeriidae, and Shansiodontidae, which were suggested by Cox (1965). The criteria for the classification are also discussed.

VERTEBRATE fossils were first found in the Ruhuhu Valley of south-western Tanzania by Stockley in 1930 (Stockley 1932). Further collections were made by German and British workers in the 1930s (Nowack 1937; Parrington 1936), and it became clear that the Permian and Triassic deposits contained a rich fauna. A joint collecting expedition of the British Museum (Natural History) and University of London therefore spent two months in the area in 1963 (Attridge *et al.* 1963). As a result, 450 specimens, weighing 2–3 tons, were collected from the Late Permian and Triassic deposits of the area. The Triassic fossils were found in the eroding land-surface (particularly in the dry stream gullies) of an area between the Mhimbasi and Lipinda streams, which ran northwards into the Rutukira River, itself a tributary of the Ruhuhu River.

The fauna of the Triassic Manda Formation (Charig 1963, 'Upper Bone Bed' of earlier workers) includes the rhynchosaur *Stenaulorhynchus* (von Huene 1938*a*), trirachodont and traversodont cynodonts (Crompton 1955, 1972), prestosuchid pseudosuchians (von Huene 1938*b*) and dicynodonts (Cruickshank 1965, 1967). This faunal assemblage suggests that the Manda Formation is of Middle Triassic age, while the similarity between the Manda pseudosuchian *Mandasuchus* and *Ticinosuchus* of Monte San Giorgio, Switzerland, suggests that its age is approximately uppermost Anisian (Cox 1973).

SYSTEMATIC PALAEONTOLOGY

Suborder ANOMODONTIA
Infraorder DICYNODONTIA
Genus *Angonisaurus* gen. nov.

Diagnosis. Skull high, medium size, approximately triangular in dorsal view. Squamosal extends far laterally. Width of skull greater than length. Snout rounded and blunt. Preorbital region short but postorbital region long (about 50 % of the length of the skull). Temporal fenestra large, rectangular. Interorbital bar wide. Intertemporal bar wide ventrally, but tapers upwards to a narrow crest on which a more narrow, deep groove exists. Tuskless, but caniniform process triangular and strong, nasal boss present. Orbits directed laterally. Occiput high and slightly oblique (height is about 65 % of its width), so that the lower jaw is short.

Derivation of name. After the local Tanzanian tribe, the Angoni.

[Palaeontology, Vol. 26, Part 2, 1983, pp. 389–406.]

Angonisaurus cruickshanki gen. et sp. nov.

Text-figs. 1–5

Diagnosis. As for genus.

Derivation of name. In honour of Dr. A. R. I. Cruickshank, who helped to collect the specimen and also prepared it.

Holotype. Skull, lower jaw, left pectoral and left pelvic girdle, vertebrae, and ribs (field number U12/1: B.M.(N.H.) R 9732).

Locality. 0·5 km north of the Hita stream-bed, and about 1·7 km south-east of the Rutukira river.

Horizon. The lowest fossiliferous level in the Manda Formation; Middle Triassic, probably uppermost Anisian.

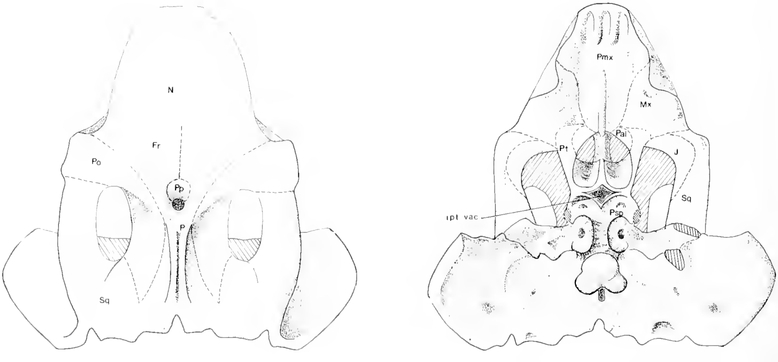
Description. The skull is almost complete, but is slightly distorted: the left side of the skull is shortened and the right side is extended, causing deformation of the shape of the orbits and angle of the occipital wing of the squamosal. Only a few parts of the skull are missing.

Dorsal view (text-fig. 1*b*). The maximum dimensions of the skull are 30 cm long and 33 cm broad. The pineal foramen lies at the bottom of a deep conical pit which includes also the preparietal bone. This pit also extends posteriorly as a deep groove down the midline of the intertemporal bar, flanked by ridges formed by the postorbitals and parietals. The orbits are directed laterally. The interorbital region is wide (13 cm). It is impossible to trace the sutures in this region because of the massive nature of the bone.

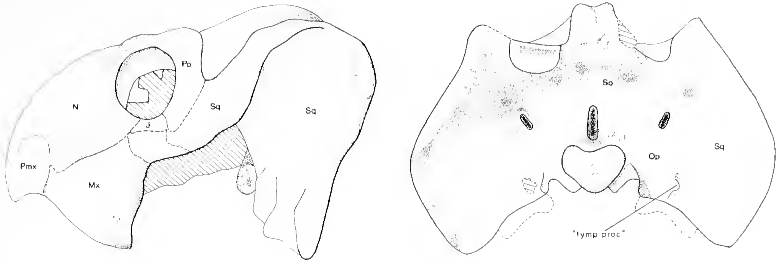
Lateral view (text-fig. 2*b*). The skull is tuskless, but the caniniform process of the maxilla is strong and has a stout, straight posterior edge. There appears to have been a low roughened boss above the external naris but the latter is damaged. The median interorbital ossification called variously the sphenethmoid (Cox 1959) or septosphenoid (Sun 1963) is well preserved. It is in contact with the processus cultriformis, so as to close the front wall of the braincase. The epipterygoid is missing.

Palatal view (text-fig. 1*a*). As preserved, the palate is narrow and rectangular. The pterygoid region is damaged, but it is clear that the interpterygoid vacuity is short, as in most Triassic dicynodonts. Two pairs of curved ridges meet anteriorly, posteriorly, and laterally to enclose the interpterygoid vacuity (text-fig. 1*b*, ipt. vac.), which is shaped like a diamond with curved sides. No labial fossa can be seen. The sutures between the basioccipital, basisphenoid, and parasphenoid cannot be distinguished.

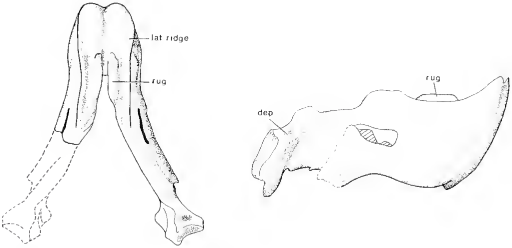
Occipital view (text-fig. 2*a*). The upper rim of the occiput turns backward strongly to form a distinct flange. The jugular foramen is absent. There is a pair of low bosses slightly dorso-lateral to the exoccipital condyle. The



TEXT-FIG. 1. *Angonisaurus cruickshanki*, type specimen. Skull in dorsal view and palatal view, ×$\frac{1}{5}$. ipt. vac., interpterygoid vacuity.



TEXT-FIG. 2. *Angonisaurus cruickshanki*, type specimen. Skull in lateral view and occipital view, × $\frac{1}{5}$. 'tymp. proc.', tympanic process.

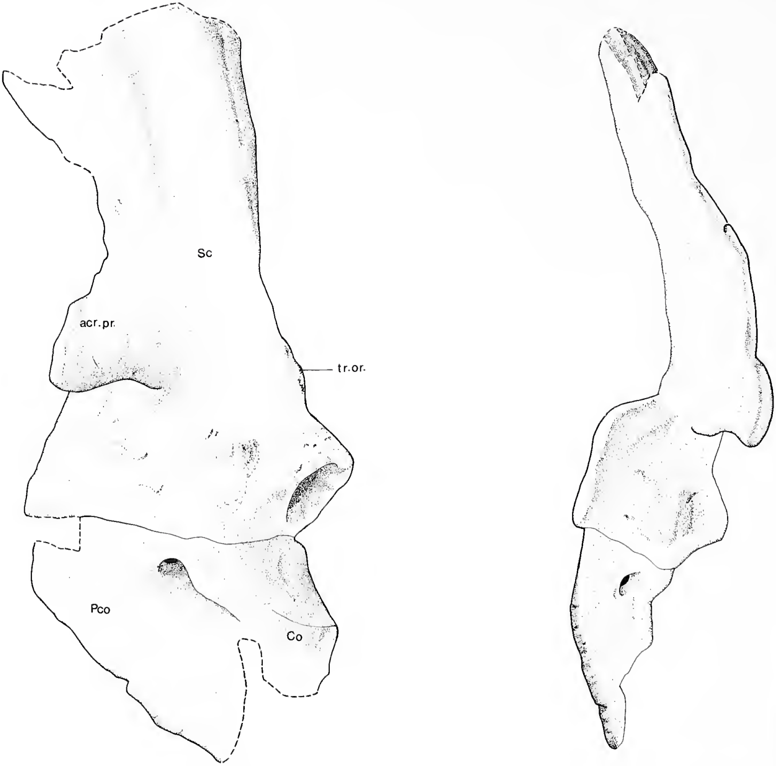


TEXT-FIG. 3. *Angonisaurus cruickshanki*, type specimen. Lower jaw in dorsal and lateral view, × $\frac{1}{5}$. dep., depression; lat. ridge, lateral ridge; rug., rugosity.

posttemporal fossa is small. The paroccipital process bears a distinct process similar to the 'tympanic process' of *Kingoria* (Cox, 1959). From this process an irregular low ridge extends up to a position lateral to the posttemporal fossa.

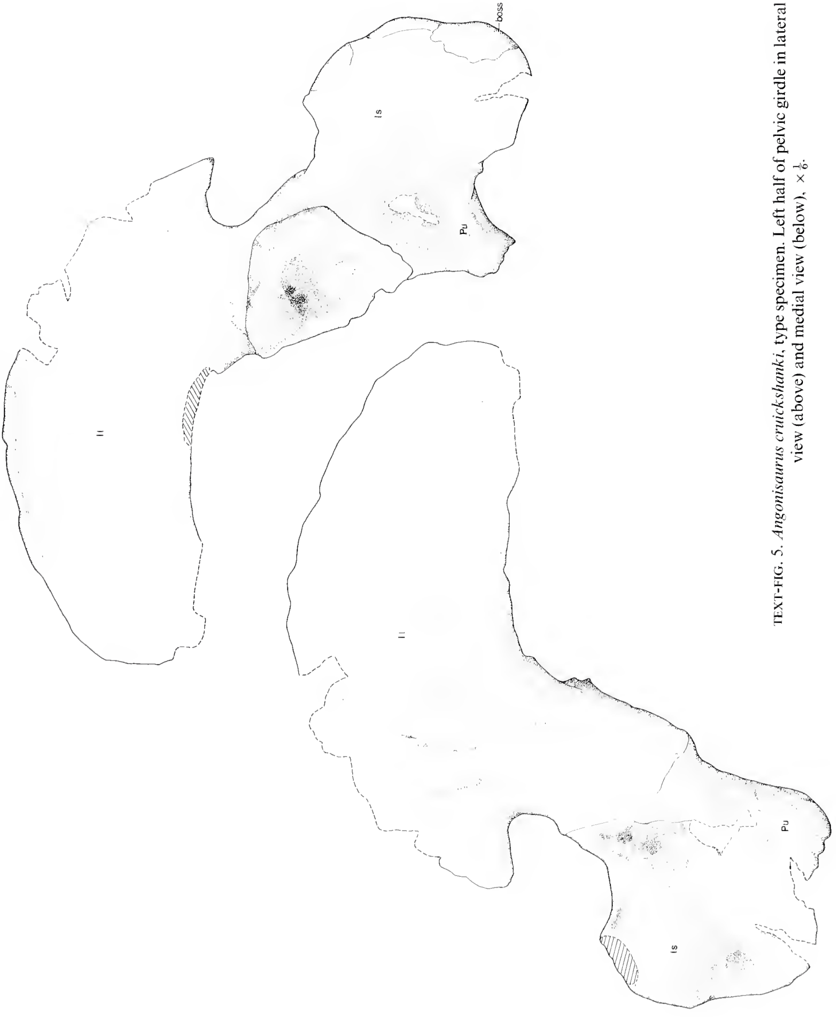
On the left side, the dorsal part of the occiput bears a strong, posteriorly directed process, the end of which is concave. There is some trace of this also on the right side, but the process is smaller and does not have a concave end. It is impossible to tell whether this difference is natural or due to damage, and such a process is unknown in other dicynodonts.

Lower jar (text-fig. 3). The posterior half of the left ramus of the lower jaw has been lost and the dorsal surface of the right ramus was damaged. The symphyseal region is rectangular in dorsal view, long and deep in lateral view. A pair of lateral dentary ridges turn a little upwards on the tip of beak. A pair of elongate rugosities lies on the inner margin of the dentary rami. The curved articular surface which corresponds with the external condyle is long and smooth. Anterior to it on the upper surface of the lower jaw there is a depression which does not show a smooth surface; this may have received the quadrate when retracted.



TEXT-FIG. 4. *Angonisaurus cruickshanki*, type specimen. Left scapulo-coracoid in lateral view (left) and anterior view (right), × $\frac{1}{6}$. acr. pr.: acromion process; tr. or.: origin of triceps muscle.

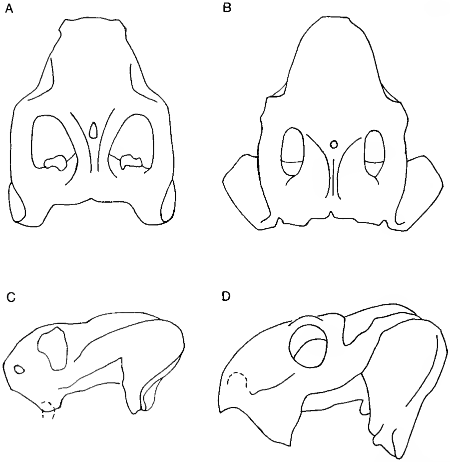
Pectoral girdle (text-fig. 4). The left scapula, clavicle, coracoid, and precoracoid are preserved, but the sternum is missing. The upper part of the scapula is not present; judging from the remaining part, it was rather stout. Its preserved length is 35 cm, the width from its antero-ventral corner to the postero-dorsal corner of the glenoid is 18 cm, and its narrowest width (at the level of the base of the acromion process) is 8 cm. It is slightly curved. The projecting acromion process has a concave distal end. Above the glenoid cavity there is a roughened ridge, running up the length of the bone for 3·5 cm (text-fig. 4, tr. or.). As to the function of this process in the related genus *Tetragonias*, Cruickshank (1967, p. 180) stated: '. . . At a point level with the acromion, and somewhat on the external face of the bone there is a knob 1 cm high and 1 cm in diameter probably marking the origin of the triceps.' In *Angonisaurus* the process is lower than the level of the base of the acromion. The upper part of the precoracoid and the lower part of the coracoid are damaged. They are fused together, but the suture cannot be traced. The coracoid foramen is small, round and opens downwards in external view.



TEXT-FIG. 5. *Angonisaurus cruickshanki*, type specimen. Left half of pelvic girdle in lateral view (above) and medial view (below), × $\frac{1}{6}$.

Pelvic girdle (text-fig. 5.) Only the left ilium, pubis, and ischium are present. The anterior part of the blade of the ilium is extremely expanded, so that this bone is larger than in other dicynodonts. The external surface is smooth and slightly curved, but the internal surface bears several irregular depressions for the attachment of the sacral ribs. The ventral pillar of the ilium is stout. It forms the upper part of the acetabulum, which is large and deep. The pubis and ischium are fused together. Only the anterior margin of the obturator foramen is preserved. The upper part of the ischium faces more dorsally than the lower part; these two surfaces meet at an angle, forming a ridge on the lateral surface. Ventral to the point where this ridge meets the posterior edge of the bone, there is a thickened boss (text-fig. 5, boss), which Cruickshank (1967) suggested may mark a point of muscular attachment. The surfaces where the ilium and pubo-ischiadic plate join together are roughened, and there is no evidence to suggest that there was movement between these two elements.

Discussion. The classification of Triassic dicynodonts in general is dealt with in a later section. For present purposes, it is sufficient to note that in its general shape, and particularly in its bluntly rounded snout, *Angonisaurus* is most similar to *Tetragonias* (Cruickshank, 1967). This genus was found in the same area as *Angonisaurus*, and the question naturally arises as to whether they represent separate taxa. However, two sets of characteristics distinguish them. First, though the length of the skull is almost identical in the two genera (28·5 cm in *Tetragonias*, 30 cm in *Angonisaurus*), the latter genus has a proportionately larger body. *Tetragonias* has a scapula 19 cm in height and an ilium 13·2 cm long, while the corresponding measurements in *Angonisaurus* are 35 cm and 38 cm respectively (the postcranial elements were in each case associated with the skull). Though this difference might suggest recognition only at species level, the differences between the skulls seem more profound (text-fig. 6). *Tetragonias* has large maxillary tusks, together with a labial fossa behind the maxilla which presumably provided access for blood vessels, etc., to the root of the tusk. *Angonisaurus* lacks both tusks and labial fossa, but instead has a much larger, more ventrally projecting maxilla. The interorbital bar of *Tetragonias* is much narrower than that of *Angonisaurus*, and its orbit is comparatively larger. Finally, the squamosals of *Angonisaurus* project laterally



TEXT-FIG. 6. Dorsal and lateral views of skulls of *Tetragonias* (left) and *Angonisaurus* (right).

much further than those of *Tetragonias*, and its whole preorbital region is much larger. These differences seem sufficient to merit generic recognition, though the two genera are clearly closely related.

FUNCTIONAL ANATOMY

Jaw function. *Angonisaurus* is tuskless, and lacks any teeth, but has strong, triangular caniniform processes. Anteriorly, the medial surface of the rim of the palate supports two palatal ridges. The symphyseal region of the lower jaw is long and massive. On the dorsal surface of the dentary it forms a medial, shallow, wide groove, lying between two short dentary tables. On the inner rim of the lower jaw, corresponding to the postcanine teeth, there is a prominent ridge ascending above the surface of the dentary. Lateral to this ridge is a shallow depression in the position of the longitudinal groove of *Lystrosaurus*. The outer rim of the lower jaw is slightly higher than the middle longitudinal depression, but it is not sharp. The anterior ends of the dentary tables turn up to form short, sharp processes. The tip of the lower jaw is not produced upward in the midline, so it forms a median depression between the two lateral processes.

Crompton and Hotton (1967) analysed the movement of the lower jaw in *Lystrosaurus*. They thought that the first step was to protract and elevate the lower jaw, but that it could not complete the jaw closure in this position. Further closure could only take place by retraction of the mandible, which forced the curved posterior end of the jaw progressively downwards against the quadrate. The whole lower jaw was simultaneously swinging about a point on the maxilla, so that its anterior end moved further dorsally to close the gape.

In *Angonisaurus* there is a depression just in front of the articular condyles; the surface of this depression is not as smooth as the articular surface. When the lower jaw was in protraction the lateral anterior processes of the mandible were probably in contact with the anterior palatal ridges. Crompton and Hotton (1967) described a similar situation in *Lystrosaurus*. As the jaw approached the retracted position, the square anterior edge of the lower beak passed close to the anterior wall of the palate, its median and antero-lateral processes intermeshing with the ridge and grooves of the palate. So retraction of the lower jaw and simple depression and elevation of it in a retracted position would have produced a cutting action between the ventral edges of the palatal rim and the symphseal end of the lower jaw.

Cluver (1975) thought that in *Chelydontops* some slicing would very likely have occurred between the lateral sides of the lower jaw beak and the palatal rim, and *Angonisaurus* shows the same condition. During the elevation of the lower jaw, the lateral edge of the lower jaw beak passed close to the inner surface of the caniniform process. Although the lateral edge of the mandible is not as sharp as the anterior edge, a slicing action could take place between the horny layers covering them. The resulting increase in the length of the cutting surface would have been a considerable advantage.

As shown above, the animal used the rims of the palate and lower jaw to cut food. Teeth are not present on either the palate or the lower jaw. Although a pair of elongate rugosities lie on the inner rim of the lower jaw, they could not contact the palatal surface, so there was no possibility of a grinding action between them. The masticatory apparatus was essentially one adapted to cutting and not to grinding.

THE TAXONOMIC POSITION OF *ANGONISAURUS* AND THE CLASSIFICATION OF TRIASSIC DICYNODONTS

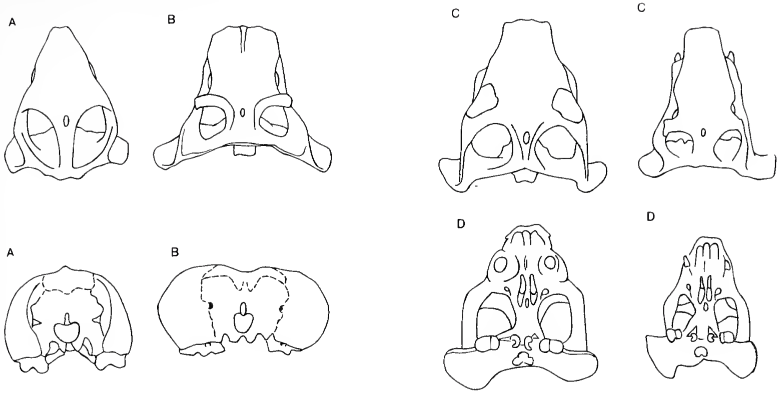
As has already been noted, *Angonisaurus* is very similar to *Tetragonias*. The latter genus (then known as '*Dicynodon*' *njalilus*), together with *Shansiodon* from the Lower Triassic of China, was placed in the family Shansiodontidae by Cox (1965). However, his classification has been criticized by Keyser and Cruickshank (1979), who provide an alternative classification in which these genera are merged into a larger sub-family, the Dinodontosaurinae (see Table 1). These conflicting views must therefore be discussed before the taxonomic position of *Angonisaurus* can be decided.

TABLE 1. Two alternative views on the classification of Triassic dicynodonts.

Cox (1965)		Keyser and Cruickshank (1979)	
		Family	Kannemeyeridae
Family	Kannemeyeriidae	Subfamily	Kannemeyerinae
	Kannemeyeria		*Kannemeyeria*
	Sinokannemeyeria		*Uralokannemeyeria*
	Parakannemeyeria		*Rabidosaurus*
	Ischigualastia		*?Rhadiodromus*
	Placerias		*?Rhinocerocephalus*
	Barysoma		*?Sangusaurus*
			?Wadiasaurus
		Subfamily	Dinodontosaurinae
			Dinodontosaurus
			Sinokannemeyeria
			Parakannemeyeria
Family	Shansiodontidae		*Dolichuranus*
	Shansiodon		*Shansiodon*
	'*Dicynodon*' *njalilus*		*Tetragonias*
			Vinceria
			Rhinodicynodon
			?Zambiasaurus
Family	Stahleckeriidae	Subfamily	Stahleckerinae
	Stahleckeria		*Stahleckeria*
	Dinodontosaurus		*Ischigualastia*
			Placerias
			Barysoma
		Subfamily	Jachalerinae
			Jachaleria

Cox (1965) suggested that most of the Triassic genera could be placed in two families, the Kannemeyeriidae (including *Kannemeyeria* and *Ischigualastia*, among others) and the Stahleckeriidae (including *Stahleckeria* and *Dinodontosaurus*). These two families were distinguished mainly on the shape of the snout and of the occiput. Cox erected a third family, the Shansiodontidae, for two genera (*Shansiodon* and *Tetragonias*, the latter at that time known as '*Dicynodon*' *njalilus*) which did not seem to fit clearly into these two families, which seemed to be more primitive and which, he stated (Cox 1965, p. 507) were 'sufficiently alike for it to be possible, for the present, to take the convenient course of placing them together in a separate family'.

