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Review of the brachiopod superfamily Plectambonitacea

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A new Arenig trilobite fauna from the Bangor area, North Wales

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CONTENTS

SYNOPSIS. A diachronous sandstone unit forms the local base of the Arenig sequence throughout north Wales. Various names have been given to this unit, and the Maes y Geirchen Sandstone Member of the Nant Ffrancon Formation is recommended for the Bangor area. Three exposures of the Maes y Geirchen Member are described and the unit is interpreted as a shallow marine deposit, thickening to the south. A bedded sandstone sequence at the base accounts for most of the thickening and is interpreted as a sand lobe deposited by storm processes in deeper water.

The fauna comprises trilobites, brachiopods and bivalves, and the five trilobite species are described in this paper. The fossils are predominantly from the bedded sandstones and were apparently transported by storm currents, with some winnowed lags developing under waning conditions. Rare specimens from the thinner, more rudaceous deposits to the north are of the same fauna.

All but one of the trilobite species are new and *Asaphellus* cf. *graffi* (Thoral) provides little age control. Three new species are described: *Annamitella sinesulcata, Neseuretus caerhunensis* and *Calymenella preboiselli*. The presence of *Azygograptus eivionicus* Elles in overlying flaggy sandstone is thought to indicate a late Moridunian to early Whitlandian age. The generic composition of the fauna suggests comparison with that from the Carmel Formation of central Anglesey, probably Fennian in age. The *Neseuretus* species of the Bangor and Anglesey faunas also show greater similarity to each other than to other members of the genus. *N. monensis* (Shirley) is redescribed. This may indicate a different lineage peculiar to the exterior margin of the Welsh Basin but Anglesey can no longer be considered as faunally distinct from the mainland.

INTRODUCTION

Throughout north Wales a shallow-water sandstone unit occurs at the base of the Arenig Series. The time of onset of deposition and magnitude of the underlying unconformity vary between areas, and these areas are thought to define separate, fault-bounded, structural blocks, active in the Lower Palaeozoic (Beckly 1987).

The only fossils hitherto described from this sandstone unit are the trilobite and brachiopod fauna of the Carmel Formation in central Anglesey (Bates 1968, Neuman & Bates 1978). The present paper describes a new trilobite fauna recently collected from the sandstone unit at the base of the Arenig sequence in the Bangor area. The *Neseuretus* and *Annamitella*