Keyser and Cruickshank (1979) do not believe that the characters used by Cox allow one to distinguish the three separate families that he recognized. Their most fundamental criticism is the opinion that the two South American genera *Stahleckeria* and *Ischigualastia* are so alike that they must be placed in a single Subfamily, not in separate Families as suggested by Cox. They stated (1979, p. 96): 'The skull of *Stahleckeria* has much wider occipital flanges than does *Ischigulastia*, and in the latter genus there is no quadrate foramen and the reflected lamina of the angular contacts the lateral condyle of the lower jaw. Apart from these facts, the differences between the two are hardly more than those used by Cox (1965) and Cruickshank (1967) to demonstrate possible sexual dimorphism in *Dinodontosaurus* and *Tetragonias* respectively' (see text-fig. 7). They show figures (1979, fig. 20) of both genera from anterolaterally and somewhat dorsally, to prove their similarity. But though this particular angle of view minimizes the differences, they can still be seen. It is clear that *Ischigualastia* has a long and narrow intertemporal bar, but it is short and wide in *Stahleckeria*; the dorsal margin of

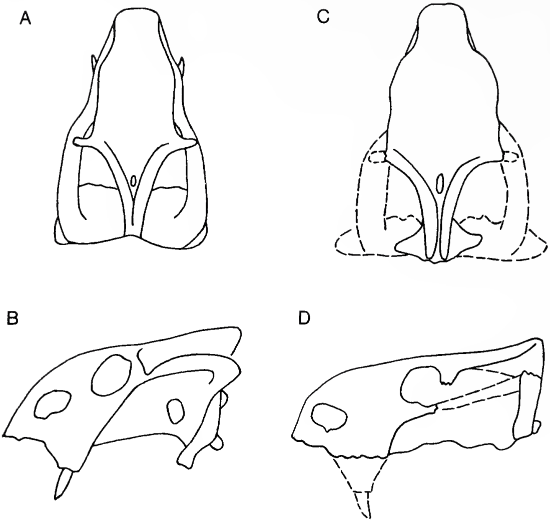


TEXT-FIG. 7. Dorsal and occipital views of skulls of A, *Ischigualastia* (after Cox 1965) B, *Stahleckeria* (after Camp and Welles 1956), C, dorsal views of skulls of presumed male (left) and female (right) of *Dinodontosaurus turpior* (after Cox 1965). D, palatal views of skulls of presumed male (left) and female (right) of *Tetragonias* (after Cruickshank 1963).

the occiput is convex in the *Ischigualastia* but it is level in the other; the former has a pointed snout, but the latter has a robust one. These characters are presumably correlated with the mechanics of the feeding process, and are therefore far more fundamental than mere sexual dimorphism. They therefore suggest that the two forms are not closely related and, as Cox suggested, *Ischigualastia* and *Stahleckeria* appear to belong in different families.

Keyser and Cruickshank (1979) in criticizing Cox's classification, also discussed the Triassic dicynodont genus *Rechnisaurus*, founded by Roy Chowdhury (1970) on a specimen from India, and placed in the family Stahleckeriidae because of its blunt snout. A second specimen, from Zambia, was described by Crozier (1970), who stated that it differed from the type specimen in having a longer, more pointed snout, and that he believed that the blunt snout of the type was due to fracture or erosion. Keyser and Cruickshank suggest that the true shape of the snout necessitates transference of the genus *Rechnisaurus* to the Kannemeyeriidae and further suggest that it is merely a species of the genus *Kannemeyeria*. Again, since they continue to use the shape of the snout as a criterion for the recognition of separate subfamilies, it is clear that they are only seeking to change the systematic level of distinction involved, rather than implying that the feature has no taxonomic value.

Keyser (1973) had described two new genera of Triassic dicynodont from South-West Africa. He stated that one of them, *Dolichuranus*, had a square, blunt tip to its snout and that it was very close to *Dinodontosaurus*, which Cox (1965) had placed in the family Stahleckeriidae; Keyser assigned *Dolichuranus* to that family. Of the other genus, *Rhopalorhinus*, Keyser (1973, p. 7.) states: 'The specimens probably belong to the family Shansiodontidae (Cox 1965) as is evidenced by the broad snout and nasal bosses and in that the intertemporal bar does not form a very prominent raised crest'—though the features that Cox used to unite the two genera he placed in the family Shansiodontidae were 'a rather short, blunt snout, a fairly narrow interorbital bar, and a very narrow intertemporal bar' (Cox 1965, p. 503). However this may be, a comparison of Keyser's figures of his two genera (text-fig. 8) shows them to be so similar that it is surprising that he found it necessary to place them in different families. It is not, therefore, surprising that further collecting 'made it clear



TEXT-FIG. 8. Dorsal and lateral views of skulls of *Dolichuranus* (left) and *Rhopalorhinus* (right), after Keyser 1973.

that *Dolichuranus* and *Rhopalorhinus* represent the extremes of a morphological series and that the two genera are synonymous' (Keyser and Cruickshank 1979, p. 96).

Though Keyser and Cruickshank (1979) placed *Shansiodon*, *Tetragonias*, and *Vinceria* in their subfamily Dinodontosaurinae, these genera can easily be distinguished from *Dinodontosaurus* in having a short preorbital region and long temporal fenestrae. Keyser (1974) discussed the evolutionary trends in Triassic dicynodonts: increase in total body size; increase in relative length of snout and secondary palate by backward growth of the premaxilla; shortening and dorsal expansion of the intertemporal bar and shortening of the postorbital bones. According to these standards, *Dinodontosaurus* with a large body, a very long preorbital region and short postorbital, should represent a progressive genus, while *Shansiodon* and *Tetragonias* show quite primitive characters. So it is necessary to maintain this group as an independent family, the Shansiodontidae, and *Angonisaurus*, since it is closely related to *Tetragonias*, clearly also belongs in this family.

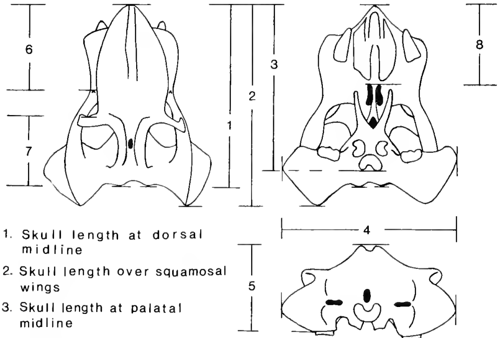
On the other hand, it does appear that the Chinese genera *Sinokannemeyeria* and *Parakannemeyeria*, which Cox placed in his family Kannemeyeriidae, are really closer to *Dinodontosaurus*, as suggested by Sun (1963) (see Table 1). These three genera are alike in having a longer preorbital region with a concomitant shortening of the temporal opening, and a strong, blunt snout. They should therefore be placed in the same group.

Keyser and Cruickshank (1979) also recognize a new sub-family for *Jachaleria* Bonaparte 1971 (which they in error refer to as *Jacheleria*), following Keyser (1974), who based this on the presence of a pterygoid process on the quadrate, and the lower jaw having a very flat profile and long symphyseal region. However, information on these points is often lacking in other genera, and *Jachaleria* itself is so poorly known that it seems best to leave it *incertae sedis*.

Irrespective of the pattern in which the individual Triassic genera are grouped together, Keyser and Cruickshank (1979) also differ in regarding all these genera as belonging to a single family, the Kannemeyeridae, divided into several subfamilies, rather than these being three separate families as recognized by Cox (1965). However, they conclude that the ancestry of two of these subfamilies lies outside the family Kannemeyeridae. Their subfamily Kannemeyerinae is derived from the Permian dicynodont *Dinanomodon*, which similarly has a 'sharply pointed snout', while their subfamily Dinodontosaurinae is derived from the Permian dicynodont *Daptocephalus* which has a 'broad, square-tipped snout'. They show these two lineages as arising in the slightly earlier Permian form *Dicynodon lacerticeps* (Keyser and Cruickshank, 1979, fig. 21). However, as pointed out by Cooper (1980), it is taxonomically unsound for the common ancestor of two subfamilies of a single family to lie outside the family itself. 'Monophyly is the essence of phylogenetic taxonomy and the only objective and natural criterion on which to establish taxonomic categories above the genus level. Thus, Keyser and Cruickshank's interpretation of the Kannemeyeriids merely entirely vindicates Cox's (1965) division of this group into two major families, the Kannemeyeriidae and the Stahleckeriidae' (Cooper 1980, p. 108). Though Cooper himself feels that the *Kannemeyeria*-like and *Stahleckeria*-like forms should be recognized as separate subfamilies rather than families, the main point at issue here is not the taxonomic rank involved but the relationship between the evolutionary relationships and the taxonomic system.

Criteria for the classification of Triassic dicynodonts. The exclusive use of any single characteristic as a basis for classification carries the danger that examples of convergent or parallel evolution may be classified together. It is therefore necessary to base taxonomic diagnoses on as wide a range of characteristics as possible. A number of numerical characters will therefore now be considered in turn. They are defined in text-fig. 9 and documented in Tables 2 and 3. Measurements within brackets were given in the original publications; the remainder are taken from the original text-figures.

Many of the genera documented in these tables have been described since Cox's (1965) classification, as follows, *Elephantosaurus* (Vyushkov, 1969); *Jachaleria* (Bonaparte, 1971); *Moghreberia* (Dutuit, 1980); *Rabidosaurus*, *Rhadiodromus*, and *Rhinodicynodon* (Kalandadze, 1970); *Shaanbeikannemeyeria* (Cheng, 1980); *Sangusaurus* and *Zambiasaurus* (Cox, 1969); *Uralokannemeyeria* (Danilov, 1971); *Vinceria* (Bonaparte, 1969) *Wadiasaurus* (Chowdhury, 1970). Following Keyser and



1. Skull length at dorsal midline
2. Skull length over squamosal wings
3. Skull length at palatal midline
4. Skull width over squamosal
5. Occipital height
6. Preorbital length
7. Postorbital length
8. Secondary palate length

TEXT-FIG. 9. Cranial features measured (see Tables 2 and 3).

TABLE 2. Skull dimensions of Triassic dicynodonts

	Skull length								
	At dorsal midline	Over squamosal wings	At palatal midline	Skull width over squamosal	Occipital height	Preorbital length	Post-orbital length	Secondary palate length	Lower jaw length
Kannemeyeria cristarhynchus	328	372	296	316	164	128	124	132	—
K. latifrons	117	129	85	85	50	45	49	36	—
Uralokannemeyeria vjuschkovia	440	473	373	460	186	207	167	173	—
Shaanbeikannemeyeria buerdongia	400	—	247	278	133	160(?)	185(?)	143	225
Wadiasaurus indicus	344	400	332	312	196	140	148	128	—
Ischigualastia jenseni	540	—	500	441	320	225	279	189	—
Placerias gigas	582	660	564	492	390	234	258	240	—
Dinodontosaurus turpior (MCZ 1670)	440	472	448	428	240	236	136	164	376
D. turpior (MCZ 1628)	480	536	500	536	276	220	164	208	—
D. brevirostris	264	300	273	—	—	99	87	99	—
'*Chanaria*' *platyceps*	300	330	—	—	—	135	108	—	—
Parakannemeyeria dolichocephala	400	(465)	—	(296)	(220)	(216)	140	—	(345)
Dolichuranus primaevus	345	360	330	240	—	135	147	132	—
Rhinodicynodon gracile	170	200	—	—	—	67	70	—	150
Stahleckeria potens	480	(590)	490	(730)	(320)	208	225	—	(440)
Sinokannemeyeria yingchiaoensis	404	(450)	424	(430)	(180)	(225)	120	168	(360)
Shansiodon wangi	150	180	—	170	100	50	86	—	114
Tetragonias njalilus	256	290	242	254	132	74	140	76	190
Angonisaurus cruickshanki	290	300	258	330	216	96	138	114	220

TABLE 3. Skull proportions of Triassic dicynodonts; all figures are percentages

	Skull breadth ÷ length (total)	Occiput height ÷ breadth	Preorbital length ÷ skull length at midline	Post orbital length ÷ skull length at midline	Secondary palate ÷ skull palatal length	Lower jaw ÷ skull length (total)	Secondary palate ÷ skull length at midline	Skull length at palatal midline ÷ skull length at dorsal midline
Kannemeyeria cristarhynchus	85	52	39	38	45	—	40	90
K. latifrons	66	59	38	41	42	—	—	73
Uralokannemeyeria vjuschkovia	97	40	47	38	46	—	40	85
Shaanbeikannemeyeria buerdongia	70	48	—	—	58	56	43	62
Wadiasaurus indicus	78	63	41	43	39	—	38	96
Ischigualastia jenseni	82	73	42	52	38	—	35	93
Placerias gigas	75	79	40	44	43	—	41	97
Dinodontosaurus turpior (MCZ 1670)	91	56	54	31	37	80	37	102
D. turpior (MCZ 1628)	100	51	42	34	41	—	45	104
D. brevirostris	—	—	38	33	36	—	38	103
'*Chanaria*' *platyceps*	—	—	45	36	—	—	—	—
Parakannemeyeria dolichocephala	64	74	54	35	—	74	—	—
Dolichuranus primaevus	67	—	39	43	40	—	38	96
Rhinodicynodon gracile	—	—	39	41	—	75	—	—
Stahleckeria potens	124	44	43	47	—	75	—	—
Sinokannemeyeria yingchiaoensis	96	42	56	30	40	80	42	105
Shansiodon wangi	94	59	33	57	—	63	—	—
Tetragonias njalilus	88	52	29	55	31	66	30	94
Angonisaurus cruickshanki	110	65	33	48	44	73	38	89

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Placerias gigas	75	79	40	44	43	—	41	97
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Angonisaurus cruickshanki	110	65	33	48	44	73	38	89

Cruickshank (1979), *Rechnisaurus* (Chowdhury, 1970) is included in the genus *Kannemeyeria*, and *Rhopalorhinus* (Keyser, 1973) is included in the genus *Dolichuranus* (Keyser, 1973). Following Keyser (1974), *Chanaria* (Cox, 1968) is included in the genus *Dinodontosaurus*. To facilitate comparison, the genera are listed in Table 6 in the systematic position finally accorded to them.

There are a number of possible sources of error in this numerical data. There may be a range of variation within a single species, either during life or resulting from post-mortem deformation. For example, though the type specimen of *Dinodontosaurus turpior* (MCZ No. 1670) has a preorbital length 54 % of that of the total skull length (Cox 1965, fig. 14), that of the 'old bull' of the species (MCZ No. 1628) is only 42 % (loc. cit., fig. 24), and Cox notes that the type specimen is very unusual in having a 'long, low shape' (1968, p. 10). Apparent differences in skull proportions may also result if different authors have chosen to draw the skull from slightly different angles.

Several different characters have, in the past, been suggested as being useful for taxonomic purposes in Triassic dicynodonts: the width and shape of the snout; the structure and relative length of the snout and secondary palate; the structure and relative length of the intertemporal bar, and the angle between the occiput and the palate. These four suggestions will now be discussed in turn.

Character 1. The significance of the width and shape of the snout has been discussed above, and it has been shown to be a more reliable characteristic than suggested by Keyser and Cruickshank (1979). It should be emphasized in any case that it is the shape of the anterior end of the palatal surface of the premaxilla that is significant, as this is the region used in feeding, rather than the shape of the more dorsal part of the preorbital region. Nevertheless, even this is not always diagnostic; for example, *Wadiasaurus* (Chowdhury 1970) from the Lower Triassic of India, has a palate that tapers anteriorly to a narrow snout but this is flat transversely, not pointed. This characteristic alone is therefore clearly not adequate as a basis for classification.

Character 2. Keyser (1974) suggested that one of the trends in the Triassic dicynodonts was an increase in the relative length of the snout and secondary palate by backward growth of the premaxillae. The ratio between the preorbital length and the total skull midline length is shown in Table 3. In most Permian dicynodonts the preorbital length is only 30–40 % of the skull length, and this is also true of a few Triassic genera (*Shansiodon*, *Tetragonias*, *Angonisaurus*), which have also retained a long temporal opening. In other Triassic genera the preorbital length is 38–56 % of the total skull length (see Table 4). As can be seen from Table 3, there is little variation in the relative length of the secondary palate, which usually ranges from 36 to 46% of the total midline skull length; only *Tetragonias* (30 %) and *Shaanbeikannemeyeria* (58 %) lie outside this range.

Keyser (1974) demonstrated that, concomitant with the elongation of the snout, there is an increase in the length of secondary palate, the extension of which is due to backward growth of the premaxilla. In some genera the prolonged premaxilla contacts the palatine, and the maxilla is excluded from the margin of the choana. But only a few genera show the palatal structure in detail, because of the massive nature of the bones. Thus the premaxilla is known to meet the palatine in *Ischigualastia*, *Placerias*, *Dinodontosaurus turpior* (MCZ No. 1670), *Dolichuranus*, *Stahleckeria*, *Tetragonias*, and *Angoniasaurus*. The two bones are known to be separated in *Kannemeyeria vanhoepeni*, *Wadiasaurus*, *Dinodontosaurus turpior* (MCZ No. 1628) and *Dinodontosaurus brevirostris*. In other forms, the situation is unclear. In any case, the variation within the genus *Dinodontosaurus* shows that this character is not reliable for taxonomic purposes.

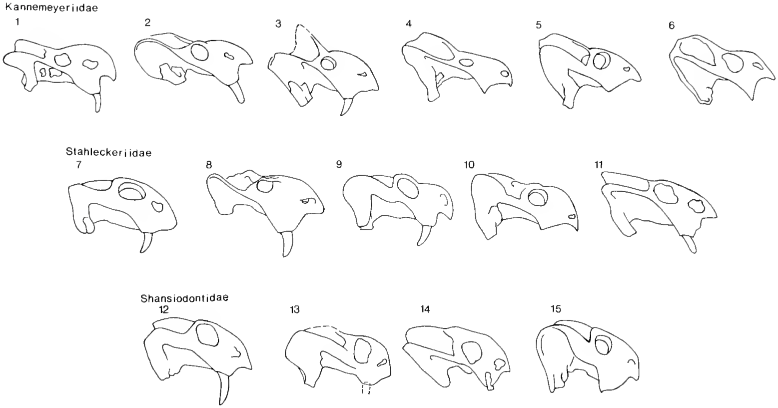
TABLE 4

	Preorbital length ÷ skull midline length (%)	Postorbital length ÷ skull midline length (%)
Stahleckeriidae	38–56	30–43
Kannemeyeriidae	39–47	33–52
Shansiodontidae	29–33	48–57

Character 3. Keyser (1974) also suggested that Triassic dicynodonts show a trend towards a crested, shortened intertemporal bar, and a shortening of the posterior rami of the postorbital bar. (Of course, the proportionate shortening of the intertemporal region is inevitably associated with the proportionate elongation of the preorbital region discussed above; see Table 4). The different genera certainly show considerable variation in each of these characters, but it is not clear that there is any connection between them, nor that any general trends exist. Thus one of the earliest Triassic forms, *Kannemeyeria* of the early Triassic, has one of the shortest, most highly crested intertemporal bars of all the genera, while the later genus *Stahleckeria* has a wide bar without any crest. A wide, short intertemporal bar is also found in *Sinokannemeyeria* of the early Triassic and in *Placerias* of the late Triassic; most other Triassic dicynodonts have an intertemporal bar bearing a longitudinal, narrow crest, though the heights and shapes of the crests vary (text-fig. 10).

The other developing trend mentioned by Keyser (1974), the shortening of the posterior rami of the postorbital bone, does not take place in all the Triassic dicynodonts. Some South American genera (*Dinodontosaurus*, *Ischigualastia*, *Placerias*), and a Russian genus (*Rhinodicynodon*) have a short postorbital, the intertemporal bar consists mainly of the parietal, and the postorbital and squamosal lose their connection. But another group retains the link between the postorbital and squamosal, i.e. *Kannemeyeria*, *Sinokannemeyeria*, *Parakannemeyeria*, and *Dolichuranus*. For this reason Sun (1963) suggested that the Asiatic genera, *Sinokannemeyeria* and *Parakannemeyeria*, had a closer relationship to *Kannemeyeria* than to *Stahleckeria*. But in his original description von Huene (1944, p. 11) stated that in *Stahleckeria* the posterior tongue of the postorbital reaches the transversely extended high edge of the squamosal (Camp 1956, fig. 45 is in error on this feature).

If one combines all the above information on the structure and shape of the intertemporal region, four different patterns emerge: (*a*) Parietal crest high and narrow; postorbital meets squamosal:



TEXT-FIG. 10. Skulls of Triassic dicynodonts in lateral view, all reduced to the same length. 1, *Kannemeyeria cristarhynchus*, after Keyser and Cruickshank 1979; 2, *Uralokannemeyeria vjushkovi*, after Danilov 1971; 3, *Rabidosaurus cristatus*, after Kalandadze 1970; 4, *Wadiasaurus indicus*, after Chowdhury 1970; 5, *Ischigualastia jenseni*, after Cox 1965; 6, *Placerias gigas*, after Cox 1965; 7, *Dinodontosaurus turpior* after Cox 1968; 8, *Sinokannemeyeria yingchaoensis*, after Sun 1963; 9, *Rhinodicynodon gracile*, after Kalandadze 1970; 10, *Stahleckeria potens*, after Camp and Welles 1956; 11, *Dolichuranus primaevus*, after Keyser 1973; 12, *Shansiodon wangi*, after Yeh 1959; 13, *Tetragonias njalilus* after Cruickshank 1967; 14, *Angonisaurus cruickshanki*.

Kannemeyeria, *Parakannemeyeria*, *Dolichuranus*. (*b*) Parietal crest narrow but not very high; postorbital does not meet squamosal: *Dinodontosaurus*, *Ischigualastia*, *Rhinodicynodon*. (*c*) Intertemporal bar wide, does not form a parietal crest; postorbital meets squamosal: *Stahleckeria*, *Sinokannemeyeria*. (*d*) Intertemporal bar wide, does not form a parietal crest; postorbital does not meet squamosal: *Placerias*.

This analysis does not help to solve the systematic problem. It only demonstrates that it is almost impossible to find any correlation between the length of the temporal fenestra and the form of parietal crest, or between the shape and the structure of the intertemporal bar. After having examined a large collection of *Dinodontosaurus*, Keyser (1974) stated that these specimens showed a great variation in the width of the intertemporal region and that the variation must be attributed to ontogenic variation in the living animals.

Character 4. As first pointed out by Cox (1965), the occiputs of stahleckeriids are almost at right angles to the plane of the palate, while that of kannemeyeriids is more obliquely inclined. Some workers suggested that this obliquity was caused by deformation during preservation, but the regular appearance of an oblique occiput in some families and the existence of a shortened lower jaw, for instance, in *Shaanbeikannemeyeria*, proves that it is a natural condition. This character can be expressed by a ratio of the lower jaw length to the skull length, but in many genera the skull lacks an

TABLE 5. The classification of Triassic dicynodonts

		Skull	Snout	Tusk	Occiput
Family	Kannemeyeriidae				
	Kannemeyeria	large	medium length, pointed	present	oblique
	Uralokannemeyeria	,,	,,	,,	,,
	Shaanbeikannemeyeria	,,	,,	,,	,,
	Rabidosaurus	,,	,,	,,	,,
	Rhinocerocephalus	,,	,,	,,	,,
	Ischigualastia	,,	,,	absent	slightly oblique
	Placerias	,,	,,	reduced	oblique
	Moghreberia	,,	,,	present	,,
	Wadiasaurus(?)	,,	medium length, flat snout end	absent	,,
Family	Stahleckeriidae				
	Dinodontosaurus	large	long, bent, blunt	present	almost vertical
	Parakannemeyeria	,,	long, bent, blunt or pointed	,,	,,
	Dolichuranus	,,	long, blunt	,,	,,
	Rhinodicynodon	medium	blunt	,,	,,
	Stahleckeria	large	wide and blunt	absent	,,
	Sinokannemeyeria	,,	long and wide	present	,,
	Zambiasaurus	,,	blunt	absent	,,
Family	Shansiodontidae				
	Shansiodon	medium	short and blunt	present	slightly oblique
	Tetragonias	,,	,,	,,	,,
	Angonisaurus	,,	,,	absent	,,
	Vinceria(?)	large	?	present	oblique
	Incertae sedis				
	Barysoma	large	?	?	?
	Elephantosaurus	,,	?	?	?
	Jachaleria	,,	?	absent	vertical
	Rhadiodromus		?	?	?
	Sangusaurus		tapers to blunt point	absent	?

associated lower jaw (Table 3). The ratio of the skull length in palatal view to dorsal skull length has therefore been used instead (Table 3). This ratio shows a clear distinction between the families. In members of the Stahleckeriidae the occiputs are almost vertical, and the ratio is usually more than 100 %. On the contrary, in the remainder, the Kannemeyeriidae and Shansiodontidae, the ratio is always less than 90 % (text-fig. 10).

Another feature of the Kannemeyeriidae which may be related to the above complex of characters is a marked angulation in the base of the braincase, the basioccipal lying below the basisphenoid so that the two are almost at right angles to one another. This was remarked on by Camp (1956) in *Placerias*, and in *Shaanbeikannemeyeria* by Cheng (1980) and Li (1980), but appears to be less noticeable in *Kannemeyeria* itself.

The above review of characters that have been suggested as useful criteria for the erection of a system for classifying Triassic dicynodonts shows that only two appear to be of value: the shape and proportions of the snout, and the relative position of the lower jaw articulation, with the consequent angle of the occiput. These characteristics can now be used to provide diagnoses of three Triassic groups (below) which in turn can be used to classify the genera (Table 5). Whether these groups should be families as Cox (1965) suggested or subfamilies, as preferred by Keyser and Cruickshank (1979), is basically a matter of personal opinion, for there is no objective method of evaluating this point. They are here viewed as families. Nevertheless, this classification must still be regarded as provisional until a more detailed analysis of the musculature and mechanics of feeding of these forms, along the lines of Crompton and Hotton's (1967) study of *Emydops* and *Lystrosaurus*, places it on a firmer functional basis.

Family Kannemeyeriidae Large sized dicynodonts: snout moderately elongated, about 39–47 % of skull length, with a strong middle ridge in some genera; jaw articulation placed anteriorly, and occiput obviously oblique, the ratio of skull length in palatal view to dorsal skull length less than 90 %.

Family Stahleckeriidae Medium to large sized dicynodonts: snout wide, blunt and pronouncedly elongated, nearly 37–56 % of skull length, bent in some genera: jaw articulation lies posteriorly, occiput almost vertical, the ratio of skull length in palatal view to dorsal skull length usually more than 100 %.

Family Shansiodontidae Medium to large sized dicynodonts; snout blunt and short, only 29–33 % of skull length; jaw articulation placed anteriorly, occiput slightly oblique, the ratio of skull length in palatal view to dorsal skull length less than 90 %.

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REFERENCES

ATTRIDGE, J. *et al.* 1963. The British Museum (Natural History)—University of London Joint Palaeontological Expedition to Northern Rhodesia and Tanganyika. *Nature, Lond.* **201,** 445–449.

BONAPARTE, J. F. 1969. Dos nuevas 'faunas' de reptiles Triassicos de Argentina. *Gondwana stratigraphy I.U.G.S. Symposium. 1967 UNESCO*, Paris, pp. 283–306.

—— 1971. Annotated check list of the South American Triassic tetrapods, *In* S. H. Haughton (Ed.). *Proc. I.U.G.S. 2nd Gondwana Symp., South Africa*, pp. 665–682. C.S.I.R. Pretoria.

CAMP, C. L. 1956. Triassic dicynodont reptiles. Part II. Triassic dicynodonts compared. *Mem. Univ. Calif.* **13,** 305–341.

CAMP, C. L. and WELLES, S. P. 1956. Triassic dicynodont reptiles. Part I. The North American genus *Placerias*. Ibid. 255–304.

CHARIG, A. J. 1963. Stratigraphical nomenclature in the Songea series of Tanganyika. *Rec. geol. Surv. Tanganyika*, **10** (for 1960), 47–53.

CHENG, ZH. W. 1980. *Mesozoic Stratigraphy and Paleontology of the Shenxi-Gansu-Ninxia basin.* Vol. 2, part 7, vertebrate fossils. Publishing House of Geology, Beijing.

CHOWDHURY, T. R. 1970. Two new dicynodonts from the Triassic Yerrapalli Formation of central India. *Palaeontology*, **13,** 132–144.

CLUVER, M. A. 1975. A new dicynodont reptile from the *Tapinocephalus* zone (Karroo system Beaufort series) of South Africa, with evidence of the jaw adductor musculature. *Ann. S. Afr. Mus.* **67,** 7–23.

COOPER, M. R. 1980. The origins and classification of Triassic dicynodonts by A. W. Keyser and A. R. I. Cruickshank. *Trans. geol. Soc. S. Afr.* **83,** 107.

COX, C. B. 1959. On the anatomy of a new dicynodont genus with evidence of the position of the tympanum. *Proc. zool. Soc. Lond.* **132,** 321–367.

—— 1965. New Triassic dicynodonts from South America, their origins and relationships. *Phil. Trans. Roy. Soc. Lond.* (B) **248,** 457–516.

—— 1968. The Chañares (Argentina) Triassic fauna IV. The dicynodont fauna. *Breviora,* **205,** 1–27.

—— 1969. Two new dicynodonts from the Triassic N'tawere Formation, Zambia. *Bull. Brit. Mus. nat. Hist.* (Geol), **17,** 255–294.

—— 1973. Gondwanaland Triassic stratigraphy. *An. Acad. bras. Cienc.* **45,** 115–119.

CROMPTON, A. W. 1955. On some Triassic cynodonts from Tanganyika. *Proc. zool. Soc. Lond.* **125,** 617–669.

—— 1972. Postcanine occlusion in cynodonts and tritylodontids. *Bull. Brit. Mus. nat. Hist.* (Geol.) **21,** 29–71.

—— and HOTTON, N. 1967. Functional morphology of the masticatory apparatus of two dicynodonts (Reptilia, Therapsida). *Postilla,* **109,** 1–51.

CROZIER, E. A. 1970. Preliminary report on two Triassic dicynodonts from Zambia. *Palaeont. afr.* **13,** 39–45.

CRUICKSHANK, A. R. I. 1965. On a specimen of the anomodont reptile *Kannemeyeria latifrons* (Broom) from the Manda Formation of Tanganyika, Tanzania. *Proc. Linn. Soc. Lond.* **176,** 149–157.

—— 1967. A new dicynodont genus from the Manda Formation of Tanzania (Tanganyika). *J. Zool. Lond.* **153,** 163–208.

DANILOV, A. I. 1971. A new dicynodont from the Middle Triassic of Southern Cisuralia. *Palaeont. Zh.* **1971,** 132–135. [In Russian.]

DUTUIT, J-M. 1980. Principaux caractères d'un genre de dicynodonte du trias marocain. *C.R. Acad. Sc. Paris,* **290D,** 655–658.

HUENE, F. VON 1938*a*. *Stenaulorhynchus*, ein Rhynchosauride der ostafrikanischen Obertrias. *Nova Acta Leopold.* **6,** 83–121.

—— 1938*b*. Ein grosser Stagonolepide aus der jüngeren Trias Ostafrikas. *Neues Jahrb. Min. Geol. Pal. Beilage-Bd.* **80,** 264–278.

—— 1944. *Die fossilen Reptilen des südamerikanischen Gondwanalandes.* C. H. Beck, München.

KALANDADZE, N. H. 1970. The new Triassic kannemeyerids, South Ural region. In: *Materials of evolution of terrestrial vertebrates*, pp. 51–57. Scientific publishers, Moscow. [In Russian.]

KEYSER, A. W. 1973. A new Triassic vertebrate fauna from South West Africa. *Palaeont. afr.* **16,** 1–15.

—— 1974. Evolutionary trends in Triassic Dicynodontia. Ibid. **17,** 57–58.

KEYSER A. W. and CRUICKSHANK, A. R. I. 1979. The origins and classification of Triassic dicynodonts. *Trans. geol. Soc. S. Afr.* **82,** 81–108.

LI, J.-L. 1980. *Kannemeyeria* fossil from Inner Mongolia. *Vert. palasia.* **18,** 94–99.

NOWACK, E. 1937. Zur Kenntnis der Karruformation in Ruhuhu-Graben (D.O.A.). *Neues Jb. Min. Geol. Paläont.* **78 (B),** 380–412.

PARRINGTON, F. R. 1936. On the tooth replacement in theriodont reptiles. *Phil. Trans. Roy. Soc.* **B, 226,** 121–142.

STOCKLEY G. M. 1932. Geology of the Ruhuhu coalfields, Tanganyika territory. *Quart. J. geol. Soc. Lond.* **88,** 610–622.

SUN, A.-L. 1963. The Chinese kannemeyerids. *Palaeont. sinica,* **147** (N.S. 17), pp. 73–109.

VJUSHKOV. 1969. New dicynodonts from the Triassic of Southern Cisuralia. *Palaeont. Zh.* **1969,** 99–106. [In Russian.]

YEH, H.-K. 1959. New dicynodont from *Sinokannemeyeria*-fauna from Shansi. *Vert. palasia.* **3,** 187–204.

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NEW LATE SILURIAN MONOGRAPTIDS FROM KAZAKHSTAN

by TATYANA N. KOREN'

ABSTRACT. Some new and previously unrecorded graptolites are described from sections through the Tokrau horizon in the north-east Balkhash area of Kazakhstan, USSR. They include *Monograptus anerosus* sp. nov., *M. balaensis* sp. nov., *M. beatus* sp. nov., *M. microdon aksajensis* subsp. nov., *M. mironovi* sp. nov., *M. nimius* sp. nov., *M. prognatus* sp. nov., *M. supinus* sp. nov., *M. willowensis* (Berry and Murphy), and *Neocucullograptus kozlowskii* Urbanek. These species were collected through approximately 750 m of section referable to the *lochkovensis*, *bouceki*, and *perneri* zones. A local zone of *M. microdon aksajensis* is established for the first time in the uppermost Silurian of Kazakhstan. The successive zonal associations contain almost all species known in the Přídolí beds of the Barrandian area. The new graptolite fauna includes monograptids having uniform or biform thecae with apertural additions of differing structures. Most of the apertural apparatuses are unusual for the Přídolían stage of graptolite evolution, although they are not new but are partly homeomorphs of those known in the Ludlow Series. The variety of thecal structures discovered in the Kazakhstan collections suggests that the Přídolían monograptid faunas are less monotonous than previously suggested.

UNTIL comparatively recently our knowledge of late Silurian (post-Ludlow) graptolites was limited to the results of investigations of Central European sections, and mainly of the Přídolí sequence of Bohemia. The first zonal subdivision established by Přibyl (1940, 1941) on the basis of the stratigraphical distribution of seven or eight species in the Přídolí sections proved to be essentially correct. It now has broad usage for subdivision and correlation of post-Ludlow deposits in different continents, with certain amendments. In the 1960s active international research began within this stratigraphical interval, and evidence of new occurrences of Přídolí monograptids has been published recently by, among others, Abduazimova (1970), Biske and Rinenberg (1973), Jackson and Lenz (1969), Jaeger (1967, 1975), Koren' (1973, 1978, 1979), Mikhajlova (1971, 1975, 1976), Paškevičius (1979), and Teller (1964, 1969). These papers mostly refer to the distribution of graptolites in sections, with systematic descriptions rarely being given. Until recently, data on the composition and morphology of Přídolí monograptids were scarce, and graptoloid associations in this stratigraphical interval were considered to be quite monotonous. Incompleteness of knowledge of Přídolí-age monograptids was clearly demonstrated by the unexpected discoveries of new monograptids ('*Saetograptus*' *pilosus* Jackson and Lenz, 1972 and '*S.*' *willowensis* Berry and Murphy, 1975) with unique apertural structures, in Yukon and central Nevada. More varied monograptid faunas were described from the lowermost Přídolí sections of the south-west Ukraine as a result of studies of drill cores (Tsegelnjuk 1976).

Study of the monograptid fauna of the upper Silurian Tokrau horizon in Kazakhstan has shown it to be the most complete and diverse of all known Přídolí graptoloid associations. It comprises not only almost all the monograptids reported from the Přídolí beds of the Barrandian, but also taxa similar or identical to those which occur in North America. In addition, there are some new monograptids important for phylogenetic reconstructions, which fill some gaps in previously suggested lineages and show more diverse trends of development and dynamics of evolution within late Silurian monograptid populations.

PREVIOUS STUDIES AND BIOSTRATIGRAPHY

The Tokrau horizon (Regional Stage of Soviet usage) is the uppermost subdivision of the Silurian in Kazakhstan (Bandaletov and Mikhajlova 1968; Bandaletov 1969). In the type area it is represented

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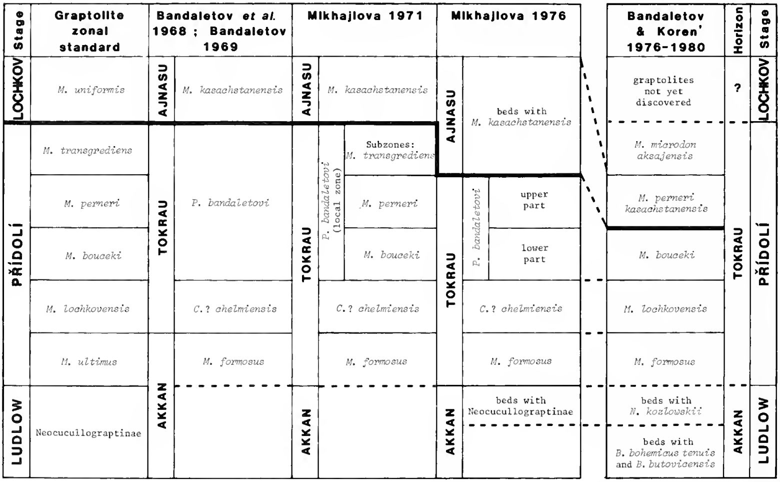
by a continuous sequence of sandstones, 750 m thick, yielding numerous graptolites at several successive stratigraphical levels. Benthic faunas (brachiopods, corals, trilobites, crinoids, and ostracodes) occur in terrigenous rocks and occasionally in lenses of organo-detrital limestones.

The age and boundaries of the Tokrau horizon were defined on the basis of graptolites first found in 1965 in the course of geological mapping. Later, beginning in 1968, they were collected and studied by Dr. N. F. Mikhajlova, and in 1974 the present author was invited to study the graptolites and the Tokrau sections. Field work in 1975 and 1978 was carried out jointly with Drs. S. M. Bandaletov and Mikhajlova as well as with other colleagues from Kazakhstan. The collections were first studied jointly with Dr. Mikhajlova in 1975–1976. However, from the outset I came to conclusions as to the age of the assemblages which were substantially different from those drawn previously by Dr. Mikhajlova (1971, 1975, 1976), mainly because of differing views on the scope and taxonomic interpretation of species important for correlation. These differences of interpretation necessitate publication of the results.



TEXT-FIG. 1. Different interpretations of the zonal subdivision and correlation of the Tokrau horizon.

Text-fig. 1 shows different interpretations of the scope, boundaries, and age of Silurian stratigraphical units based on successive studies of the composition and distribution of graptolites in the sections in north-east Balkhash. In the upper part of the section, assigned to the boundary beds of the Tokrau and Ajnasu horizons, two graptolite zones, *Pseudomonoclimacis bandaletovi* and *Monograptus kasachstanensis* have been established (Bandaletov and Mikhajlova 1968; Mikhajlova 1971). The index species were described later by Mikhajlova (1975). Among the graptolites characteristic of the *M. kasachstanensis* Zone, *Monograptus uniformis uniformis*, *M. u. angustidens* and *M. aequabilis* were identified by Dr. Mikhajlova, and these occurrences were taken as evidence for assignment of the *M. kasachstanensis* Zone to the Lower Devonian. The Silurian–Devonian boundary in Kazakhstan was placed at the base of this graptolite zone (Resheniya . . . 1976). Later, on the basis of occurrences of *M. transgrediens* in the assemblage, the *M. kasachstanensis* Zone was correlated with two standard zones, *M. transgrediens* and *M. uniformis*. Thus, the correlation of the Silurian–Devonian boundary in Kazakhstan became less definite (Mikhajlova 1976).

Since 1974 more detailed biostratigraphical research has been carried out in north-east Balkhash. Bed by bed sampling was carried out in the stratotype section of the Tokrau horizon in the Kokbajtal Mountains, as well as in other sections including a new area near the Aksaj and Sarybiik mountains. The major aim of this work was the study of graptolites in the upper part of the section in connection with the problem of the Silurian–Devonian boundary in Kazakhstan. As a result, extensive and diagnostic collections were made, mostly from numerous artificial trenches. The graptolites are preserved better on fresh bedding planes. During this period a re-study was also made of graptolites collected before 1973 and housed in the Palaeontological Museum of the Central Kazakhstan Geological Survey and in the Central Geological Tschernyshev Museum (Karaganda and Leningrad respectively). The main results of my palaeontological and stratigraphical studies can be summarized as follows (see also text-fig. 2).

1. The Tokrau succession begins with the *formosus* Zone. In the underlying sequence of the Akkan horizon the presence of the *Neodiversograptus kozłowskii* Zone is established for the first time. *Monograptus ultimus*, previously identified from these sections (Mikhajlova 1976, p. 100), together with *M. parultimus* Jaeger, which is characteristic of the base of the Přídolí, were not confirmed in the boundary beds of the *kozłowskii–formosus* zones in Kazakhstan.

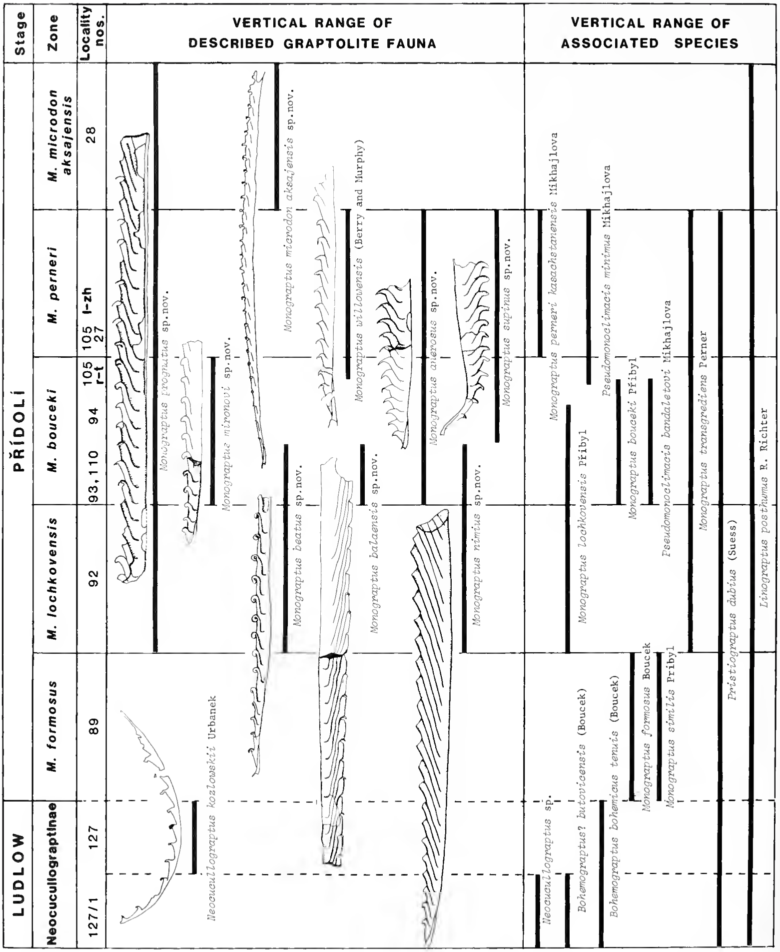
2. Strata above the last occurrences of *M. formosus* Bouček (loc. 92 in the stratotype section) are assigned to the *M. lochkovensis* Zone. This is characterized by the zonal species in association with numerous and diverse monograptids, including *M. transgrediens* Přibyl. The latter was previously identified as *M. chelmiensis* Teller and strata bearing it were considered as the *chelmiensis* Zone (text-fig. 1).

3. The local zone of *Pseudomonoclimacis bandaletovi* (locs. 110, 94) corresponds to the *bouceki* Zone of the standard scale. It contains numerous specimens of *M. bouceki* Přibyl in several sections within the region.

4. *M. kasachstanensis* Mikhajlova, as noted in the original description of the species, is 'identical in rhabdosome shape and size' to *M. perneri* Bouček (Mikhajlova 1975, p. 155). Difficulties in distinguishing these forms are increased by the inadequate preservation. The Barrandian specimens are mostly flattened compared with the Kazakhstan material, which is beautifully preserved in full to low relief. With the help of Dr. H. Jaeger, who kindly provided type material, photographs, and detailed measurements of the Bohemian *M. perneri*, I have concluded that it is most probably identical to *M. kasachstanensis*. However, in adopting caution and bearing in mind the different preservation of the taxa under comparison, the Kazakhstan form is referred to here as a geographical variant *M. perneri kasachstanensis*. The strata bearing it correlate with the *perneri* Zone of the graptolite standard. This correlation is supported by the stratigraphical position in the Tokrau section above the *bouceki* Zone, as well as by the presence in the assemblage of *M. willowensis* (Berry and Murphy) and species closely similar morphologically to *M. pilosus* (Jackson and Lenz). Both these North American monograptids are characteristic of the middle Přídolí (Berry and Murphy 1975; Jackson and Lenz 1969).

5. The presence of *M. uniformis uniformis* Přibyl, *M. uniformis angustidens* Přibyl, and *M. aequabilis* Přibyl mentioned by Mikhajlova (1975) in the upper part of the section has not been confirmed. The specimens described as these species (CGM Leningrad N10290) have different apertural structures and belong to the new species *M. anerosus*, *M. mironovi*, and *M. prognatus* (see synonymies). The latter is closely similar to *M. uniformis angustidens* and *M. praehercynicus* Jaeger. It differs in having uniformly developed hoods, a thinner proximal extremity, and greater overlap of interthecal septae in the distal part of the rhabdosome.

6. The Přídolí graptolite-bearing succession terminates with the new local zone of *M. microdon aksajensis*. Among the impoverished zonal assemblage, *M. transgrediens* does not occur. A similar situation is known in the Upper Silurian–Lower Devonian sections of central Nevada (Berry and



TEXT-FIG. 2. Stratigraphical distribution of monograptids in the Tokrau horizon of the north-east Balkhash area. Locality numbers in the third column are the numbers of exposures in the stratotype section of the Tokrau horizon at Kokbajtal Mountain (127–105) and those of the section near Aksaj Mountain (27, 28).

Murphy 1975). Here the local *M. birchensis* Zone is recognized in strata immediately underlying beds with the first appearance of *M. uniformis*. Within this topmost Silurian zone, *M. transgrediens* is not found. As in Kazakhstan, *M. microdon* R. Richter is the most common species in the zonal assemblage.

MORPHOLOGY

The morphology of the Tokrau monograptids can be determined only from specimens preserved in the rock. Nevertheless, the collections are represented by numerous specimens of different astogenetic stages, well preserved in relief or flattened. Many specimens studied give a general idea of the apertural structures, though investigation of some morphological problems awaits the recovery of isolated material.

The new Tokrau monograptids and some previously known Přídolí species can be classified into morphological groups on the basis of shape and degree of development of the apertural structures. There is not enough data to judge whether the morphological similarity reflects phylogenetic affinities or whether it exemplifies convergent evolution. No doubt both took place, and some of these groups unite monograptids belonging to different lineages.

Monograptus similis group. In the assemblages studied, monograptids possessing uniformly developed hoods of *M. uncinatus* type are most common. They span the complete stratigraphical interval from the *formosus* Zone to the *microdon aksajensis* Zone (inclusive). A maximum of development is observed in the *lochkovensis–bouceki* zones. *M. similis* Bouček is the oldest member of the group. The other members appear successively as follows: *M. prognatus* sp. nov., *M. beatus* sp. nov., *M. mironovi* sp. nov., and *M. balaensis* sp. nov. These species belong to at least two lineages. The first consists of *M. similis* and *M. prognatus*, connected by gradual morphological transition observed at the *formosus–lochkovensis* boundary. To this group probably belongs *M. birchensis* Berry and Murphy. These species most probably represent the Přídolí links in the lineage ancestral to the early Devonian *M. uniformis* group. Their Ludlow forerunners are still unknown. The morphological gap between the last Silurian and early Devonian monograptids having thecae of *M. uncinatus* type is not significant and it is expressed in the degree of development of hoods within the colony. *M. mironovi* and *M. balaensis* apparently represent short-lived offshoots. The second lineage includes *M. beatus* and *M. microdon aksajensis* and probably derives from *M. kallimorphus* Kraatz (late Ludlow). The morphological gap between the latter and *M. beatus* is possibly to be filled by an intermediate link.

Monograptus anerosus sp. nov. group. In the *bouceki* and *perneri* zones there occur the peculiar spiny monograptids *M. anerosus* sp. nov. and *M. supinus* sp. nov., closely similar to *M. pilosus* (Jackson and Lenz) from the Přídolí sequence of Canada. They have uniform apertural structures developed initially as dorso-lateral hoods, becoming later folded or separated by a mesial slit. In the last stage they terminate in long, paired apertural processes as *M. supinus*, a possible descendant of *M. anerosus*. The morphological changes at the transition are insignificantly small, manifested only in gracilization and dorsal curvature of the proximal end of the rhabdosome. There are intermediate specimens in the collections studied (Pl. 49, fig. 2; text-fig. 3*f*). The origin of the *M. anerosus* group is unclear but one can assume a relationship with the *M. lochkovensis* group, as well as affinities with *M. bouceki*.

M. transgrediens–M. lochkovensis group. Among the graptolite associations of the *lochkovensis* and *boučeki* zones there occur numerous biform graptolites like *M. lochkovensis* Bouček, *M. transgrediens* Perner and *M. nimius* sp. nov. *M. willowensis* occurs in the *M. perneri kasachstanensis* Zone. These species are characterized by similar apertural structures of the proximal thecae. The structures are distinct in detail and in the degree of penetrance within the colony. *M. nimius* has small lateral elevations at the first theca and in this respect it is closely similar to *M. transgrediens*. The other species, *M. willowensis*, is closer to the *M. lochkovensis* group and probably evolved from it. It inherits well-developed apertural structures at about thecae ten-twelve, which terminate with paired lateral spines. Distal thecae are simple tubes in both species.

Some common tendencies are characteristic of the different morphological groups. One of the strangest trends is the thecal elongation developing towards the distal end. *M. nimius*, *M. balaensis*, and *M. microdon aksajensis* display this feature in different Přídolí time intervals. In extreme cases the thecae became more than 5 mm long, greatly overlapping each other. The elongation of thecae does not correlate with changes in their shape. The elongated thecae can be straight (*M. nimius*), distinctly undulating (*M. balaensis*), or sigmoidally curved (*M. microdon aksajensis*).

There are also some other morphological types which are not considered in this paper. The peculiar monograptids with climacograptid-like thecae devoid of any apertural additions are worth mentioning. They have been discovered in the *bouceki-perneri kasachstanensis* level and were assigned to *Pseudomonoclimacis* Mikhajlova, 1975. They are not known outside Kazakhstan within the Přídolí.

The new late Přídolí monograptids are associated with long-lived *P. dubius* (Suess) (*formosus* to *perneri kasachstanensis* zones inclusive) and *Linograptus posthumus* R. Richter (throughout the sequence studied).