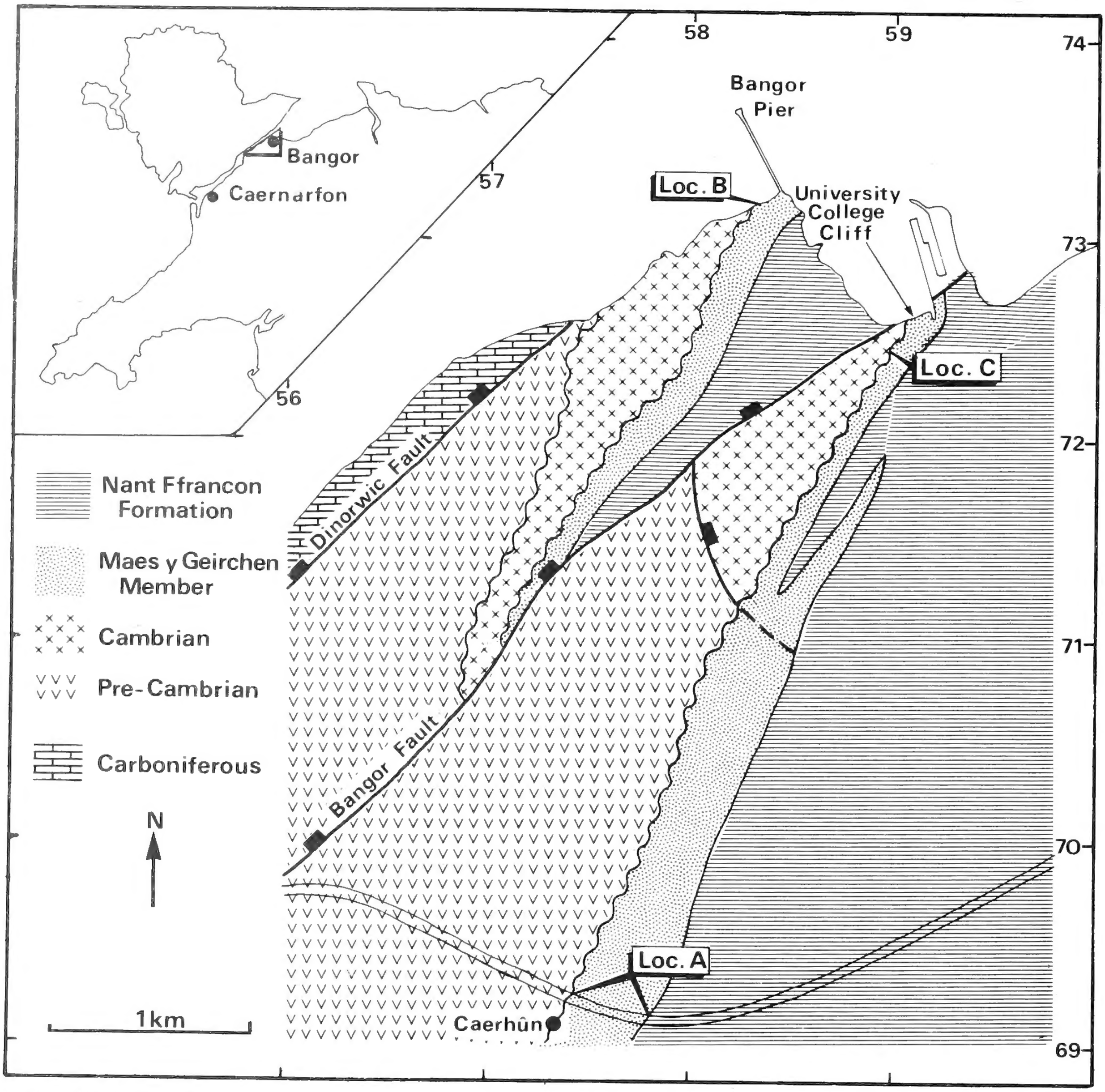

Fig. 1 Simplified geological map of the Bangor area. Loc. A, cutting on A5 near Caerhûn; Loc. B, foreshore section west of Bangor Pier; Loc. C, inland from Penrhyn Dock.

species display features that suggest a comparison with the Anglesey fauna. However, the overall generic composition is typical of later shallow-marine facies around Gondwana, and notably *Calymenella* is recorded for the first time below the Caradoc. *Neseuretus monensis* (Shirley) is also redescribed (p. 13). Specimens are deposited in the Dept of Palaeontology, British Museum (Natural History), apart from the material of *N. monensis* which is held by the British Geological Survey.

Localities

The basal unconformity is exposed in three places near Bangor (see Fig. 1):

(A) the cutting on the A5 just east of the flyover at Caerhûn (NGR SH 576692) (Fig. 2),

(B) the cliff section approx. 100 m west of Bangor Pier (SH 583732) (Figs 3, 4), and

(C) a small exposure at the foot of the wood 150 m inland from the University College Cliff section figured by Greenly (1944: 80; fig. 2) (SH 5901 7247) (Fig. 5).

Apart from a single cranidium of each of *Calymenella preboiselli* sp. nov. and *Nesueretus* indet. from Loc. B, all material came from Loc. A. The majority of material was collected during road construction and much of it came from loose blocks taken from the cutting.

Lithostratigraphy

A single lithostratigraphic terminology has been used for the Arenig Series over the entire Bangor Sheet (Howells *et al.* 1985), though the type localities for these units lie to the east of the Aber-Dinlle fault. Such a uniform view is questionable. There is evidence that the Aber-Dinlle fault was active during the Lower Palaeozoic (Webb 1983), and the basal sandstone in the Bangor area is more similar to the Carmel Formation of central Anglesey than to the type Graianog Sandstone