All the species described in this paper with hoods (*M. similis* group), those with lateral lobes (*M. transgrediens* group), and those having more complicated intermediate structures (*M. lochkovensis* and *M. anerosus* groups) are considered within the scope of the genus *Monograptus s.l.* (Bulman and Rickards 1970). The affinities of the apertural structures in some of the newly discovered Přídolí monograptids with early Ludlow saetograptids can be considered a clear example of homeomorphy. They do not serve as an evolutionary basis for discussing the Přídolí monograptids. More detailed knowledge of morphology, affinities, and biozonation of Přídolí monograptids is necessary before creating new genera which would have more value than mere technical validity.

SYSTEMATIC PALAEONTOLOGY

Material. Well-preserved graptolites in the collections are in greenish-grey siltstone and sandstone lithologies. They are preserved either as flattened, undeformed specimens or in low to full relief infilled with limonite. Abundant specimens of successive astogenetic stages represent most taxa. The material was collected by S. M. Bandaletov, A. I. Mironov, L. M. Paletz, M. A. Olenicheva, N. F. Mikhajlova, and the author, and is housed in the Central Geological Tschernyshev Museum, Leningrad (CGM), under accession number 10876. The photographs are by Mr. B. S. Pogrebov, Leningrad University, and A. P. Reuss, VSEGEI; drawings were prepared by the author.

Symbols and abbreviations. L—length of rhabdosome, thecae, sicula, etc.; S—width of rhabdosome, thecae, etc.; Σ—distance from the top of th^1 hood to the sicular aperture; th^1, th^2 . . . the first, second . . . thecae. All measurements are given in mm. Dimensions included in brackets after the figures for rhabdosome width in some species give the dorso-ventral width across the aperture excluding the thecal hoods.

Suborder MONOGRAPTINA Lapworth, 1880
Family MONOGRAPTIDAE Lapworth, 1873
Genus MONOGRAPTUS Geinitz, 1852

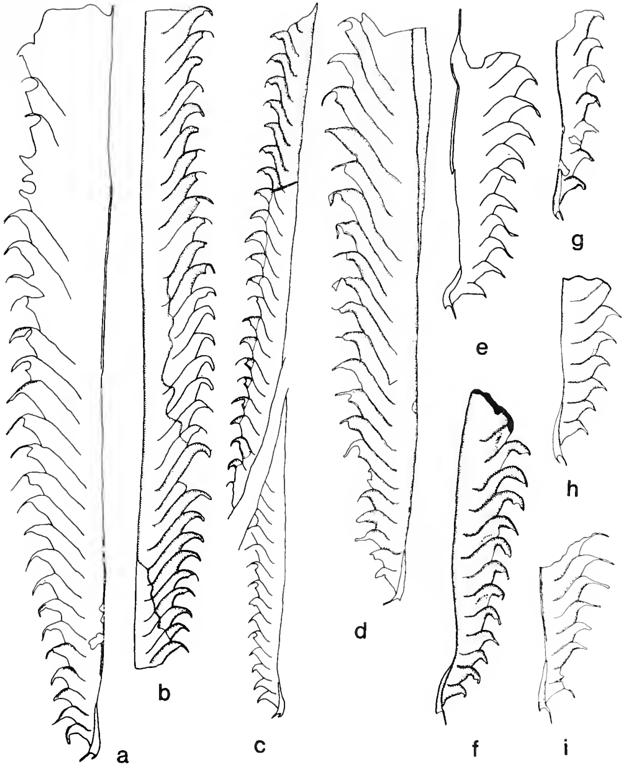
Monograptus anerosus sp. nov.

Plate 49, figs. 1-5; text-fig. 3

1975 *Monograptus uniformis*; Mikhajlova, p. 153, pl. 37, figs. 4-6.
1975 *Monograptus angustidens*; Mikhajlova (*pars*), p. 154, pl. 37, fig. 1, *non* figs. 2, 3.
1976 *Monograptus* aff. *uniformis*; Mikhajlova, pl. 2, fig. 19.
1976 *Monograptus* cf. *uniformis*; Mikhajlova, pl. 3, fig. 5.

Derivation of name. Latin *anerosus*, meaning fat.

Holotype. CGM 1/10876; Pl. 49, fig. 1, text-fig. 3*a*; *bouceki* Zone, Tokrau horizon, from the Bala well.



TEXT-FIG. 3. *Monograptus anerosus* sp. nov.; *a*, holotype, 1/10876, × 6; *b*, distal part of rhabdosome, 5/10290, × 4; *c*, 1/10290, × 4; *d*, rhabdosome in low relief, 6/10876, × 6, loc. 94/1; *e*, flattened young rhabdosome, 7/10876, × 6, loc. 35; *f*, *g*, rhabdosomes in full and low relief, transitional to *M. supinus* sp. nov. on account of the curvature of the proximal end, 8/10876, 2/10876, × 6, loc. 105; *h*, *i*, 9/10876, loc. 68, 10/10876, loc. 105, × 6.

Description. Rhabdosome straight, large, more than 35 mm long, with comparatively thin extreme proximal end at th$^{1-2}$. Dorsal edge displays slight dorsal curvature between th$^{3-5}$ with sicula becoming distinctly curved ventrally. Width across the aperture (including hood and lobe structures but excluding spines) at th^{1} 0·75–0·95, above the aperture of th^{1} 0·5–0·7, at th^{2} 1·0–1·2, th^{3} 1·2–1·5, th^{4} 1·3–1·6, th^{5} 1·45–1·75, at 5 mm 1·8–2·3, at 10 mm 2·0–2·5; maximum width 2·5–3·0, sometimes 2·1–2·2 in rhabdosomes 35 mm long.

Long (up to 3·5 mm), straight thecae parallel-sided (0·4–0·5 mm), inclined towards virgula at 50–60° at the extreme proximal end and 35–45° distally. They end with distinctive apertural structures that are beak-like in profile and uniform within the rhabdosome. The degree of thecal overlap increases from $\frac{1}{2}$ proximally to $\frac{3}{4}$ and $\frac{4}{5}$

distally. At the proximal end interthecal septae are slightly curved, lying almost normal to the axis. At 5 mm a horizontal line at the aperture level crosses one septum, distally—not more than two. Subapertural part of thecae is isolated and projected in ventral direction, while the free ventral wall lies at low angle to the axis. Although numerous specimens are available, details of the apertural structure are unclear, since the preservation in rock gives no possibility of observing these features in ventral view. Judging from specimens in relief, one can assume that in the initial stages the short shield was under construction as a result of the subsequent development of both dorsal and lateral thecal walls. Later the mesial slit appears, and paired curved lateral lobes are formed. The latter terminate in stout spines projecting ventrally. The apertural structures described are similar to those in *M. lochkovensis*. The length of the isolated subapertural part of the thecae and that of the lobes is about 0·5–0·85; length of apertural processes is equal in all thecae, 0·3–0·5. Thecal spacing 7·5–8·0 in 5 mm proximally, 9–10 in 10 mm distally.

Sicula curved distinctly ventrally, with apex reaching the upper edge of the apertural structure of th^2. Dimensions, L 1·3–1·6, sometimes 1·8, S aperture 0·15–0·2. Stout virgella 0·6–0·7 mm long is directed ventrally downward. There is a short (0·15 mm) curved dorsal process. The first theca is very short (0·7–0·75), Σ 0·8–1·05.

Discussion. The long, straight thecae at a gentle angle to the axis and the robust nature of the rhabdosome distinguish *M. anerosus* from other Přídolí monograptids. The complicated dorsolateral apertural structures are unusual for late Silurian graptoloids, and their reconstruction given in the description above is not the only possibility. It could have been an undivided, hood-like structure with a deep fold but no slit in the middle, and terminating with long, paired processes situated dorsolaterally—a structure similar to that described by Tsegelnjuk (1976) for '*Acanthograptus*' *spineus* and '*A*.' *aculeatus*. From the first growth stages the paired lateral lobes terminating with long spines could be formed—a structure homeomorphic to that of *Saetograptus*. This second possibility is less probable, but isolated material is needed for a more detailed analysis of morphology. In the shape of its apertural structures as seen in lateral view *M. anerosus* is similar to '*Saetograptus*' *pilosus*, described from post-Ludlow beds in the Yukon (Jackson and Lenz 1972). The structure is interpreted by those authors as paired lateral lobes. However, the real nature of the apertural additions cannot be reconstructed from the material preserved as silver-coloured films in shales. Thus, the assignment of this species to *Saetograptus* cannot be proved even on a morphological basis, to say nothing of phylogenetic criteria. This case seems to serve as a good example of convergent evolution, with the homologous thecal structure appearing independently. Comparison with some specimens of '*S*.' *pilosus* kindly provided by Professor A. Lenz shows that the new species differs in its larger size of rhabdosome, especially in its width. Further differences are in the straighter proximal extremity and in the closer thecal spacing, 7·5–8 in the first 5 mm as compared to 5–6 in the Yukon material. *M. anerosus* differs from *M. bouceki* in having paired apertural processes and larger rhabdosome size. Comparison with *M. supinus* sp. nov., which is closely similar morphologically and probably phylogenetically, is given in the description of the latter.

Distribution. Tokrau horizon, *M. bouceki–M. perneri kasachstanensis* zones, north-east Balkhash.

Material. More than fifty specimens well preserved as limonitic moulds in full to low relief, also flattened; Kokbajtal Mountains, locs. 93/1, 93/2, 255, 94, 105, 65, 41, 69; Kiikbaj Mountains, loc. 35; Bala well, loc. 209; Ashchi-Azek, loc. 47; Sarybiik Mountains, loc. 23.

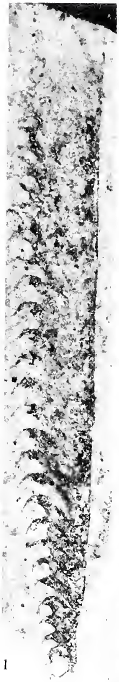
EXPLANATION OF PLATE 49

Tokrau horizon, *M. bouceki* (locs. 209, 20, 92, 94) and *M. perneri* (loc. 105) zones.

Figs. 1–5. *Monograptus anerosus* sp. nov. 1, holotype, 1/10876, × 5, loc. 209. 2–5, paratypes. 2, 2/10876, loc. 105, × 10. 3, 3/10876, loc. 105, × 5. 4, 4/10876, loc. 209, × 10. 5, 5/10876, loc. 105, × 5.

Fig. 6. *Monograptus balaensis* sp. nov., holotype, 11/10876, loc. 20, × 10.

Figs. 7–10. *Monograptus beatus* sp. nov. 7, 7*a*, holotype, 12/10876, loc. 20, × 5, × 10. 8–10, paratypes. 8, 9, early growth stages, locs. 92, 110, × 20. 10, 15/10876, loc. 94/3, × 10.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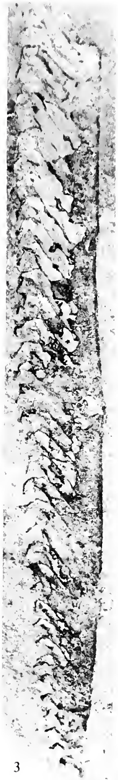
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KOREN', *Monograptus*

Monograptus balaensis sp. nov.

Plate 49, fig. 6; text-fig. 4*a*

Derivation of name. After the Bala well, north-east Balkhash.

Holotype. CGM 11/10876; Pl. 49, fig. 6, text-fig. 4*a*; 2·3 km south-west of the Sarybiik Mountains, loc. 20, Tokrau horizon, *bouceki* Zone.

Description. A large, straight monograptid, 35–40 mm long with proximal end weakly curved dorsally between th$^{1-6}$. Width increasing gradually: at th^1 0·75(0.6), th^2 0·8–0·9(0·65–0·7), th^3 0·8–1·0(0·7–0·8), th^4 0·9–1·1(0·8), th^5 1·15(0·9), at 10 mm 1·2(1·0)–1·5(1·2), at 15 mm 1·45(1·2)–1·7(1·45) and maximum width at 20 mm 1·65(1·45)–2·0(1·65).

Thecae long and narrow, strongly overlapping. The most distinctive feature is the strong, progressive elongation of thecae, from th^1 being 1 mm long to the distal thecae up to 4·5–5·5 mm long. Distally the thecal width to length ratio is 1 : 10. The thecal overlap reaches $\frac{4}{5}$ their length distally. Interthecal septa are straight and overlap strongly distally. A horizontal line at 10 mm from the sicular aperture crosses one septum, at 15 mm one septum and the base of the second, and further on distally it crosses two to three septa. Free ventral walls of the thecae are almost parallel to the axis. Metathecae strongly curved sigmoidally, displaying a sharp geniculum and shallow, semicircular apertural excavations. Thecal apertures 0·15–0·2 mm wide, and lie horizontally or are slightly everted. Thecae are furnished with short, down-curved hoods hanging closely above the apertures. They occur at a rate of 6 in 5 mm and 11·5–12·0 in 10 mm proximally, and 10–11 in 10 mm distally.

Sicula curved weakly ventrally, with the apex almost reaching the aperture of th^2. Dimensions, L 1·5–1·75, S aperture 0·15–0·2, Σ 1·25.

Discussion. This species is distinct from any previously reported Přídolí monograptids in having long and extremely narrow thecae that overlap each other strongly in the middle and distal part of the rhabdosome.

Distribution. Tokrau horizon, middle part, *lochkovensis–bouceki* zones, north-east Balkhash.

Material. Ten specimens in full to low relief, Bala well, locs. 209, 201; Sarybiik Mountain, loc. 20.

Monograptus beatus sp. nov.

Plate 49, figs. 7–10; Plate 50, figs. 1–5; text-fig. 4*b–g*

1975 *Monograptus* n. sp. aff. *microdon* R. Richter; Jaeger, p. 115, pl. 2, figs. 1, 2, text-fig. 5*d*.
1975 *Monograptus aequabilis* Přibyl; Mikhajlova (*pars*), pl. 38, fig. 6.

Derivation of name. Latin *beatus* meaning beautiful.

Holotype. CGM 12/10876; Pl. 49, fig. 7, text-fig. 4*b*; 2·3 km south-west of Sarybiik Mountain, loc. 20, *bouceki* Zone.

Description. Rhabdosome narrow, straight, 20–25 mm long. Dorsal edge displays slight dorsal curvature between th$^{2-4}$ whereas the proximal extremity at th^1 and sicula are curved ventrally. At th$^{1-2}$ the rhabdosome is of equal width, which is characteristic of the species. The width increases gradually between th$^{3-10}$; thereafter it may remain constant or show a slight decrease distally. Width at th^1 0·55–0·65, above the th^1 hood 0·3–0·35, at

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EXPLANATION OF PLATE 50

Figs. 1–5. *Monograptus beatus* sp. nov., Tokrau horizon, *M. lochkovensis* (loc. 92) and *M. bouceki* (locs. 15, 20, 110, 94) zones, paratypes. 1, 16/10876, loc. 20, × 10. 2, 17/10876, loc. 15a, × 10. 3, 18/10876, loc. 94/1, × 10. 4, 19/10876, loc. 110, × 10. 5, 20/10876, loc. 110, × 10.

Figs. 6–14. *Monograptus microdon aksajensis* subsp. nov., Tokrau horizon, eponymous zone, loc. 28. 6, holotype, 26/10876, × 5. 7–14, paratypes. 7, 8, 27/10876, 28/10876, × 20. 9, 29/10876, × 10. 10, 11, 30/10876, 31/10876, × 10. 12, rhabdosome in relief, distal fragment, 32/10876, × 20. 13, 33/10876, × 20. 14, 34/10876, × 10.


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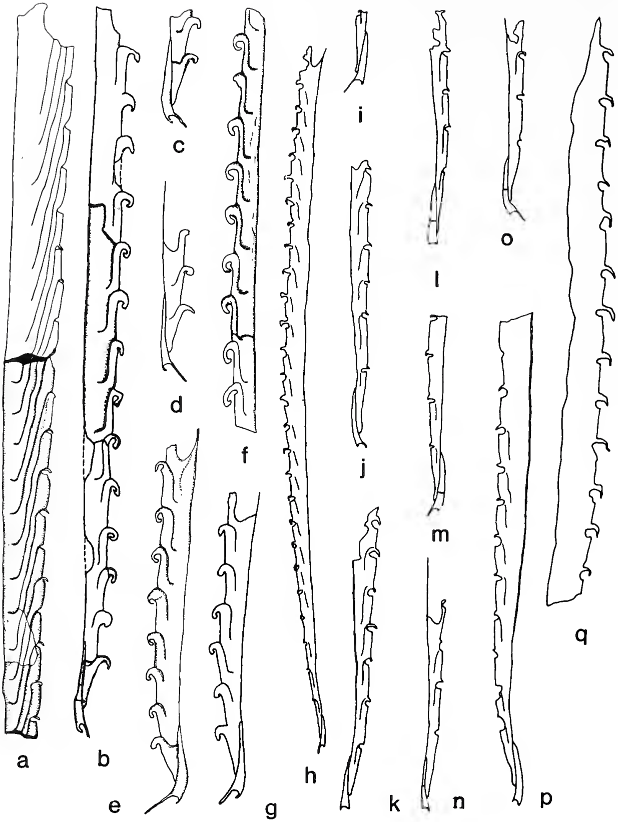
KOREN', *Monograptus*



TEXT-FIG. 4. *a*, *Monograptus balaensis*, sp. nov., holotype, rhabdosome in relief, 11/10876, × 6; *b–g*, *Monograptus beatus* sp. nov.; *b*, holotype, fragment of proximal part, 12/10876; *c–e*, *g*, young rhabdosomes with the characteristic shape of the distal end, 21/10876, 22/10876, 23/10876, 25/10876, locs. 20, 15; *f*, distal fragment of rhabdosome in full relief, 24/10876, loc. 15; *h–q*, *Monograptus microdon aksajensis* subsp. nov., loc. 28; *h*, holotype, 26/10876, × 4; *i–o*, young rhabdosomes at different growth stages, 35/10876, 36/10876, 27/10876, 33/10876, 28/10876, 37/10876, 38/10876, × 10; *p*, proximal fragment of adult rhabdosome, 34/10876, × 10; *q*, distal fragment with well-developed hoods, 39/10876, × 10.

th^2 0·55–0·75, th^3 0·65–0·75, th^4 0·65–0·8, at 5 mm 0·8–0·85, at 10 mm 0·85–0·95, with a maximum of 0·85–1·0 across the hood and 0·7–0·75 above it. A prominent, free nema is commonly thin.

Thecae long, narrowing to the aperture and strongly curved sigmoidally, displaying a sharp geniculum. The ventral walls are parallel to the axis. Dimensions, L 1·5–1·7, S aperture 0·1–0·15. Thecae overlap half of the succeeding thecae, the base of the interthecal septum is at the level of the hood of the preceding theca. Apertural structures develop as dorso-lateral hoods, which are down-curved, extending ventrally and obscuring the apertures both ventrally and laterally; beginning with th$^{2-3}$ they are retroverted to face and almost to touch the ventral edge of the aperture. Their dorso-ventral width accounts for $\frac{1}{2}$ to $\frac{1}{3}$ the total width of the rhabdosome. Thecae occur at a rate of 6–7 in 5 mm and 11·5–12·0 in 10 mm proximally, and 10·5–11·0 in 10 mm distally.

Prosicula very narrow and short (0·3 mm), metasicula weakly or distinctly curved ventrally, more strongly so in the subapertural part with the aperture facing down ventrally. Dimensions, L 1·4–1·5, S aperture 0·17–0·2. The sicula carries a stout virgella 0·55–0·65 mm long, and a narrow, weakly curved dorsal tongue (0·15 mm). Apex extends to a level between the hoods of th$^{1-2}$, Σ 1·25–1·4. The ventral wall of th^1 at 1 mm length is 0·2–0·25 mm above the aperture.

Discussion. M. beatus differs from *M. kallimorphus* Kraatz and *M. balticus* Teller (the latter being possibly a junior synonym of the former) in having a comparatively straight proximal end and larger rhabdosome. It can also be distinguished by its longer thecae and lesser degree of thecal hood retroversion. Compared with *M.* cf. *balticus* Teller from the Road River Formation of the Yukon (Jackson and Lenz 1972) the Kazakhstan species differs in having a thinner proximal extremity and a greater thecal count. The long, retroverted hoods and short thecae separate this species from late Přídolí-Lochkov monograptids such as *M. microdon*. One can suggest that *M. kallimorphus* (late Ludlow), *M. beatus* (middle Přídolí) and *M. microdon* (which are all similar morphologically) belong to one lineage with some unknown links within the Ludlow–Lochkov interval.

Distribution. Tokrau horizon, middle part, *lochkovensis–bouceki* zones, north-east Balkhash.

Material. Eighty-six specimens at various growth stages, well preserved in low to full relief or flattened; Kokbajtal Mountains, locs. 92, 110, 93/1–4; Sarybiik Mountains, locs. 15a, 20a; Aksaj Mountains, loc. 75.

Monograptus microdon aksajensis subsp. nov.

Plate 50, figs. 6–14; text-fig. 4*h–q*

Derivation of name. After the Aksaj Mountains of north-east Balkhash.

Holotype. CGM 26/10876; Pl. 50, fig. 6, text-fig. 4*h*; Aksaj Mountains, loc. 28, the eponymous zone in the upper part of the Tokrau horizon.

Description. Rhabdosome straight, thin, reaching 30 mm in length. The proximal end between th$^{1-5}$ varies from straight to weakly curved dorsally, while the sicula has a ventral curvature. The width increases imperceptibly up to a maximum of 0·7–0·95 (0·55–0·8) mm at a distance of 10 mm from the first theca, thereafter being constant. Successive increase in width, at th^1 0·25(0·2), th^2 0·3(0·22–0·25), th^3 0·3–0·4(0·25–0·35), th^4 0·4–0·45(0·3–0·4), th^5 0·45–0·5(0·4–0·45), at 10 mm 0·7–0·95(0·55–0·8).

Uniform thecae are strongly curved near the apertures of preceding thecae, forming a sharp geniculum. They overlap significantly, with the interthecal septae noticeably undulating. Thecae have short dorso-lateral hoods 0·15–0·3 mm long and 0·05–0·1 mm high hanging above the apertures, with their edges extending beyond the ventral walls of thecae at 0·1–0·2 mm. Straight apertures of proximal thecae are exposed laterally. Distal hoods are more strongly developed laterally and obscure the thecal apertures. The middle part of the hood resembles a weakly down-curved shield. Protheca expanded, bottle-like at the base, narrowing sharply to the aperture. At the base of the lateral side of the protheca a distinct wrinkle can be observed (Pl. 50, fig. 12), directed ventrally downwards from the nema. Metathecae are of equal width over most of their length, narrowing sharply towards the aperture. The free part of the metatheca is convex, with the subapertural part introverted. Thus, hoods grow first dorsally, then they turn upwards ventrally. Most of the hood is under the geniculum of the succeeding theca. This distinctive outline of the subapertural part of the thecae is well seen at the growing end of the rhabdosome (Pl. 50, figs. 9, 11, 13). Towards the dorsal end the thecae have a strong tendency to elongation, which is expressed in a greater degree of thecal overlap. Dimensions of distal thecae, L 2·1–2·15 (metatheca occupies $\frac{2}{3}$ the whole length), S metatheca from 0·25–0·27 above geniculum to 0·1 near the aperture. The base of the interthecal septum of th^{n} and th^{n+1} almost reaches the upper edge of the th^{n-2} hood. A horizontal line across the hood distally crosses not more than one septum. The thecal count ranges from 6·0–6·5 in 5 mm and 12·5–13·0 in 10 mm proximally, to 12·0–12·5 in 10 mm distally.

The extreme proximal end is very thin. The sicula is short with its apex reaching the level of the th[1] aperture. The base of th[1] is at 0·17–0·22 mm above the sicular aperture. The sicula is provided with a virgella 0·3–0·5 mm long and with a short dorsal tongue. Dimensions of sicula, L 1·0–1·2, S aperture 0·12–0·15(0·2), Σ 1·3–1·4.

Discussion. Numerous well-preserved specimens both in low relief and flattened allow details of the distinctive thecal structure to be studied for the first time. Previous knowledge of the morphology of *M. microdon* was based on studies of flattened and often deformed material preserved mainly as silver films in black shales. A thin rhabdosome and small, barely noticeable hoods are considered to be diagnostic features of this species. Differentiation of subspecies is based on the shape of the proximal end—straight, curved dorsally, or curved ventrally (*M. m. microdon* R. Richter; *M. m. silesicus* Jaeger). In my material it is possible to see the extensive range of variation in the curvature of the proximal end, from straight to distinctly curved dorsally. On the same bedding planes there are straight rhabdosomes similar to *M. m. microdon* and dorsally curved forms typical of *M. m. silesicus*, with all transitions. This therefore casts doubt on the possibility of using the shape of thin, flexible proximal extremities as a reliable taxonomic criterion. The new Kazakhstan subspecies differs from *M. m. microdon* in having a thinner proximal end at the level of th^{1-5} and a lesser maximum width not exceeding 1 mm. It also has more closely spaced thecae, 13–12 in 10 mm as compared with 10·5–8·5 characteristic of the type subspecies from the uppermost Silurian and Lower Devonian (Thuringia, Urals, central Nevada).

From monograptids of the *M. similis* group, with uniform thecae having hoods of the *M. uncinatus* type, this subspecies can be distinguished by its longer and thinner thecae with sigmoidal curvature, by its smaller hoods, and its thinner proximal end; also, the maximum rhabdosome width is lower. Comparison with *M. beatus* sp. nov., to which it is probably related, is given in the description of the latter species.

Distribution. Uppermost part of the Tokrau horizon, the eponymous local zone, north-east Balkhash. This local zone terminates the continuous Silurian succession of terrigenous rocks. The level of the Silurian–Devonian boundary is not proved biostratigraphically since graptolites are not found in the overlying strata, but one would predict the appearance of *M. uniformis* close to this level.

Material. Eighty specimens at various growth stages preserved both flattened and sometimes as limonitic moulds in full relief; Aksaj Mountain, loc. 28.

Monograptus mironovi sp. nov.

Plate 51, figs. 1–3; text-fig. 5*a–e*

1975 *Monograptus aequabilis*; Mikhajlova (*pars*), pl. 38, figs. 1, 2.

Derivation of name. In honour of the Kazakhstan geologist A. I. Mironov.

Holotype. CGM 40/10876; Pl. 51, fig. 1, text-fig. 5*a*; Kokbajtal Mountains, loc. 94/1, Tokrau horizon, *bouceki* Zone.

EXPLANATION OF PLATE 51

Figs. 1–3. *Monograptus mironovi* sp. nov., Tokrau horizon, *M. bouceki* Zone, loc. 94/1. 1, 1*a*, holotype, 40/10876, × 10, × 5. 2, 3, paratypes, 41/10876, 42/10876, × 10.

Figs. 4–7. *Monograptus nimius* sp. nov., Tokrau horizon, *M. bouceki* Zone, loc. 44. 4, paratype, 47/10876, × 5. 5, holotype, 48/10876, × 5. 6, 7, 49/10876, 50/10876, × 5.

Figs. 8–14. *Monograptus prognatus* sp. nov., Tokrau horizon, *M. microdon aksajensis* local Zone, loc. 28. 8, holotype, 51/10876, × 5. 9, 10, early growth stages, 52/10876, 53/10876, × 10. 11, 13, paratypes, 54/10876, 56/10876, × 10. 12, 14, 55/10876, 57/10876, × 10.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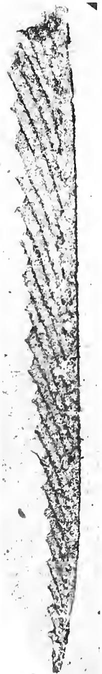
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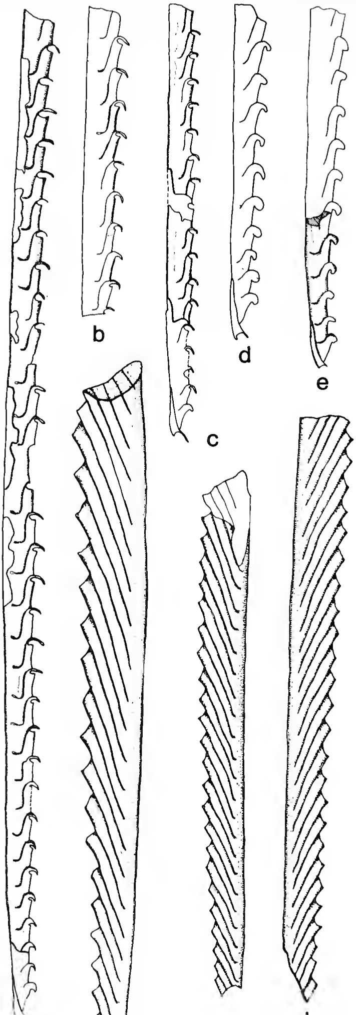
KOREN', *Monograptus*



TEXT-FIG. 5. *a–e*, *Monograptus mironovi* sp. nov., × 6; *a*, holotype, 40/10876; *b*, distal fragment, 43/10876, loc. 94/1; *c–e*, rhabdosomes in full and low relief, 44/10876, loc. 94/1, 45/10876, loc. 15, 46/10876, loc. 75; *f–h*, *Monograptus nimius* sp. nov.; *f*, holotype, 48/10876, × 6; *g*, *h*, distal fragments of rhabdosomes in relief, 50/10876, × 4.

Description. Rhabdosome straight, medium sized, 20–30 mm long. The dorsal edge between th$^{2-4}$ is weakly curved dorsally, the ventral edge is straight. A slight increase of width within the rhabdosome is characteristic of the species. Successive width measurements, at th^{1} 0·75–0·8(0·5–0·65), above the hood of th^{1} 0·55, at th^{2} 0·65–0·8(0·5–0·6), th^{3} 0·75–0·85(0·6–0·75) th^{4} 0·75–0·85(0·55–0·75), th^{5} 0·8–0·9(0·65–0·75), maximum width 0·8(0·6)–1·0(0·8) between th$^{6-8}$, sometimes reaching 1·25(1·0) and thereafter constant.

Thecae comparatively short (1·8–1·9), slightly curved sigmoidally, overlapping for half of their length. The ventral walls and interthecal septa are parallel or inclined slightly to the axis. In the middle and distal parts of the rhabdosome the bases of the interthecal septa are at the level of the preceding thecal hood. Dorsal apertural hoods hang over the aperture and extend down slightly below its ventral edge. The hood of th^{1} is slightly larger than the others and its length corresponds to one-third of the whole dorso-ventral width of the rhabdosome. Thecal hoods are equally developed along the rhabdosome, including the extreme dorsal end; they are 0·3–0·35 mm long and 0·35–0·4 mm high. Thecae number 6·5–7·5 in 5 mm and 13–14 in 10 mm proximally, and 10·5–12·0 in 10 mm distally.

The extreme proximal end is not thin in comparison to the small size of the rhabdosome. Sicula straight or slightly curved ventrally. The first theca is short and broad at its base, originating at 0·15 mm above the sicular aperture. The sicula terminates with a stout virgella 0·5–0·6 mm long and a short dorsal tongue; the apex extends to the level of the th^{2} aperture. Dimensions of sicula, L 1·3–1·6, S aperture 0·2–0·25, Σ 1–1·2.

Discussion. This species is comparable to *M. similis* Přibyl in general structure and rhabdosome shape. It differs, however, in being narrower at th^{1} and in the distal part of the rhabdosome. Its maximum width is 1·0(0·8) as compared with 1·2–1·5(1·0–1·2) in *M. similis.* It can also be distinguished from *M. similis* by its shorter thecae, shorter sicula, and larger size of hoods projecting considerably and uniformly beyond the free ventral wall. It has close affinities with *M. beatus* sp. nov. but it can be distinguished by: 1, shorter hoods that are not retroverted at the edges; 2, greater width of the extreme proximal end (0·55 above th^{1} hood as compared with 0·3–0·35 mm); 3, straight extreme proximal end including the sicula itself; and 4, more closely packed thecae. It differs from *M. prognatus* sp. nov. in having a smaller rhabdosome, a slight increase in width within the rhabdosome, and in having the free ventral walls of the thecae lying parallel to the axis.

Distribution. Middle part of the Tokrau horizon, *bouceki* Zone, north-east Balkhash.

Material. Forty-eight well-preserved specimens, both flattened and in low relief; Kokbajtal Mountains, locs. 94/1–3; Bala well, loc. 75; Sarybiik Mountains, locs. 15a, 20.

Monograptus nimius sp. nov.

Plate 51, figs. 4–7; text-fig. 5*f–h*

Derivation of name. Latin *nimius* meaning extraordinary.

Holotype. CGM 48/10876; Pl. 51, fig. 5, text-fig. 5*f*; Ashchi–Azek, loc. 44, Tokrau horizon, *bouceki* Zone.

Description. Rhabdosome large, 25–35 mm long. The extreme proximal end between th$^{5-6}$ is slightly curved ventrally. Width increases rapidly within the first 10 mm, thereafter more slowly up to the distal end. Width measurements, at th^{1} 0·75–0·85, th^{2} 0·85–1·0, th^{3} 0·95–1·1, th^{4} 1·1–1·2, th^{5} 1·15–1·3, at 5 mm 1·2–1·4, at 10 mm 1·6–1·65, at 15 mm 1·75–2·1, maximum width 2·25–2·65 (specimens in relief) and 2·85 (flattened) for rhabdosomes more than 20 mm long. The extreme proximal end appears to taper in comparison with the remainder of the rhabdosome.

Thecae biform, the first three to four provided with paired lateral lobes, each small and rounded; remaining thecae are simple tubes with even, retroverted apertures. Thecae long and slender, parallel-sided over most of their length and distinctly widening towards the apertures. The progressive astogenetic elongation of thecae accompanied by development of thecal overlap is the most characteristic morphological feature. Length of successive thecae, th^{1} 1·25, th^{5} 2·25, th^{10} 3·5, th^{15} 4·5, and th^{20} 5·5. Average size of distal thecae: L 5·0, S aperture of protheca 0·4, S aperture of metatheca 0·5; S : L more than 1 : 10. Overlap increases from $\frac{1}{2}$ proximally to $\frac{5}{6}$ of the succeeding thecae distally. A horizontal line across the thecal aperture at 5 mm from the sicula crosses two interthecal septa, at 10 mm it crosses two and the base of the third, at 20 mm and thereafter not less than three. Angle of thecal inclination 18–23°. Thecae number 5·5–6·5 in 5 mm and 10·5–11·5 in 10 mm proximally, 8–9 in 10 mm distally.

Sicula slightly curved ventrally, with apex reaching a level between the apertures of th^1 and th^2. Dimensions of sicula, L 1·75, S aperture 0·25–0·3, Σ 1·5.

Discussion. M. nimius differs from closely similar biform monograptids such as *M. transgrediens* Perner and *M. lochkovensis* Bouček in having extremely long and strongly overlapping thecae with a small angle of inclination to the axis. In both *M. lochkovensis* and *M. transgrediens* a horizontal line across the thecal aperture crosses two interthecal septa at the most. A ratio of thecal width to length of 1:10 is unknown among previously recorded Přídolí monograptids, except for *M. balaensis* sp. nov. described herein. *M. lochkovensis* is most similar to *M. nimius*, but the latter is distinguished by having a lower number of proximal thecae provided with paired lateral additions that are smaller and have no processes.

Distribution. Middle part of the Tokrau horizon, *lochkovensis–bouceki* zones, north-east Balkhash.

Material. Thirty well-preserved specimens both in relief and flattened; Kokbajtal Mountains, locs. 92, 110, 93/4, 94/1; Sarybiik Mountains, loc. 15a; Ashchi-Azek, loc. 44.

Monograptus prognatus sp. nov.

Plate 51, figs. 8–14; Plate 52, figs. 1–5, 8–10; text-fig. 6

1975 *Monograptus angustidens*; Mikhajlova (*pars*), p. 154, pl. 37, figs. 2, 3.
1976 *Monograptus angustidens*; Mikhajlova, pl. 1, fig. 21.
1969 ?*Monograptus* aff. *angustidens*; Jackson and Lenz, p. 21, pl. 3, figs. 6–9, pl. 5, fig. 7.
1978 ?*Monograptus* aff. *angustidens*; Jackson, Lenz and Pedder, p. 21, pl. 3, figs. 4, 11.

Derivation of name. Latin *prognatus* meaning deriving from somebody.

Holotype. CGM 51/10876; Pl. 51, fig. 8; from the *microdon aksajensis* Zone, uppermost part of the Tokrau horizon, Aksaj Mountains, loc. 28.

Description. Rhabdosome straight, large, 30–40 mm or up to 50–60 mm long. The extreme proximal end is very thin, dorsal edge displays slight dorsal curvature between th$^{3-5}$. A stout, free nema continues beyond the distal thecae for more than 10 mm. Width at th^1 0·6–0·85(0·45–0·65), above th^1 hood 0·35–0·55, at th^2 0·65–0·95(0·5–0·75), th^3 0·7–1·0(0·6–0·8), th^4 0·75–1·0(0·6–0·85), th^5 0·8–1·1(0·6–0·85), at 5 mm 0·95–1·25(0·75–1·15), at 10 mm 1·35–1·65(1·1–1·4), maximum width in specimens 20–50 mm long is 1·6–2·0(1·3–1·75), in those up to 60 mm long is 2·0–2·3(1·75–1·8). The noticeable variation in dorso-ventral width can be explained partly by different states of preservation. Thecae are weakly curved sigmoidally and have long dorsal hoods. They project 0·3 mm beyond the ventral edge of the rhabdosome and extend down below the aperture for 0·2–0·3 mm; they are 0·5–0·75 mm long and 0·2–0·3 mm high. Hoods are well developed and uniform within the whole rhabdosome, being 0·75 mm long on the extreme distal thecae (Pl. 52, figs. 8–10). Apertures are clearly visible in ventral view beginning with th$^{3-4}$. Proximally the hoods occupy $\frac{1}{3}$ and distally $\frac{1}{4}$ to $\frac{1}{5}$ of the dorso-ventral width of the rhabdosome, and they have small excavations 0·15–0·2 mm long and 0·25–0·3 mm wide. The overlap of interthecal septa increases distally. At 5 mm from the sicula the septum between th^n and th^{n+1} reaches the level of the th^{n-1} hood, and a horizontal line across the aperture does not cut any septum; at 10 mm it crosses the base of one septum, at 15–20 mm it cuts one septum and sometimes the base of another, and at the extreme distal end it cuts two septa. Thecal overlap increases from $\frac{1}{4}$ to $\frac{2}{3}$ of their length. The distal thecae are 3·0–3·5 mm long, 0·25–0·35 mm wide; the angle of inclination to the axis reaches 10–15°, sometimes 20°. Free ventral walls

EXPLANATION OF PLATE 52

Figs. 1–5, 8–10. *Monograptus prognatus* sp. nov., Tokrau horizon, *M. lochkovensis* (loc. 92), *M. bouceki* (locs. 15, 20) and *M. microdon aksajensis* (loc. 28) zones. 1, 58/10876, loc. 28, × 10. 2, 59/10876, loc. 20, × 10. 3, 60/10876, loc. 15a, × 10. 4, 61/10876, loc. 28, × 10. 5, paratype, 62/10876, loc. 92, × 10. 8–10, distal fragments of adult rhabdosomes with well-developed hoods, 63/10876, 64/10876, loc. 28, × 10; 65/10876, loc. 92, × 5.

Figs. 6, 7, 11, 12. *Monograptus supinus* sp. nov., Tokrau horizon, *M. bouceki* Zone, loc. 94/1. 6, 7, 12, young rhabdosomes, 75/10876, 76/10876, × 20; 78/10876, × 10. 11, holotype, 77/10876, × 10.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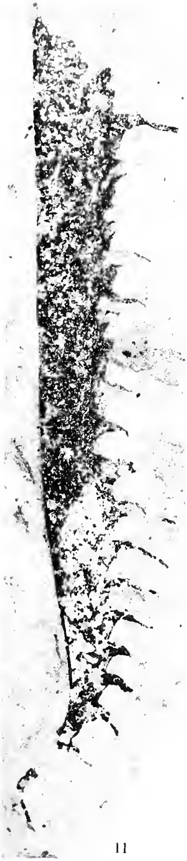
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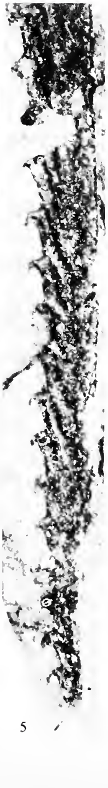
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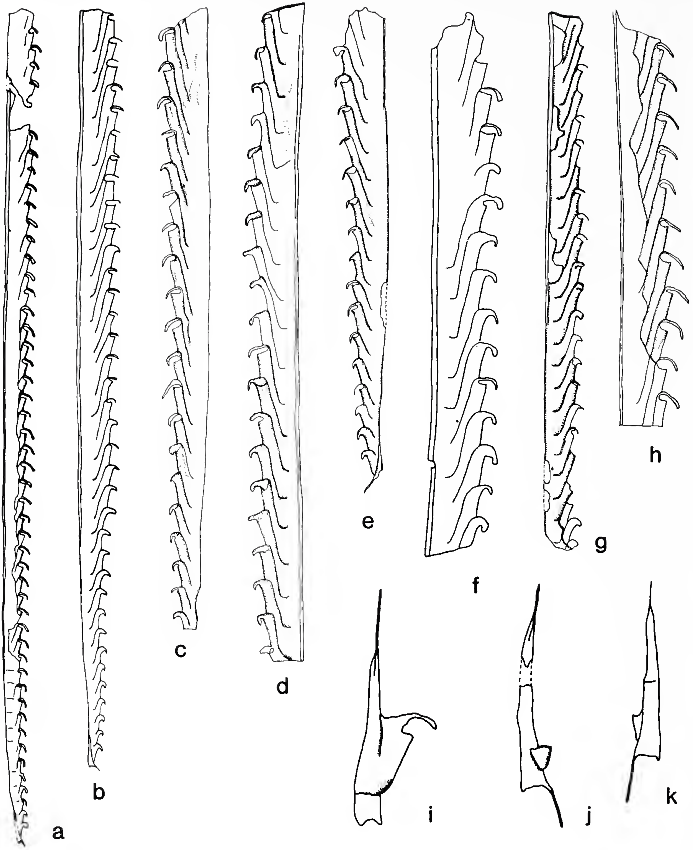
KOREN', *Monograptus*



TEXT-FIG. 6. *Monograptus prognatus* sp. nov.; *a*, *b*, adult rhabdosomes, 66/10876, ×3, loc. 28, 67/10876, ×4, loc. 92; *c*, *d*, distal rhabdosome fragments, 68/10876, loc. 92, 69/10876, loc. 15, ×6; *e*, 62/10876, ×6, loc. 92; *f–h*, distal fragments of adult rhabdosomes, 70/10876, loc. 15, 2/10290, 71/10876, loc. 77, ×6; *i–k*, early stages of development, 72/10876, 73/10876, 74/10876, ×20, loc. 28.

are straight and inclined at 10° to the nema. The thecal count is 6·0–6·5 in 5 mm and 11·0–12·5 in 10 mm proximally, 9–10 in 10 mm distally.

Sicula straight or weakly curved ventrally. Dimensions, L 1·35–1·8, S aperture 0·2–0·3, L virgella 0·5–0·65, L dorsal tongue 0·1, Σ 1·1–1·35. Apex reaches the level of the base of the septum between th$^{2-3}$ or between the hoods of th$^{1-2}$. The base of th^1 is 0·2 mm above the sicula aperture, its length being about 0·85–1·05 mm.

Discussion. *M. prognatus* is fairly close to *M. uniformis angustidens* Přibyl, *M. praehercynicus* Jaeger and *M. birchensis* Berry and Murphy in thecal shape and hood structure. From all these species it differs, however, in one important feature, namely in the uniform development of hoods within the whole rhabdosome. This feature is more or less typical of Přídolí monograptids, as opposed to the *M. uniformis* group and others displaying a distinct decrease of hoods distally. From *M. u. angustidens* and *M. praehercynicus* it also differs in having a thinner proximal extremity and greater overlap of thecae distally. From the latter, *M. prognatus* can be distinguished by its lower distal width, more closely packed proximal thecae, smaller sicula, and shorter distance between sicular aperture and the upper edge of th^1 hood. From *M. birchensis* it differs in having a thinner and commonly straight proximal end within the first 10 mm, as well as having a narrower sicular aperture and shorter distance to the hood of th^1. In contrast to *M. birchensis* the new species displays a lower thecal inclination to the axis (28–33° in *M. birchensis*) and a greater overlap of distal interthecal septae. *M. prognatus* is comparable with *M. uncinatus* Tullberg in having hoods developed equally within the rhabdosome. It differs, however, in having smaller hoods and less strongly curved thecae with free ventral walls inclined to the axis. The length of thecae and their overlap are markedly greater than in *M. uncinatus*. The well-developed hoods on the distal thecae, slender proximal extremity, very gradual increase in rhabdosome width, lesser thecal overlap and angle of inclination separates *M. prognatus* from *M. u. uniformis* Přibyl. It also differs in having more closely spaced thecae and a shorter sicula that never reaches 2 mm. The larger rhabdosome and the longer thecae displaying stronger overlap distinguish *M. prognatus* from *M. similis* Přibyl. The material studied makes it possible to trace a morphological transition between *M. similis* and *M. prognatus*, expressed in increase in rhabdosome size together with thecal elongation and stronger thecal overlap. Stratigraphically, the new species succeed *M. similis*, appearing just above its last occurrences at the top of the *formosus* Zone and occurring thereafter through the whole Přídolí sequence. It can be assumed that *M. prognatus* is a precursor of the Lower Devonian monograptids of the *M. uniformis* group. *M. similis*, *M. prognatus* and *M. uniformis* could have been successive members of the same lineage developing within Přídolí–Lochkov times. The representatives of this lineage were conservative in the general morphology of their thecae, possessing similar hoods that are homeomorphs of those in *M. uncinatus* throughout the whole time span. They underwent insignificant morphological modification, namely a change of thecal size and proportions, appearance of thecal bioformity expressed in distal decrease and then complete reduction of hoods, and in a small variation in rhabdosome size.

Distribution. Tokrau horizon, *lochkovensis*, *bouceki*, *perneri*, *kasachstanensis* and *microdon aksajensis* zones, north-east Balkhash, most abundant in the uppermost local zone where it occurs with *M. microdon aksajensis*, and *Linograptus posthumus*. The marked impoverishment of the graptolite association suggests an immediate stratigraphical proximity to the *M. uniformis* level.

Material. More than 170 specimens of different astogenetic stages, well preserved, mainly flattened and sometimes in low relief; Kokbajtal Mountains, locs. 92, 110, 93/1, 105, 65, 69, 30, 41; Kiikbaj Mountains, loc. 7a; Aksaj Mountains, locs. 27, 28; Sarybiik Mountains, locs. 15a, 20, 22; Ashchi-Azek, loc. 47.

Monograptus supinus sp. nov.

Plate 52, figs. 6, 7, 11, 12; text-fig. 7

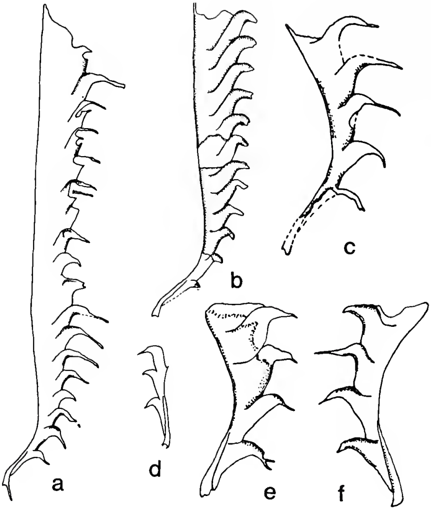
1976 *Monograptus* sp.; Mikhajlova, pl. 2, fig. 15.

Derivation of name. Latin *supinus* meaning curved dorsally (back).

Holotype. CGM 77/10876; Pl. 52, fig. 11, text-fig. 7*a*; Kokbajtal Mountains, loc. 94/1, middle part of Tokrau horizon, *bouceki* Zone.

Description. Rhabdosome of medium-size with slender proximal end, sharply curved dorsally (45°) within the first three to five thecae. Dimensions of adult rhabdosomes, L 20–40, S maximum 2·0–2·25. Successive measurements of width, at th^1 0·6, above the th^1 aperture 0·3, at th^2 0·7–0·8, th^3 1·0–1·1, th^4 1·3, th^5 1·4, at 5 mm 1·5–1·6, at 10 mm 1·7–1·9, maximum width attained distally.

Thecae have uniform apertural additions identical to those of *M. anerosus*. The proportions of the thecae and their inclination to the axis change within the rhabdosome due to the marked curvature of the proximal end. The first three or four thecae have long prothecal sections and overlap for not more than $\frac{1}{4}$ of their length. Distally the thecal overlap increases to $\frac{3}{4}$ of the length. The angle of inclination to the axis changes from 50° to 30–35° distally. A horizontal line across the thecal aperture proximally does not meet any septum; distally it crosses two septa.

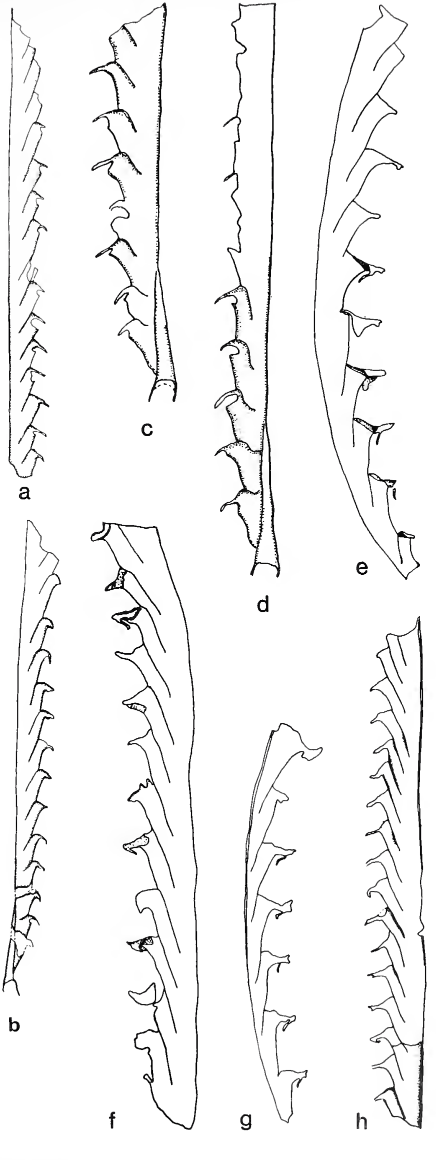


TEXT-FIG. 7. *Monograptus supinus* sp. nov.; *a*, holotype, 77/10876, ×6; *b*, rhabdosome in relief, 79/10876, ×6, loc. 22; *c–f*, young rhabdosomes, 76/10876, ×12, 80/10876, ×6, 78/10876, ×12, 75/10876, ×12, loc. 94/1.

The beak-like apertural structures project ventrally, terminating in straight processes 0·8–1·0 mm long and 0·1–0·2 mm thick at the base. Sometimes a bifurcation of processes can be observed and their ends are connected by membranes. Details of apertural spine structures are not clear in the material studied. They are probably similar to monofusellar processes, with edges folded together into a tube, as described previously as a characteristic feature of *Saetograptus chimaera* (Urbanek 1958). Thecae are spaced at 7 in 5 mm and 13–14 in 10 mm proximally, and at 11–12 in the distal 10 mm.

Sicula weakly curved ventrally with apex reaching the level of the th^1 aperture or slightly above. Dimensions, L 1·15–1·2, S aperture 0·15–0·2, L virgella 0·25–0·35, Σ 1·4–1·5.

Discussion. Although possessing the general form of the thecal structures of *M. anerosus*, this species is distinct in having a markedly thinner proximal end and in its stronger dorsal curvature. Some specimens transient from *M. anerosus* to *M. supinus* are present in the collections studied. They display an intermediate degree of proximal end width and curvature (Pl. 49, fig. 2; text-fig. 3*f*). *M. supinus* has obvious affinities in thecal structure with '*Saetograptus*' *pilosus* Jackson and Lenz. However, besides the distinction already mentioned it has more fully developed apertural processes, more closely spaced proximal thecae, and a larger rhabdosome. All three species (*M. anerosus*, *M. supinus*, '*S.*' *pilosus*) are considered to be closely similar and phylogenetically related. They



TEXT-FIG. 8. *a–d*, *Monograptus willowensis* (Berry and Murphy), loc. 105; *a*, *b*, distal and proximal fragments of adult rhabdosomes, 84/10876, 87/10876, × 6; *d*, proximal fragments of rhabdosomes in relief, 81/10876, 82/10876, × 12; *e–h*, *Neocucullograptus kozlowskii* Urbanek, loc. 127; *e*, 95/10876, × 10; *f*, *g*, 96/10876, 97/10876, × 10; *h*, 98/10876, × 6.

possess distinctive spinose thecal structures that are not known otherwise beyond the end of the early Ludlow.

Distribution. Tokrau horizon, *bouceki* and *perneri kasachstanensis* zones, north-east Balkhash.

Material. Fifteen specimens at different stages of development, preserved both in half relief and flattened; Kokbajtal Mountains, locs. 94, 94/1, 105p; Sarybiik Mountains, loc. 22.

Monograptus willowensis (Berry and Murphy, 1975)

Plate 53, figs. 1–6; text-fig. 8*a–d*

1975 *Saetograptus willowensis* Berry and Murphy, p. 79, pl. 7, fig. 7, text-fig. 18*d*.

Holotype. University of California at Riverside 6043/1, upper part of the Roberts Mountain Formation, Přídolí, Willow Creek, Nevada, USA.

Description. Rhabdosome straight, medium sized, 35–50 mm long. Dorsal margin between th^{1-5} weakly curved dorsally. Rhabdosome widens rapidly in the first 5 mm, thereafter width increases more slowly to a maximum in the distal part. Successive width measurements (exclusive of apertural processes), at th^1 0·75–0·85, above the aperture 0·45–0·55, at th^2 0·8–0·95, th^3 0·95–1·0, th^4 1·0–1·1, th^5 1·0–1·1, at 5 mm 1·05–1·25, at 20 mm 1·2–1·6, maximum 1·4–1·75, sometimes 1·85.

Thecae are distinctly biform. The proximal 12–14 thecae have distinctive apertural structures similar to those described in *M. anerosus*. Distal thecae are simple tubes with extroverted, even apertures. In lateral view the apertural additions of proximal thecae appear as beak-like structures terminating in paired spines. Details of thecal morphology are not clear as the specimens studied are preserved in rock. The apertural structures could have been formed either as paired, completely separate lateral lobes or as more complicated dorso-lateral additions. They are 0·6–0·65 mm long at the most (including spines), decreasing distally where they become less visible, giving place first to small lateral additions and then disappearing. Their overlap increases distally from $\frac{1}{4}$ to $\frac{2}{3}$ of their length, and the angle of inclination also increases. The base of the interthecal septum in the distal part of the rhabdosome reaches to the middle of the free ventral wall of the succeeding theca. A horizontal line crosses not more than one septum. Dimensions of thecae, L 2·5–3·0, S 0·35–0·45, S:L 1:6, inclination 20–25°. Thecae spaced at 6·0–6·5 in 5 mm and 11–12 in 10 mm proximally, and at 9–10 in 10 mm distally.

Sicula large, thin apically and widening markedly, almost flaring, at the aperture. A 0·25 mm long dorsal tongue is strongly incurved and well developed. Dimensions of sicula, L 2·0–2·1, S aperture 0·35, L virgella 0·5–0·55. Apex lies between the apertures of th^{2-3}, the base of th^1 is 0·2–0·25 mm above the sicular aperture, Σ 1·25–1·4.

Discussion. The distinctive biformity of the thecae, and the proximal apertural structures make the assignment of specimens to *M. willowensis* quite evident. Only slight variations in rhabdosome size were discovered when comparing the Kazakhstan specimens with typical material from Nevada (Willow Creek section), kindly provided by Dr. H. Jaeger. They differ insignificantly in their lower rhabdosomal width and more closely spaced thecae having a lower angle of inclination to the axis. The sicular aperture of the Kazakhstan form is less flared and the feature itself can be observed only in some specimens. These differences are probably due to the different preservations—flattened specimens from central Nevada and in full to low relief in Kazakhstan.

EXPLANATION OF PLATE 53

Figs. 1–6. *Monograptus willowensis* (Berry and Murphy), Tokrau horizon, *M. perneri kasachstanensis* Zone, loc. 105. 1, 81/10876, × 10. 2, 82/10876, × 10. 3, young rhabdosome, 83/10876, × 10. 4, distal fragment, 84/10876, × 5. 5, 6, rhabdosomes in half relief, 85/10876, 86/10876, × 10.

Figs. 7–14. *Neocucullograptus kozlowskii* Urbanek, Akkan horizon, eponymous zone, loc. 127. 7, 8, 9, 11, distal fragments, 88/10876, 89/10876, 90/10876, 92/10876, × 5. 10, 12, 14, fragments of middle parts of rhabdosomes, 91/10876, 93/10876, 95/10876, × 10. 13, proximal part of rhabdosome with no sicula, 94/10876, × 10.

KOREN', *Monograptus*, *Neocucullograptus*

As discussed above, the thecal structure is not unique to Přídolí monograptids, but similar apertural additions are characteristic of synchronous species belonging to the *M. lochkovensis* and *M. anerosus* groups. From the closely similar *M. lochkovensis*, *M. willowensis* differs in having a smaller rhabdosome and thecae, a lower degree of septal overlap distally, and in its sicular shape. Although having apertural processes similar to those of the *M. anerosus* group, it can be distinguished by the well-expressed thecal biformity and the different shape of the proximal end and sicula.

The original assignment of this species to *Saetograptus* (Berry and Murphy 1975) does not seem to be justified. It was based on the apertural structures of the proximal thecae, reminiscent of *Saetograptus fritschi linearis*. Even now it seems premature to determine the generic assignment of such species as *M. willowensis*, *M. anerosus*, *M. lochkovensis*, and other similar forms because details of their thecal morphology are not clear. Neither the *M. lochkovensis* nor *M. anerosus* groups are linked phylogenetically with the lower Ludlow saetograptids. One can suggest instead that similar apertural structures appear independently at later stages of evolution.

Distribution. Roberts Mountain Formation of central Nevada, the eponymous zone corresponding to the middle part of the Přídolí. In Kazakhstan it occurs at approximately the same level in the uppermost part of the *bouceki* Zone (rare) and in the *perneri kasachstanensis* Zone (common).

Material. Thirty-six specimens at different stages of development, preserved in relief; Kokbajtal Mountains, locs. 105, 69, 30, 13a, 41; Kiikbaj Mountains, loc. 35.

Genus NEOCUCULLOGRAPTUS Urbanek, 1970

Neocucullograptus kozlowskii Urbanek, 1970

Plate 53, figs. 7–14; text-fig. 8*e–h*

1970 *Neocucullograptus kozlowskii* n. sp. Urbanek, p. 348, pls. 37–39, figs. 18–20.
1976 *Neocucullograptus kozlowskii*; Tsegelnjuk, pl. 41, fig. 11.
1976 *Neocucullograptus* sp. n. Mikhajlova, pl. 1, figs. 4–7.

Holotype. Urbanek 1970, text-fig. 20A–B, Palaeozoological Institute, Warsaw; lower part of the Siedlce Beds, the eponymous zone, Melnik borehole (873.40–854.60).

Description. Fragmentary rhabdosomes more than 30 mm long with no proximal extremities preserved. They are straight distally and broadly arcuate proximally (up to 130°). They widen gradually within the greater part of their length, distally they are parallel-sided. Maximum width of the observed proximal fragments measured across the aperture 0·4, above it 0·2, distally 1·0–1·2 and 0·9–1·0 respectively.

Thecae are slender tubes, 2·0–2·2 mm long, parallel-sided in the metathecal part. Free ventral walls are straight and inclined to the axis at 15–20°. Overlap of the thecae increases from $\frac{1}{3}$ to $\frac{1}{2}$ distally. Thecal count ranges from 9·0 to 10·5. The straight interthecal septa begin at the level of the succeeding thecal aperture. Only general features of the apertural apparatus structure can be observed in specimens preserved in rock. From the lateral lobes characteristic of this species only left hypertrofied structures 0·8–0·85 mm long are usually observed in the material studied. These have a well-developed tongue-like ventral process that conceals the aperture almost completely. In some cases one can distinguish the edges of a short gular process. Prominent rostral processes are usually clearly visible; these are straight, 0·5 mm long and projected ventrally.

Discussion. The structure of the lateral lobes is taken as the main diagnostic feature for the discrimination of neocucullograptid species (Urbanek 1970). Details of this structure were studied on the material isolated from the matrix. *N. kozlowskii* is distinct from other species in having strikingly asymmetrical lateral lobes of a more complicated structure. The left apertural lobe possesses ventral and long rostral processes. These characteristic morphological details are distinguishable in the Kazakhstan material and thus confirm the specific identification.

Distribution. N. kozlowskii was first described from the eponymous zone in the upper part of the Siedlce Beds of Poland. Later it was found in the uppermost part of the Kopanina beds below the first occurrence of *M. ultimus* in the Barrandian area, as well as in synchronous deposits of Lithuania and the south-west Ukraine (Paškevičius 1979; Tsegelnjuk 1976). In Kazakhstan it occurs in the uppermost part of the Akkan horizon in beds above the last occurrences of ?*Bohemograptus butovicensis* Bouček and below the first appearance of *M. formosus* Bouček.

In its known localities the vertical range of *N. kozlowskii* does not overlap with the ranges of *M. ultimus* and *M. formosus*.

Material. More than sixty specimens in low to full relief preserved in coarse-grained sandstones; Kokbajtal Mountains, loc. 127.

Acknowledgements. I thank Dr. S. M. Bandaletov for making possible my study of the Přídolí sections in Kazakhstan, and Dr. D. Kaljo for support in publishing the results. I am greatly indebted to Dr. H. Jaeger for helpful suggestions made while he examined the collections, and to both him and Professor A. Lenz for providing comparative material. Professors A. Urbanek and L. Teller gave me friendly co-operation during comparative studies of graptolites in Warsaw and Leningrad. For critically reading the manuscript and for their helpful suggestions I thank Dr. I. F. Nikitin, Dr. O. P. Kovalevskii, Dr. G. A. Stukalina, and Dr. R. B. Rickards. The English translation was improved and edited by Dr. M. G. Bassett.

REFERENCES

ABDUAZIMOVA, Z. M. 1970. Graptolity verchnego venloka, ludlova i nadludlova nekotorykh regionov Yuzhnogo Tyan'-Shanya. *In*: *Biostratigrafia osadochnykh obrazov. Uzbekistana, sb. 9.* Nedra, Leningrad, 34–73.

BANDALETOV, S. M. 1969. *Silur Kazakhstana.* Akad. Nauk Kazakh. SSR, Nauka, Alma-Ata, 156 pp.

—— 1979. Regional'nye stratigraficheskie podrasdelenia silura Kazakhstana i britanskij standart silurijskoj sistemy. *Izv. Akad. Nauk Kazakh. SSR.* ser. geol., **4–5,** 58–65.

—— and MIKHAJLOVA, N. F. 1968. Verkhnij silur i granitsa silura i devona v Kazakhstane. Ref. dokladov k III Mezhdunarodnomu simpoziumu po granitse silura i devona i stratigrafii nizhnego i srednego devona, VSEGEI, Leningrad, 25–28.

BERRY, W. B. N. and MURPHY, M. A. 1975. Silurian and Devonian graptolites of central Nevada. *Univ. Calif. Publs geol. Sci.* **110,** 109 pp., 15 pls.

BISKE, G. S. and RINENBERG, R. E. 1973. Nakhodki graptolitov v nadludkovskikh otlozheniyakh rajona Baubashaty (Yuzhnyj Tyan'-Shan'). *In* SAPELNIKOV, V. P. and CHUVASHOV, B. I. (eds.). Materialȳ po paleontologii srednego paleozoya Uralo-Tyan'shanskoy oblasti. Sbornik vo voprosam stratigrafii No. 18. *Trudȳ instituta geologii i geokhimii,* **99,** 169–175.

BULMAN, O. M. B. and RICKARDS, R. B. 1970. Classification of the graptolite family Monograptidae Lapworth, 1873. Pp. 149–157. *In* TEICHERT, C. (ed.). *Treatise on Invertebrate Paleontology, Part V, 2nd edition, Graptolithina.* xxxii + 163 pp. Kansas.

JACKSON, D. E. and LENZ, A. C. 1969. Latest Silurian graptolites from Porcupine River, Yukon territory. *Contr. Can. Palaeont.*, **182,** 17–29.

—— —— 1972. Monograptids from the Upper Silurian and Lower Devonian of Yukon territory, Canada. *Palaeontology*, **15**(4), 579–597.

—— —— and PEDDER, A. E. H. 1978. Late Silurian and early Devonian graptolite, brachiopod and coral faunas from northwestern and Arctic Canada. *Spec. Pap. geol. Ass. Can.* **17,** 1–159.

JAEGER, H. 1959. Graptolithen und Stratigraphie des jüngsten Thüringer Silurs. *Abh. dt. Akad. Wiss. Berl.*, Kl. Chem. Geol. Biol. **1959**(2), 1–197.

—— 1967. Preliminary stratigraphical results from graptolite studies in the Upper Silurian and Lower Devonian of southeastern Australia. *J. geol. Soc. Aust.* **14**(2), 281–286.

—— 1975. Die Graptolithenführung im Silur/Devon des Cellon-Profils (Karnishe Alpen). Ein Beitrag zur Gleichsetzung der Conodonten- und Graptolithenzonen des Silurs. *Carinthia II,* **165/85,** 111–126.

KOREN' T. N. 1973. Pozdnesilurijskie-rannedevonskie graptolity Ural'skoj skladchatoj oblasti. *In* SAPELNIKOV, V. P. and CHUVASHOV, B. I. (eds.). Materialȳ po paleontologii srednego paleozoya Uralo-Tyan'shanskoy oblasti. Sbornik po voprosam stratigrafii No. 18. *Trudȳ instituta geologii i geokhimii,* **99,** 132–161.

—— 1978. Early Devonian graptolites of South Fergana, Central Asia. *Čas. Miner. Geol.* **23**(2), 113–127.

—— 1979. Late monograptid faunas and the problem of graptolite extinction. *Acta palaeont. pol.* **24**(1), 79–106.

MIKHAJLOVA, N. F. 1971. Graptolitovye zony silurijskikh otlozhenij Kazakhstana. Strat. Sov. po dopaleozoyu i paleozoyu Kazakhstana (tezisy dokladov), Alma-Ata, 115–117.

—— 1975. Graptolity. *In* MENNER, V. V. (ed.). Kharakteristika fauny pogranichniykh sloev siluria i devona Tsentral'nogo Kazakhstana. *Materialy po geologii Tsentral'nogo Kazakhstana,* **12,** 151–158.

—— 1976. Postludlovskie graptolity Kazakhstana. Pp. 99–104. *In* KALJO, D. L. and KOREN', T. N. (eds.). *Graptolity i stratigrafiya.* Akad. Nauk Estonskoi SSR, Institut Geologii, Tallin, 256 pp.

PAŠKEVIČIUS, J. 1979. *Biostratigrafia i graptolity silura Litvy.* Mosklas, Vilnius, 230 pp.

PŘIBYL, A. 1940. Die Graptolithenfauna des mittlere Ludlows von Böhmen (oberes eβ_2). *Vest. st. geol. Ust. csl. Repub.* **16**(2-3), 63-73.

—— 1941. Über einige neue Graptolithenarten aus dem böhmischen Obersilur. *Bull. int. Acad. tchéque Sci.* **51**(7), 1-9.

Resheniya Mezhvedomstvennogo soveshchaniya po razrabotke unifitsirovannykh stratigraficheskikh skhem dokembria i paleozoya Vostochnogo Kazakhstana. 1976. Leningrad.

TELLER, L. 1964. Graptolite fauna and stratigraphy of the Ludlovian deposits from Chelm borehole, Eastern Poland. *Studia geol. pol.* **13,** 1-84.

—— 1969. The Silurian biostratigraphy of Poland based on graptolites. *Acta geol. pol.* **19**(3), 393-501.

TSEGELNJUK, P. D. 1976. Pozdnesilurijskie i rannedevonskie monograptidy yugo-zapadnoj okrainy Vostochno-Evropejskoj platformy. Pp. 91-132. *In*: *Paleontologiya i stratigrafiya verkhnego kembria i niznego paleozoya yugozapada Vost.-Evrop. platformy.* Naukova Dumka, Kiev.

URBANEK, A. 1958. Monograptidae from erratic boulders of Poland. *Palaeont. pol.* **9,** 1-105.

— 1970. Neocucullograptinae n. subfam. (Graptolithina)—their evolutionary and stratigraphic bearing. *Acta palaeont. pol.* **15**(2-3), 163-388.

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NEW STRATIGRAPHICALLY SIGNIFICANT FORAMINIFERA FROM THE DINANTIAN OF GREAT BRITAIN

by A. R. E. STRANK

ABSTRACT. Four new genera of foraminifera are described. Two of these, *Gigasbia* (Earlandiidae) and *Bibradya* (Endothyridae), are diagnostic guides to the Asbian Stage, and a third, *Melatolla* (Endothyridae), characterizes Brigantian strata. *Biorbis*, the fourth new genus is of uncertain affinities and has been found in strata of Arundian to Brigantian age. *Cribrospira denticulata* sp. nov. is confined to Asbian strata.

THIN-SECTION studies of Lower Carboniferous (Dinantian) limestones in several regions of Great Britain have revealed many undescribed taxa of smaller foraminifera. This paper describes six new species, five belonging to new genera, which have a restricted stratigraphical range within the British Dinantian.

Unless stated otherwise all registration numbers quoted are of thin sections in the collections of the Institute of Geological Sciences at Leeds. Grid references to the localities are in square brackets. Dimensions given in the descriptions represent the range observed in known specimens and may not be the maxima or minima attained by each taxon. This paper is published by permission of the Director, Institute of Geological Sciences (N.E.R.C.).

Family EARLANDIIDAE Brady, 1884
Genus GIGASBIA gen. nov.

Type species. Gigasbia gigas sp. nov.

Derivation of name. From *gigas* = giant (Latin) and Asbian (Dinantian Stage, of which this genus is characteristic).

Diagnosis. A very large, thick differentiated walled earlandiid, with a spherical chamber followed by a long straight cylindrical chamber.

Description. Test free. Wall calcareous, microgranular to granular. Outer layer of wall thin, dark, and finely microgranular, gradually coarsening to produce a thicker, more robust, less dense, granular inner layer. Innermost layer of spherical chamber thin, dark, and microgranular. Calcareous granules in wall of elongate chamber aligned parallel to the peripheral curvature of the spherical chamber. Walls of cylindrical chamber parallel or slightly subparallel. Wall of spherical chamber not in contact with elongate chamber, tends to be uniformly microgranular and less differentiated than the rest of the test. Diameter of spherical chamber: external 420–670 μm, internal 280–500 μm. Maximum width of elongate chamber 580 μm. Maximum width of internal tube 250 μm. Maximum length observed 2000 μm (note that the large, elongate nature of this genus makes it difficult to find complete specimens in random thin sections. Probably none of those figured shows a complete specimen.)

Remarks. This genus is much larger than *Earlandia* Plummer, 1930, and also differs from it by having a more robust and clearly differentiated wall structure, alignment of grains in the wall, and a parallel aspect to both the internal and external portions of the wall.

[Palaeontology, Vol. 26, Part 2, 1983, pp. 435–442, pls. 54–55.]

Gigasbia gigas sp. nov.

Plate 54, figs. 1–5

Holotype. ARE 1194, early Asbian Stage, Potts Beck Limestone, 54 m below sandstone which occurs at the top of this formation, Groups Hollows [NY 6988 0827], near Newbiggin-on-Lune, Cumbria.

Description. As for the genus, only one species recognized.

Occurrence. This species has been found in most regions of the British Lower Carboniferous. It is quite common in Britain, though it has not been recorded elsewhere. To date the species has only been found in Asbian Limestones and tends to be more common in early Asbian strata, equivalent to the Potts Beck Limestone of Cumbria. The distinctive size and shape make it easy to recognize in thin section, and hence it is a useful guide fossil for the Asbian. The species is present in both basin and shelf facies.

Recorded occurrences include the following: Bc 3766s, Asbian, Alport Borehole [SK 1360 9105], Derbyshire, depth 1780–81 ft; Bk 4671, late Asbian, Hotwells Limestone, Ashton Park Borehole [ST 5633 7146], Bristol, depth 1928 ft; ARE 730, Asbian, Urswick Limestone, 12·5 m below top, Stainton Quarry [SD 2490 7280], Dalton-in-Furness, Cumbria; ARE 1102, Asbian, Urswick Limestone, 1 m above base, Old Park Wood Quarry [SD 3381 7750], Holker, Cumbria; ARE 1430, early Asbian, Strandhall shore [SC 2513 6870], Isle of Man; ARE 34, late Asbian, Urswick Limestone, 4 m above base, Trowbarrow Quarry [SD 4800 7575], Silverdale, Cumbria; LL 2157, early Asbian, Potts Beck Limestone, 78·21 m above base, Little Asby Scar [NY 6988 0827], near Newbiggin-on-Lune, Cumbria; KR 9998, late Asbian, Oxwich Head Limestone, 2 m above base, St. Govan's Head [SR 9668 9283] Pembrokeshire; ARE 1000, 1011, 1013, late Asbian, Oxwich Head Limestone, 4·5 m, 15 m and 17 m respectively, above base, Pwlldu Head [SS 570 863], West Glamorgan, South Wales; ARE 426, Asbian, Chee Tor Rock, 21 m above base, Hay Dale/Dam Dale [SK 1127 7781], Derbyshire.

Family ENDOTHYRIDAE Brady, 1884
Genus BIBRADYA gen. nov.

Type species. Bibradya inflata sp. nov.

Derivation of name. Bi refers to the bifurcating septa, *bradya* after H. B. Brady and intended also to emphasize its membership of the Subfamily Bradyininae.

Diagnosis. An endothyrid with bifurcating septa, inflated final chambers and cribrate aperture.

Description. Test free. Wall thin, microgranular or very finely granular, dense and compact, increasing slightly in thickness with growth. Septa thick, blunt, swollen, more robust than surrounding wall and clearly bifurcating close to their origin. Sutures well defined. Chambers rounded and slightly swollen, increasing rapidly in size in the final whorl, rendering the latter the most important part of the test. Coiling irregular. Initial 2½ volutions arranged in a tight, irregular-coiling formation which is totally encompassed by the highly inflated final whorl; 5–6 chambers in final whorl. Aperture cribrate.

EXPLANATION OF PLATE 54

All figures ×75.

Figs. 1–5. *Gigasbia gigas* gen. et sp. nov. 1, holotype, ARE 1194, early Asbian, Potts Beck Limestone, 54 m below sandstone horizon, Groups Hollows, Cumbria. 2, LL 2157, early Asbian, Potts Beck Limestone, 78·21 m above base, Little Asby Scar, Cumbria. 3, ARE 1102, Asbian, Urswick Limestone, 1 m above base, Old Park Wood Quarry, Cumbria. 4, ARE 1000, late Asbian, Oxwich Head Limestone, 45 m above base Pwlldu Head, Gower, South Wales. 5, ARE 730, early Asbian, Urswick Limestone, 12·5 m below Woodbine Shale, Stainton Quarry, Cumbria.

Figs. 6, 7. *Bibradya inflata* gen. et sp. nov. 6, holotype, ARE 335, early Asbian, Tandinas Limestone, level 9, Tandinas Quarry, Anglesey. 7, ARE 403, Asbian, Chee Tor Beds, 2 m above base, Hay Dale/Dam Dale section, Derbyshire.

Fig. 8. *Cribrospira denticulata* sp. nov., holotype, ARE 335, early Asbian, Tandinas Limestone, cycle 9, Tandinas Quarry, Anglesey.

PLATE 54


1

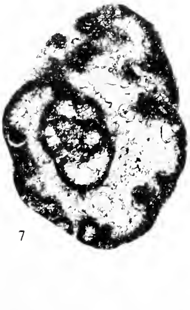

2


3


4


5


6


7


8

STRANK, Dinantian foraminifera

Remarks. The most characteristic feature of this genus is the bifurcating septa. The chamber shape and wall structure are endothyroid. The cribrate aperture and bifurcating septa distinguish it from *Plectogyranopsis*. The overall shape and coiling are very similar to those of *Janischewskina*, which has a thin, delicate wall in the initial whorls and a very inflated final whorl. The septal structures of *Janischewskina* are distinguished by their complex sutural apertures. *Bibradya* is also similar in coiling and shape to *Cribrospira*. Mamet (1973, pl. 7, fig. 27) figured as *Janischewskina* sp. an example with only one truly bifurcating septum, the other septa being normal or showing only initial signs of bifurcation (see Pl. 55, fig. 4), and this form would appear to be an early morphological praecursor of *Bibradya*. The example was found in Mamet's Zone 13 (= Asbian) which is at the same level to which *Bibradya* is confined in Britain. It would appear that *Bibradya* may have evolved from *Cribrospira* (or *Holkeria*) and is possibly a predecessor of *Janischewskina* characteristic of the Brigantian.

Bibradya inflata sp. nov.

Plate 54, figs. 6, 7

Holotype. ARE 335, early Asbian Stage, Tandinas Limestone, Tandinas Quarry, SH 5800 8200, Anglesey.

Derivation of name. Latin *inflata*, referring to the inflated chambers and final whorl.

Description. Wall thin, microgranular. Septa thick, blunt and clearly bifurcating. Sutures well defined. Chambers rounded and swollen, increasing rapidly in size in final whorl. Coiling irregular, initial $2\frac{1}{2}$ whorls totally covered by inflated final whorl. 5–6 chambers in final whorl. Aperture cribrate. Diameter 560–650 μm. Wall thickness 20–30 μm. Height of final chamber 300 μm.

Occurrence. The species has been found in several British localities. It is confined to Asbian strata and is especially characteristic of the early Asbian. Records of the species include, in addition to the holotype, the following: ARE 1244, late Asbian, Oxwich Head Limestone, 15 m above base, Mumbles Head [SS 6318 8725], Gower, South Wales; ARE 1000, late Asbian, Oxwich Head Limestone, 4·5 m above base, Pwlldu Head [SS 570 863] West Glamorgan, South Wales; ARE 403, Asbian, Chee Tor Limestone, 2 m above base, Hay Dale/Dam Dale section [SK 1234 7662], Derbyshire.

Bibradya grandis sp. nov.

Plate 55, figs. 1–3

Holotype. Bk 4213, Asbian Stage, depth 1844 ft 11 in, Hotwells Limestone, Ashton Park Borehole, ST 5633 7146, near Bristol, Avon.

EXPLANATION OF PLATE 55

All figures × 75 unless otherwise stated.

Figs. 1–3. *Bibradya grandis* sp. nov. 1, holotype, Bk 4213, Hotwells Limestone, Ashton Park Borehole, depth 1844 ft 11 in. 2, ARE 335, Tandinas Limestone, cycle 9, Tandinas Quarry, Anglesey. 3, Bk 4229, late Asbian, Hotwells Limestone, Ashton Park Borehole, Avon, depth 1850 ft 9 in.

Fig. 4. *Janischewskina*? Reproduced from Mamet 1973, pl. 7, fig. 27. Mamet Zone 15 (Asbian).

Fig. 5. *Melatolla whitfieldensis* gen. et sp. nov., holotype, ARE 503, early Brigantian, Single Post Limestone, 1 m above base, Whitfield Gill, near Askrigg, Yorkshire.

Fig. 6. *Melatolla* sp. Reproduced from Conil *et al.* 1980, pl. xix, fig. 12. PS 2136 (IGS Edinburgh collection), late Asbian, Archerbeck Beds, Archerbeck Borehole, Canonbie, Dumfriesshire, depth 1860 ft.

Fig. 7. *Melatolla* sp. × 70. Reproduced from Rozovskaia, 1963, pl. v. fig. 6. Venev-Mikhailov, USSR.

Figs. 8–12. *Biorbis duplex* gen. et. sp. nov. 8, LL 2130, early Asbian, Potts Beck Limestone, 12·00 m above base, Little Asby Scar, Cumbria. 9, ARE 46, early Asbian, Urswick Limestone, 8 m below recognized base of section, Trowbarrow Quarry, near Silverdale, Cumbria. 10, LL 2151, early Asbian, Potts Beck Limestone, 45·5 m above base of bed i, Little Asby Scar, Cumbria. 11, holotype, ARE 691, late Asbian, Knipe Scar Limestone, 24 m above base, Little Asby Scar, Cumbria. 12, HR 3440, early Brigantian, Oxford Limestone, Spittal Shore, near Berwick, Northumberland.

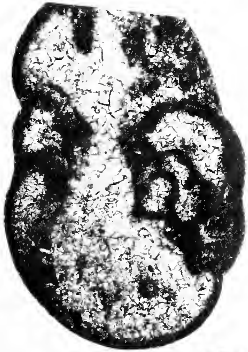
PLATE 55


1


2


4


6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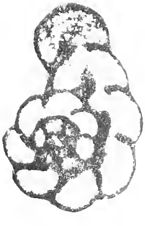
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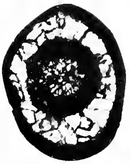
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STRANK, Dinantian foraminifera

Derivation of name. Latin *grandis* referring to the large size of this species.

Description. Wall microgranular or very slightly granular. Septa very thick, robust, blunt, swollen, and bifurcating in most cases. Sutures moderately defined. Chambers mildly rounded, increasing rapidly in size in the final whorl, rendering the latter the most important part of the test compared with inner, irregularly coiled whorls. Coiling irregular. Final whorl covers the whole test. 5–7 chambers in final whorl. Aperture probably cribrate. Diameter 850–1100 μm. Height of final chamber up to 600 μm.

Occurrence. To date this species has only been found in Asbian strata. Records of the species include, in addition to the holotype, the following: Bk 4209, Bk 4213, and Bk 4333, from depths 1844 ft 11 in, 1850 ft 8 in and 1867 ft respectively, late Asbian, Hotwells Limestone, Ashton Park Borehole [ST 5633 7146], near Bristol; ARE 335, early Asbian, Tandinas Limestone cycle 9, Tandinas Quarry [SH 8200 5800], Anglesey.

Remarks. Larger than *B. inflata*, with thicker, more robust septa and higher inflation of final whorl.

Genus CRIBROSPIRA von Möller, 1878

Cribrospira denticulata sp. nov.

Plate 54, fig. 8

Holotype. ARE 335, early Asbian Stage, Tandinas Limestone, cycle 9, Tandinas Quarry, SH 5800 8200, Anglesey.

Derivation of name. Latin *denticulata*, meaning set with small teeth (referring to regular tooth-like septa).

Description. Test free. Wall granular, calcareous. Septa short, relatively thick, usually pointed, slightly irregular in shape but often at right angles to the chamber wall. Sutures become better defined with growth. Chambers not very swollen, slightly rounded, increasing rapidly in size in the final half-whorl, giving the aperture a raised appearance. Coiling initially irregular, with final whorl totally encompassing the inner coiled portion. 7–8 chambers in final whorl. Aperture cribrate. Diameter 450–650 μm. Thickness of wall up to 20 μm. Height of final chamber up to 250 μm.

Remarks. A closely related form belonging to the genus *Cribrospira* is found occurring in the same horizon as *Bibradya*. Since it is very similar to *Bibradya* in some sections, this new species is described here in order to avoid confusion. This species differs from *B. inflata* in not having bifurcating septa, and from *C. pansa* in having differently shaped septa, and being larger in size.

Occurrence. ARE 335, early Asbian, Tandinas Limestone cycle 9, Tandinas Quarry [SH 8200 5800], Anglesey; ARE 984, late Asbian, Danny Bridge Limestone, 117 m below top of section, River Clough [SD 7000 9119], near Sedbergh.

Genus MELATOLLA gen. nov.

Type species. Melatolla whitfieldensis sp. nov.

Derivation of name. Greek *melas*, meaning black, dark; and Latin *tollere* to lift or raise.

Diagnosis. A partially uncoiled endothyrid with extremely heavy supplementary deposits in the form of floor coverings and spines in the final whorl. Final aperture cribrate.

Description. Test free. Wall calcareous, dark, micrograngular. Septa rounded *in continuum* with chamber shape with slightly inflated ends. Sutures deep and well defined. Chambers inflated and well rounded. Coiling regular, planispiral in final whorls—may be initial oscillations. Terminal raising of whorl height into an incoiled portion of varying development. Supplementary deposits very well developed in final whorl. Floor coverings rapidly increasing in thickness and density to form massive, robust, blunt spines in the final chambers. Aperture cribrate in uncoiled portion. Maximum observed diameter of coiled portion 715 μm. Nine chambers in final whorl.

Remarks. This genus differs from *Endothyra* in that it is partially uncoiled and cribrate, from *Rectoparaendothyra* in being more robust and having a larger coiled section, and from *Mikhailovella* in being much larger, and in having very well-developed supplementary deposits. It also differs from *Corrigotubella* in not having a thick, granular, agglutinated wall, and from *Endothyranella* in having prominent basal deposits, and being more massive. One form in the literature which appears to belong to this genus is that figured by Rozovskaia (1963, pl. v, fig. 6) as *Mikhailovella gracilis* (Rauser-Chernoussova, 1948): the well-developed supplementary deposits (see Pl. 55, fig. 7) distinguish this specimen from true *M. gracilis* (Rauser-Chernoussova, 1948). The only other example figured is that in Conil *et al.* (1980) (see Pl. 55, fig. 6) described as gen. nov. In USSR the genus occurs in the Mikhailov/Venev horizon, correlated with the Brigantian Stage of Britain.

Melatolla whitfieldensis sp. nov.

Plate 55, fig. 5.

1980 gen. nov. Conil and Longerstaey *in* Conil, Longerstaey and Ramsbottom, pl. xix, fig. 12.

Holotype. ARE 503, early Brigantian, Single Post Limestone, 95 cm above base, Whitfield Gill, SD 9350 9204, Askrigg, North Yorkshire.

Diagnosis. *Melatolla* with well-developed supplementary deposits, more robust than *M. sp.* of Rozovskaia, the only other known form.

Occurrence. This species has been recorded so far only in Britain, where it is rare. Recorded occurrences, in addition to the holotype, include: PS 2136 (IGS Edinburgh collection), late Asbian, Archerbeck Beds, depth 1260 ft, Archerbeck Borehole [NY 416 782], near Canonbie, Dumfriesshire; KR 6744, late Asbian, Danny Bridge Limestone, 160 m below top of section, River Clough [SD 7000 9119], near Sedbergh. HR 3077, Brigantian, Smiddy Limestone, River Eden, Janny Wood [NY 7830 0370], near Kirkby Stephen, Cumbria.

Family uncertain

Genus BIORBIS gen. nov.

Type species. *Biorbis duplex* sp. nov.

Derivation of name. From *bi*, meaning double, and *orbis*, meaning ring or circle.

Diagnosis. A double concentric sphere with an outer wall of large diameter enclosing an inner wall of smaller dimensions.

Description. Test free. Wall calcareous, granular to microgranular, consisting of two annuli of different diameters, one enclosing the other. The outer ring has a dark microgranular external layer which decreases in density to a granular appearance towards another dark, dense, microgranular layer on the internal margin of this wall. The nature of the internal ring is identical although the microgranular layers are often not quite so well developed. Cross sections through the test are often circular or ellipsoidal. Diameter of circular sections 250–350 μm. Thickness of outer wall 40–50 μm. External diameter of inner ring 120–180 μm. Thickness of inner wall 20–40 μm.

Remarks. There are several possibilities for the overall shape of this test. It could be a spherical object, in which case it should be classed with the calcispheres. The ellipsoidal sections could then be explained as being squashed specimens. Alternatively, the rings could be cross sections through an elongate, cylindrical '*Earlandia*'-type form, in which case they would be classed as Earlandiidae. However, none of the corresponding elongate sections of this has ever been found, although examples similar to these figured are quite common. In addition, the wall structure is differentiated into layers, whereas the small earlandiids described originally by Plummer (1930) have a uniform wall structure and texture. The external dark layer is similar to that found in *Gigasbia* gen. nov., but the internal microgranular layer is missing in the cylindrical portion, and the dimensions of *Gigasbia* are much larger. Vachard (1980, p. 14, fig. 10) figured a form with three rings inside one another which he stated was formed of three specimens of *Earlandia* wedged inside each other. His figure is not good enough to see the wall structure but it looks uniformly microgranular, unlike these samples. It seems unlikely, therefore, that these are cross sections through tubes of *Earlandia*, and they can be described as a new genus. Differs from *Eovolutina* Antropov 1950 in that the latter has a less differentiated and complex wall structure.

Biorbis duplex sp. nov.

Plate 55, figs. 8–12

Holotype. ARE 691, late Asbian, Knipe Scar Limestone 24 m above base [NY 6988 0827], Little Asby Scar, near Newbiggin-on-Lune, Cumbria.

Derivation of name. *duplex*, referring to the double wall of the shell.

Description. As for the genus, only one species being known.

Occurrence. This species occurs commonly in strata ranging from Arundian to Brigantian in age. Occurrences include: Arundian—KR 3330, Embsay Limestone, Embsay Beck SE 006 537, Yorkshire. Asbian—LL 2139 and LL 2151, from 5·89 and 45·5 m above the base of the Potts Beck Limestone at Little Asby Scar; ARE 36 and ARE 23, 2 m and 15 m respectively above base of section (below Woodbine Shale), Trowbarrow Quarry [SD 4800 7575], Silverdale, Cumbria. Brigantian—HR 3440, Oxford Limestone, Spittal Shore [NU 0120 5090], near Berwick, Northumberland.

Acknowledgements. I acknowledge the help given by both Dr. W. H. C. Ramsbottom and Dr. F. M. Broadhurst, who kindly read and commented on the manuscript. Much appreciation also goes to Professor R. Conil who verified the proposed new genera and species.

REFERENCES

ANTROPOV, I. A. 1950. New species of Foraminifera from the Upper Devonian of certain areas of the eastern Russian platform. *Akad. Nauk. Geol. Dist. Kazan, Izvestiya Kazanskoop Filiala*, **1,** 21–33.

CONIL, R., LONGERSTAEY, P. J. and RAMSBOTTOM, W. H. C. 1980. Matériaux pour l'étude micropaléontologique du Dinantien de Grande-Bretagne. *Mém. Inst. géol. Univ. Louvain* **30,** 1–187.

MAMET, B. L. 1973. Microfaciès viséens du Boulonnais (Nord, France). *Revue Micropaléont.* **16,** 101–124.

PLUMMER, H. J. 1930. Calcareous foraminifera in the Brownwood shale near Bridport, Texas. *Bull. Texas Univ.* **3019,** 5–21.

RAUSER-CHERNOUSSOVA, P. M. 1948. The genus *Haplophragmella* and similar forms. *Trudy̆ Inst. Geol. Akad. Nauk. S.S.S.R.* **62,** 159–165. [In Russian.]

ROZOVSKAIA, S. E. 1963. The earliest fusulinids and their ancestors. *Trudy̆ Paleont. Inst.* **97,** 1–127. [In Russian.]

SOMERVILLE, I. D. 1979. Sedimentary cyclicity in early Asbian (Lower D_1) Limestones in the Llangollen district of North Wales. *Proc. Yorks. Geol. Soc.* **42,** 397–404.

VACHARD, D. 1980. Tethys et Gondwana au paléozoique supérieur les donnés afghanes. *Docum. et Trav. IGAL.* Paris No. 2. 463 pp.

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PATHOLOGICALLY DEFORMED *GRAPHOCERAS* (AMMONITINA) FROM THE JURASSIC OF SKYE, SCOTLAND

by NICOL MORTON

ABSTRACT. Successive populations of *Graphoceras* from the *concavum* Zone (Aalenian, Middle Jurassic) at Bearreraig (Isle of Skye, N.W. Scotland) contain an unusually high proportion (8·1 %) of pathologically deformed specimens, in which the whorls grew over to one side after initial normal growth. Size-frequency distributions and proportions of dimorphs are similar among deformed and normal ammonites, and are consistent with random affliction of members of the populations. The most likely cause of the deformity is disease or parasitic infestation.

IN THE course of systematic and biostratigraphical work on the Aalenian and Bajocian ammonite faunas of the Bearreraig Sandstone in Skye and Raasay, western Scotland, successive populations of *Graphoceras* were collected from nodules in the *concavum* Zone (topmost Aalenian) in the lowest 9 m of the Udairn Shale Member (Morton 1965, 1976). The nodules formed at a very early stage of diagenesis, so that there is minimal post-burial crushing of fossils, and realization that the asymmetrical specimens described below were biologically deformed prompted careful examination to determine the frequency and types of deformity present.

PREVIOUS WORK

There is in the literature on Mesozoic ammonites a long history of observation, description and illustration of various types of deformity, reviewed and summarized by Spath (1945), Hölder (1956, 1970), Theobald (1958), Guex (1967), Bayer (1970), and Kennedy and Cobban (1976). Of relevance here, Buckman (1887–1907) discussed (Supplement p. 97) and figured (pl. 9, figs. 8–10) a specimen of *Graphoceras* from the Inferior Oolite of Bradford Abbas, Dorset, which shows irregular ribbing and umbilicus wider on one side but is otherwise symmetrical; also a *Fontannesia* from the same locality which shows deformity similar to that described below (pl. 47, figs. 8, 9). The only comprehensive studies of deformity in large samples of ammonites that I know of are by Guex (1967) and Bayer (1970).

Guex (1967) found 160 deformed specimens (2 %) among some 8000 ammonites from the Toarcian of Aveyron, France, including 20 (2·5 %) of 800 from the *bifrons* Zone. He found a wide variety of types of deformity all interpreted as resulting from injuries, and classified them according to the type of injury and the response of the animal into four groups: temporary (Group 1) or permanent (Group 2) disfigurement especially of ornament as a result of injury to the mantle only; imperfect replacement of a broken part of the shell (Group 3); and disruption of symmetry as a result of damage also to the 'centres of equilibrium' (Group 4). In the *Graphoceras* samples from Bearreraig the range of deformities is very much more limited, being confined to only Group 4 of Guex's study, in which the plane of symmetry of growth is affected. Incidentally, it can now be stated (cf. Guex 1967, p. 4) that this type of deformity can also occur in moderately involute as well as in evolute ammonites.

Bayer (1970) studied Aalenian and Bajocian ammonites from Swabia, southern Germany. Deformities related mainly to injuries were found to be most common (9·7 %) in Stephanocerataceae (excluding Sphaeroceratidae), much less frequent in Sphaeroceratidae (1·4 %) and Sonniniidae

[Palaeontology, Vol. 26, Part 2, pp. 443–453, pl. 56.]

TABLE 1. Stratigraphical position and abundance of pathological ammonites, *concavum* Zone, Bearreraig, Isle of Skye.

Sample no.	Height above base of Udairn Shale Member	Total no. of ammonites recovered	Frequency of pathological ammonites	
			Number	Percentage
75/8	8·8 m	151	9	6·0
75/5	8·0 m	80	11	13·8
NES-B8	*c.* 6·0 m	5	1	(20·0)
75/4	5·4 m	69	4	5·8
75/3	5·0 m	68	5	7·4
NES-B5	3·0–4·5 m	24	2	8·3
Total	—	397	32	8·1

TABLE 2. Summary of details of deformed *Graphoceras* from the *concavum* Zone, Bearreraig, Isle of Skye.

Explanation of column heading abbreviations:

S. No.—Sample number (see Table 1 for stratigraphical details). M. No.—Allocated museum number, Hunterian Museum, University of Glasgow. Dim.—Dimorphic status (see Table 3): m—microconch with lappets; m?—probably microconch because of morphological similarity and closer final sutures; M or M?—probably juvenile macroconch because of morphological differences from microconchs of same size (see p. 3); ?—juveniles of uncertain dimorphic status [(m) more similar to microconch, (M) more similar to macroconch, but cannot be reliably assigned]. Max. D.—Maximum preserved diameter of specimen (A indicates aperture preserved). D. phr.—Diameter at end of phragmocone, beginning of body chamber. D. def.—Diameter at beginning of deformity. Wh. def.—whorl height at beginning of deformity. A. def.—Angular length (about axis of coiling) of deformed part, in brackets if incompletely preserved; T indicates deformity temporary. Dirn. def.—Direction of deformity, described as direction of displacement of keel from plane of symmetry, looking along venter towards aperture: R—displaced to right; L—displaced to left. Max. K-S.—Maximum distance of keel from projected plane of bilateral symmetry (defined from unaffected inner whorls). Beg. def.—Beginning of deformity: A—abrupt; G—gradual.

S. No.	M. No.	Dim.	Max. D.	D. phr.	D. def.	Wh. def.	A. def.	Dirn. def.	Max. K-S.	Beg. def.
NES-B8-4	S15319/2	?(m)	20·2	17·3	*c.* 10·5	4·2	(360)	L	1·5	A
NES-B5-6	S15322	m?	15·4	12·7	10·6	4·3	(190)	R	*c.* 2·1	A
NES-B5-7	S15325/1	m?	22·7	—	*c.* 11·7	*c.* 5·1	*c.* 390	R	2·8	?G
75/3-9	S26431/1	?	A20·8	15·6	*c.* 13·4	5·9	190	R	0·7	A
75/3-11	S26431/2	?(M)	16·0	15·1	12·4	5·5	34T	L	0·2	A
75/3-31	S26432	?	frag. of body chamber			15·5	?	R	?	G
75/3-54	S26433/1	?(m)	13·2	10·0	*c.* 8·5	?	*c.* 240	R	1·6	?
75/3-68	S26433/2	?	13·6	12·3	12·3	5·4	(60)	R	?	A
75/4-24	S26434/1	?(m)	15·3	12·2	*c.* 7·8	3·4	317	R–?L	1·0	G
75/4-44	S26434/2	m?	13·2	11·3	*c.* 5·9	*c.* 2·5	(410)	R–L–R–L	1·6	?G
75/4-55	S26434/3	?	11·0	8·4	9·9	4·3	(67)	R	1·2	A
75/4-57	S26434/4	?	21·8	?	< 14·8	?	(180)	L	0·6	?G
75/5-3	S26435/1	m	A25·0	*c.* 18·6	19·7	7·4	152	R	1·4	A
75/5-5	S26435/2	?(m)	21·7	15·2	?	?	(180)	R	2·1	?
75/5-17	S26436	M?	A34·4	*c.* 24·2	*c.* 14·0	?	*c.* 520	R	7·2	?G
75/5-20	S26437/1	M?	23·8	> 23·8	18·1	8·2	(165)	R	0·8	G
75/5-31	S26437/2	?	16·2	15·0	*c.* 10·7	4·4	60T	L	0·3	A
75/5-38	S26438	m	A34·2	24·0	*c.* 23·4	9·3	175	R–L	1·0	A
75/5-41	S26439/1	M?	30·2	*c.* 19·9	20·3	8·9	(193)	R	2·5	A
75/5-46	S26439/2	M?	25·2	*c.* 25·0	*c.* 8·7	*c.* 3·6	(526)	L–R	3·1	?
75/5-50	S26439/3	?	*c.* 22·4	17·2	*c.* 18·6	*c.* 8·7	(94)	R	1·1	G
75/5-56	S26440/1	m?	*c.* 21·6	19·7	*c.* 17·8	*c.* 7·8	(147)	L	1·4	G
75/5-64	S26440/2	?	12·9	11·3	10·4	4·6	(119)	R	0·5	A
75/8-22	S26441	M?	A *c.* 19·5	?	?	?	?	R	2·4	?
75/8-50	S26442/1	m?	15·9	*c.* 11·4	*c.* 11·4	?	(123)	R	0·9	A
75/8-57	S26442/2	m	A20·5	14·7	?	?	> 540	R	?	?
75/8-58	S26442/3	m?	16·0	15·3	*c.* 14·4	*c.* 5·4	(110)	R	1·3	?A
75/8-63	S26443	M?	27·1	*c.* 23·0	20·0	9·0	(166)	R	2·6	G
75/8-76	S26444	?(m)	23·1	?	21·1	8·9	(65)	L	1·0	G
75/8-81	S26445	M?	A *c.* 13·7	?	10·9	5·3	124	L	1·0	G
75/8-119	S26446/1	M?	*c.* 22·0	?	*c.* 15·0	7·4	(180)	L	0·7	?
75/8-124	S26446/2	?(m)	13·5	?	*c.* 9·2	3·8	(254)	L	0·7	A

(1·0%), and most rare in Graphoceratidae (0·3%). Variation in frequency of deformities was thought to be related to different modes of life.

OCCURRENCE

The stratigraphical levels of the *Graphoceras* samples (mainly from a shallow gully 300 m south of Bearreraig Point at grid reference NG 5186 5245) with total numbers of ammonites obtained and deformed specimens are given in Table 1. Details of the deformed ammonites are summarized in Table 2, including the Hunterian Museum (University of Glasgow) reference numbers. Measurements and other data on which Tables 2–4 and text-figs. 1–4 are based are deposited with the British Library, Boston Spa, Yorkshire LS23 7BQ as Supplementary Publication No. SUP 14019 (5 pages). These data may be purchased from the British Library; prepaid coupons for such purposes are held by many libraries throughout the world.

The frequency of occurrence of deformed ammonites in the samples from Skye is much higher than that found by Guex (1967) in the Toarcian of Aveyron, but is of the same order (9·7%) as that found by Bayer (1970) for Bajocian stephanoceratids in Swabia. The contrast between frequency of deformity in Swabian graphoceratids (0·3%) reported by Bayer compared with that for Skye *Graphoceras* is most striking. So also in comparison is the rarity of deformity in other Aalenian–Bajocian ammonite faunas from Skye. I know of no other published data with which to compare.

Detailed description and discussion of the fauna will be given elsewhere. There is a great range

TABLE 3. Dimorphic status (see text and Table 2 for explanation of categories) of deformed ammonites in each sample, with totals (and percentages) for each dimorphic category for deformed and normal ammonites; *concavum* Zone, Bearreraig, Isle of Skye.

Sample no.	m	m?	M?	?(m)	?(M)	?
75/8	1	2	4	2	—	—
75/5	2	1	4	1	—	3
75/4	—	1	—	1	—	2
75/3	—	—	—	1	1	3
NES-B8	—	—	—	1	—	—
NES-B5	—	2	—	—	—	—
deformed	3 (9·4%)	6(18·8%)	8(25·8%)	6(18·8%)	1 (3·1%)	8(25·0%)
Totals						
normal	59(16·2%)	28(7·7%)	82(22·5%)	18(4·9%)	14(3·8%)	163(44·8%)

TABLE 4. Direction of deformity of pathological ammonites; *concavum* Zone, Bearreraig, Isle of Skye (right–left convention used as looking along venter towards aperture).

Sample no.	Deformed to left	Deformed to right	Deformity direction varies
75/8	4	5	0
75/5	2	7	2
75/4	1	1	2
75/3	1	4	0
NES-B8	1	0	0
NES-B5	0	2	0
Totals	9	19	4

of variation within each population, but relatively little change between successive populations, so that for the present all are classified as variants of *Graphoceras* aff. *concavum* (Buckman). There is very marked dimorphism in the populations—microconchs with lappets (cf. *Graphoceras* (*Ludwigella*) *rudis* (Buckman)) are common, also apparently juvenile macroconchs of small to medium size, but large mature macroconchs (cf. *Graphoceras* (*Graphoceras*) *concavum* (Buckman) *sensu stricto*) are relatively rare. In general, microconchs tend to be more evolute and to have fewer ribs per whorl than macroconchs of comparable size, but there is much overlap in the ranges of variation so that many specimens cannot be identified with certainty as either dimorph. Of the 32 deformed specimens: 3 can be identified with certainty as microconchs because they show lappets (e.g. Pl. 56, figs. 5, 6); 6 are probably microconchs because of morphological similarity and supporting evidence of closer last two or three sutures (and in one specimen a constriction just behind the broken aperture; Pl. 56, figs. 17, 18); 8 are probably juvenile macroconchs because they are more involute and have closer ribbing and other morphological similarities (e.g. Pl. 56, figs. 1–4, 7, 8, etc.). The remaining 15 are dimorphically indeterminate juveniles, although 7 of these are more similar to one or other dimorph but without indicative morphological features. The numbers of specimens of each dimorphic category per sample are given in Table 3, with totals for each of deformed and normal specimens. The relative proportions of microconchs (m + m?) among deformed specimens is slightly higher than for the rest of the fauna (28·2% cf. 23·9%), but of macroconchs is of the same order (25·0% cf. 22·5%). It would appear, therefore, that the deformity has not been selective in which part of the populations was affected. Microconchs and macroconchs are deformed in almost equal proportions (9·4% and 8·9% respectively of each recognizable dimorph).

Comparison of the size-frequency distributions of deformed and normal ammonites (text-fig. 1), using diameter at the end of the phragmocone as the standard for comparison, shows no significant differences in range (except for the smaller and larger ends of the distribution) or mean diameter, though the latter is a statistic of doubtful significance in such a dimorphic set of populations. The modal classes are very nearly identical. Again it is evident that deformity does not selectively

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EXPLANATION OF PLATE 56

Pathologically deformed specimens of *Graphoceras* aff. *concavum* (Buckman), *concavum* Zone, Aalenian, Middle Jurassic, Bearreraig Sandstone Formation, Udairn Shale Member, 8·0 m above base (except fig. 9 from 5·0 m above base, and figs. 10, 11 from *c.* 6·0 m above base), south of Bearreraig Point, Trotternish, Isle of Skye.

Figs. 1–4. Juvenile macroconch, deformed to right so that umbilical diameter differs on opposite sides and with asymmetrical whorl cross-section; length of deformed part *c.* 520°; sample no. 75/5-17 (HMS 26436).

Figs. 5, 6. Microconch with lappets, deformed to right on last part of phragmocone and body chamber; sample no. 75/5-38 (HMS 26548).

Figs. 7, 8. Juvenile macroconch(?), deformed to right with gradual displacement of keel and venter; sample no. 75/5-20 (HMS 26437/1).

Fig. 9. Dimorph uncertain, temporarily deformed to left; sample no. 75/3-11 (HMS 26431/2) × 2·9.

Figs. 10, 11. Dimorph uncertain, deformed to left, whorl cross-section remaining approx. symmetrical; sample no. NES-B8-4 (HMS 15319/2).

Figs. 12–13, 15. Juvenile macroconch(?), deformed to left on inner whorls (fig. 13) then to right on outer whorl with abrupt change in direction of keel and ventral lobe of suture ‘anticipating’ deformity; angular length of deformed part 526° of phragmocone plus body chamber; sample no. 75/5-46 (HMS 26439/2); fig. 15 only × 2·3.

Fig. 14, 19. Juvenile macroconch(?), deformed to right with abrupt change in direction of keel; sample no. 75/5-41 (HMS 26439/1).

Fig. 16. Dimorph uncertain, deformed to right, but with gradual and abrupt slight changes in direction of keel; sample no. 75/5-64 (HMS 26440/2), × 3·8.

Figs. 17–18. Microconch with constriction behind aperture, deformed to right on body chamber with slight irregularity of coiling geometry of venter; sample no. 75/5-3 (HMS 26435/1).

All figs × 1·5 unless otherwise stated; specimens coated with ammonium chloride except figs. 2 and 15; + marks beginning of body chamber, and arrow indicates beginning of deformity.


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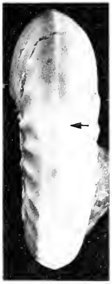
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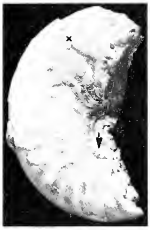
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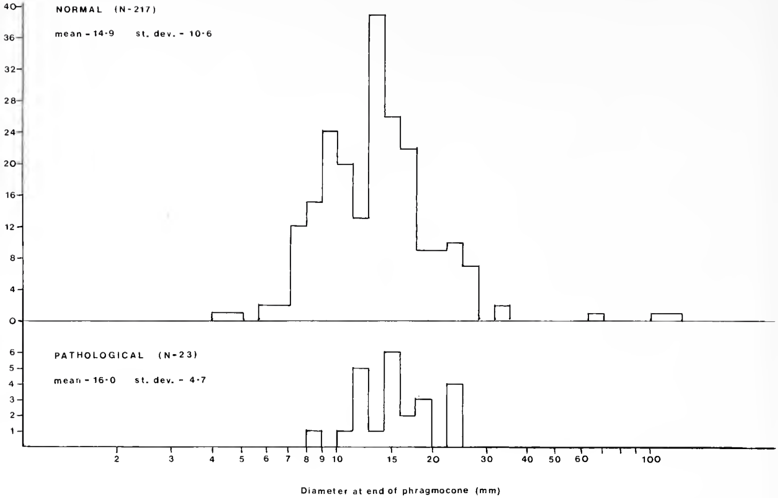
MORTON, deformed *Graphoceras*



TEXT-FIG. 1. Size-frequency distribution of normal and pathological ammonites, *Graphoceras* aff. *concavum* (Buckman), *concavum* Zone, Bearreraig, Skye.

affect particular sizes within the populations. Nor, as is shown later, does it appear that the onset of deformity affected growth.

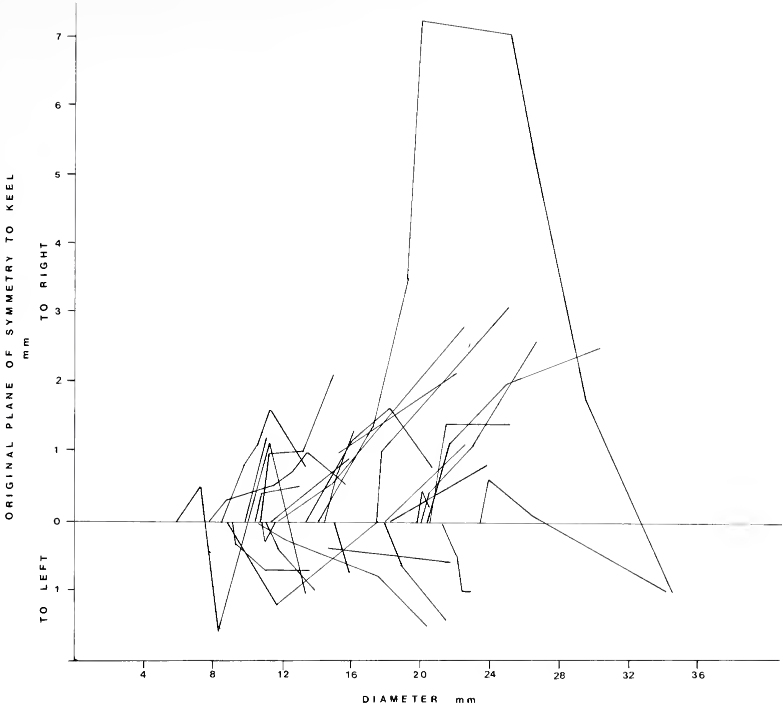
It has to be concluded from the above discussion that the deformity which affected the *Graphoceras* populations in Skye was non-selective in terms of dimorphism or size, and presumably also in age of individual. The distributions are consistent with random affliction.

DESCRIPTION OF DEFORMITY

The deformity found in the Skye *Graphoceras* populations is of only one type, affecting the bilateral symmetry of coiling of the specimens. Other types of deformity are extremely rare (one specimen shows evidence of slight injury affecting the ribbing temporarily) and are not discussed further.

Keel and Venter. Onset of deformity is particularly evident in departure of the keel (marking the mid-venter position) from the plane of bilateral symmetry as determined from the unaffected inner whorls. In most specimens where it can be estimated the maximum distance from the projected plane of symmetry to the position of the keel is less than 3 mm (see text-fig. 2), but in one (Pl. 56, figs. 1–4) it reaches a maximum of 7·2 mm at diameter 20·0 mm before decreasing.

The direction of displacement of the keel (looking along the venter towards the aperture) remains constant in most, with 19 displaced to the right (e.g. Pl. 56, figs. 14, 19), and 9 to the left (e.g. Pl. 56, figs. 10, 11) (see Table 4). The significance of this bias, which was found in all but one of the samples, is unknown. There remain 4 specimens in which the displaced keel and venter cross the original plane of symmetry from right to left or vice versa (e.g. Pl. 56, figs. 12, 13, 15). One (75/4–44) has the keel displaced to the right, then left, right and finally (at the last part preserved since the body chamber is incomplete) to the left. The right and left extremes of displacement are

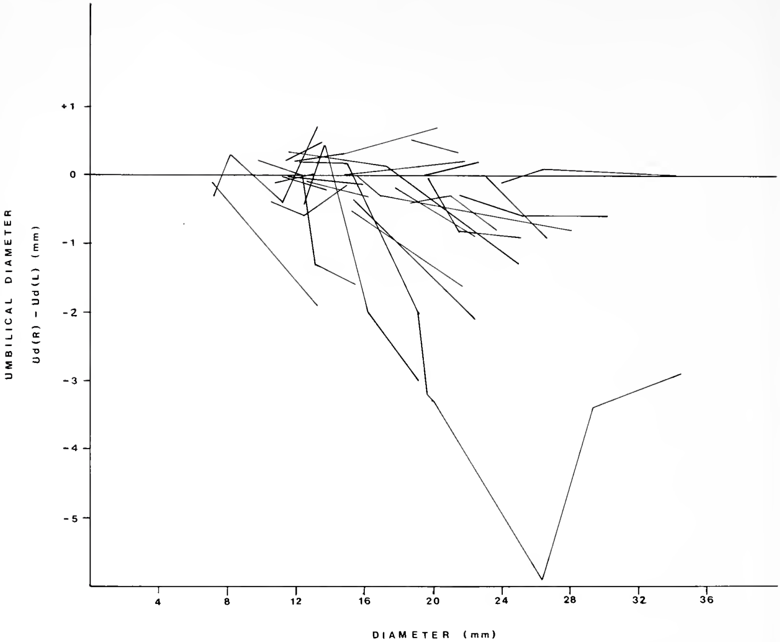


TEXT-FIG. 2. Deformity of *Graphoceras* from the *concavum* Zone, Bearreraig, Skye, measured as the deviation of the keel from the original plane of bilateral symmetry.

each one half whorl apart, but right and left 'axes' are not quite at right angles (70°). In none of the specimens has the deformity resulted in a new axis or plane of coiling being developed. In just over half (17, with 3 unknown) there is more than one change in direction of the keel, either increasing or decreasing the rate of departure from the original plane of bilateral symmetry.

The beginning of the deformity can be either abrupt, in the sense that there is an obvious change in the direction of the keel (e.g. Pl. 56, figs. 14, 19), or it can be so gradual that it can be difficult to see exactly where the keel first diverged from the original plane of symmetry (e.g. Pl. 56, figs. 7, 8). There are approximately equal numbers of the two categories (14 abrupt change, 12 gradual, and 6 indeterminate because of breakage, see Table 2). In some specimens both gradual and abrupt changes in direction of the keel are present (e.g. Pl. 56, fig. 16).

Once affected few recovered, and only two specimens show a return to the normal bilateral symmetry. In both the keel abruptly changes direction (both to left) followed by a more gradual change back to the original line, after angular distances of 34° (75/3-11, Pl. 56, fig. 9) and 60°

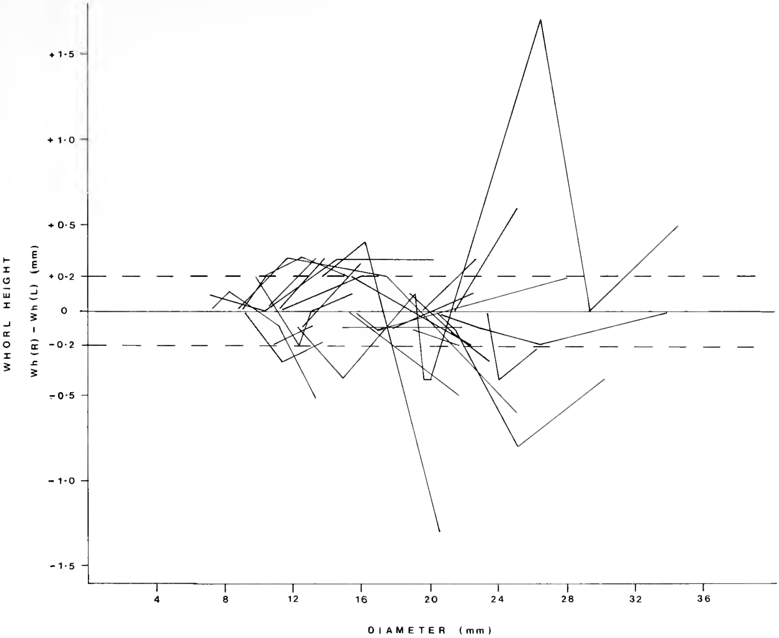


TEXT-FIG. 3. Deformity of *Graphoceras* from the *concavum* Zone, Bearreraig, Skye; loss of bilateral symmetry measured as the effect on umbilical diameter by subtracting Ud. on the left side from Ud. on the right side at the same position (Right/Left convention explained in text).

(75/5-31). Only 8 specimens have the deformed part completely preserved (i.e. including aperture) and in these the angular length of the affected part varies from 124° to about 520° (Pl. 56, figs. 1-4) or more. Another specimen (Pl. 56, figs. 12, 13, 15) shows 526° of phragmocone affected but lacks the body chamber. Clearly deformity did not cause cessation of growth—in the last case for at least a further two whorls. Only the body chamber is affected in 9 specimens (e.g. Pl. 56, figs. 17, 18); the last part of the phragmocone is also affected in 7 (e.g. Pl. 56, figs. 5, 6); but at least a quarter of a whorl of phragmocone is affected in 11 specimens (e.g. Pl. 56, figs. 10, 11).

Whorl shape and Umbilicus. In most specimens displacement of the keel and venter is followed by tilting of the whorl so that the umbilicus becomes narrower on one side than the other (text-fig. 3) (also compare Pl. 56, figs. 1 and 3). In some specimens the whorl shape remains basically symmetrical (e.g. Pl. 56, fig. 11) but with the plane of symmetry tilted to one side. In more extreme cases of deformity the upper part of the whorl is more pushed over, resulting in loss of symmetry with the whorl sides of differing height (text-fig. 4) and convexity (Pl. 56, fig. 2).

Shell geometry. Apart from aspects described above, the coiling geometry of the shell is little affected. Where there is a distinct or abrupt change in the direction of the keel, a notch in the



TEXT-FIG. 4. Deformity of *Graphoceras* from the *concavum* Zone, Bearreraig, Skye; loss of bilateral symmetry of whorl cross-section measured as the difference in whorl height on either side, by subtracting Wh. on the left side from Wh. on the right side at the same position (Right/Left convention explained in text). A difference of more than 0·2 mm results in visible asymmetry of the whorl cross-section.

spiral of the venter is just perceptible in side view (e.g. Pl. 56, fig. 17), sometimes with a very slight indentation. A few specimens also show a slight irregularity in the umbilical edge of the whorl.

Ribbing. Development of ribbing is not affected on deformed specimens more than is necessary to accommodate to varying whorl heights etc. on opposite sides (e.g. compare Pl. 56, figs. 1 and 3).

Sutures and Septa. Sutures and septa formed at the same time as the deformity began (i.e. half to three quarters of a whorl behind) are unaffected until the deformed part of the shell is reached. Then where visible the basic shape remains, even on the most severely deformed phragmocones, with only relative compression of the lobes and saddles on one side to accommodate to varying whorl heights. The centre of the external (ventral) lobe usually follows the divergence of the keel from the plane of symmetry, with a few exceptions. One (NES-B5-6) has the first three sutures after displacement of the keel remaining in the original plane of symmetry so that the keel is off centre of the external lobe, septal asymmetry being delayed. Conversely, another (75/5–46, Pl. 56, fig. 15) has two sutures before the deformity begins 'anticipating' the asymmetry so that the external lobes are further over to one side than the keel.

DISCUSSION

The deformities found in these *Graphoceras* from Skye are sufficiently similar to be interpreted as having the same cause. Occurrence has been shown to be random within the populations. Unexplained is the bias for displacement of keel and venter to the right rather than to the left—the ammonites are not thought to have had any asymmetry of organs which could have been differentially affected, nor is there any explanation in the suggested mode of life such as tendency to lie on one side.

Once affected, recovery was rare, with only two specimens showing a return to bilateral symmetry. However, continued growth was not influenced significantly, and sexual maturity (as microconchs) was attained by nine specimens. Therefore, although the effect on the animal's symmetry was dramatic, vital functions were not impaired.

The beginning of deformity is extremely gradual in some specimens and abrupt in others, but this is thought not to be significant because there are intermediate and varying conditions, and they are otherwise identical. In no case is there evidence of a distinct trauma, even after careful examination, and no evidence of shell repair, for example. Only the direction of shell growth is affected by the deformity, but not other aspects of shell morphology related to the growing edge (such as ribbing) or elsewhere (e.g. septal formation).

INTERPRETATION

Deformities of growth can result from three possible causes—genetic, injury, or infestation. Genetic defects must be regarded as highly unlikely, since all the deformed specimens have inner whorls which are normal, and only became affected by deformity in the outer whorls. I know of no genetic mechanism which will result in such abnormal growth after a relatively long period of normal growth.

Deformity as a result of injury is common among ammonites and well documented, with some groups more liable to be affected than others (Bayer 1970), and with a wide variety of types of deformity (e.g. Guex 1967; Hölder 1970). The effects of injuries on the shell are immediate and traumatic, involving a variety of repair mechanisms. Injury as a cause of the deformity in the Skye *Graphoceras* specimens described here seems unlikely for two main reasons. First, the deformities are all of one type, and it is more likely that injury, by whatever cause, would result in a greater variety of effects. Secondly, the beginning of deformity is as often as not gradual with no evidence of trauma, and this is not what would be expected as a result of an injury.

There remains the possibility that deformity was caused by part of the population being infested by parasites or infected by disease. This seems to me to be the most likely explanation because it would fit in with the random distribution through the population, with restriction of deformity to only one type, and with gradual or more abrupt beginning depending on the speed at which infestation took place. Attack by parasites was suggested by Keupp (1976, 1979) as the explanation for a variety of deformities among Jurassic ammonites from Franconia, southern Germany. None of these is comparable with that described here, either in type or in frequency of occurrence within a population. I know of no criteria to decide between infestation by disease or by parasites, but favour some form of infestation as being the most plausible explanation for the deformed *Graphoceras* in these populations from Skye. There is little evidence of similar deformity in modern *Nautilus* or coleoids, even among those affected by parasites. Living cephalopods offer little guidance to interpretation of the phenomenon described here.

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REFERENCES

BAYER, U. 1970. Anomalien bei Ammoniten des Aaleniums und Bajociums und ihre Beziehung zur Lebensweise. *Neues Jb. Geol. Paläont. Abh.* **135,** 19–41.

BUCKMAN, S. S. 1887–1907. A monograph of the ammonites of the Inferior Oolite Series. *Palaeontogr. Soc.* [*Monogr.*], 1–456, pls. 1–124.

GUEX, J. 1967. Contribution à l'étude des blessures chez les ammonites. *Bull. Labs. Géol. Géogr. phys. Minér. Univ. Lausanne* **165,** 1–16, pls. 1–7.

HÖLDER, H. 1956. Über Anomalien an jurassischen Ammoniten. *Paläont. Z.* **30,** 95–107.

—— 1970. Anomalien an Molluskenschalen, insbesondere Ammoniten, und deren Ursachen. Ibid. **44,** 182–195.

KENNEDY, W. J. and COBBAN, W. A. 1976. Aspects of ammonite biology, biogeography, and biostratigraphy. *Spec. Pap. Palaeont.* **17,** 94 pp., 11 pls.

KEUPP, H. 1976. Neue Beispiele für den Regenerationsmechanismus bei verletzten und kranken Ammoniten. *Paläont. Z.* **50,** 70–77.

—— 1979. Nabelkanten-Präferenz der forma *verticata* Hölder 1956 bei Dactylioceraten (Ammonoidea, Toarcien). Ibid. **53,** 214–219.

MORTON, N. 1965. The Bearreraig Sandstone Series (Middle Jurassic) of Skye and Raasay. *Scott. J. Geol.* **1,** 189–216.

—— 1976. Bajocian (Jurassic) stratigraphy in Skye, Western Scotland. Ibid. **12,** 23–33.

SPATH, L. F. 1945. Problems of ammonite-nomenclature X. The naming of pathological specimens. *Geol. Mag.* **82,** 251–255.

THEOBALD, N. 1958. Quelques malformations chez les ammonites. *Annls scient. Univ. Besançon*, 2^e sér., Géol. **8,** 19–28, pls. 1–2.

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