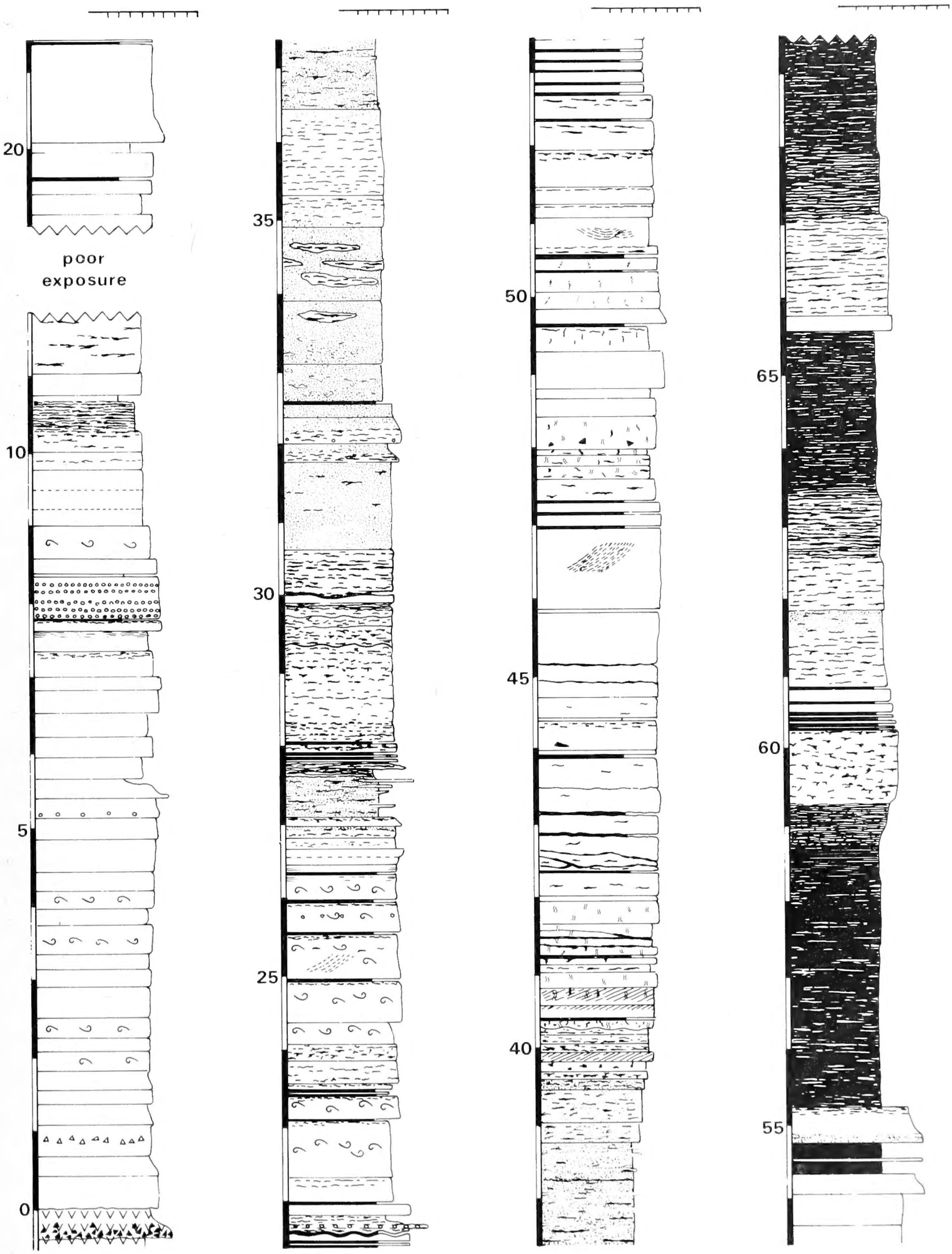

Fig. 2 Sedimentary log of the Maes y Geirchen Sandstone Member in cutting on A5 near Caerhûn. Key given with Fig. 5, p. 7.

Member. However, no fewer than four other names have been used for the intervening exposures of basal Arenig sandstone on Anglesey (Bates 1972) and unless all are placed in a single lithostratigraphic unit there appears no alternative but to have a separate name in the Bangor area. It is therefore recommended that the name Maes y Geirchen Quartzite Member (Reedman *et al.* 1983) be changed to the Maes y Geirchen Sandstone Member and extended to include the entire basal sandstone sequence. The overlying siltstone sequences are more difficult to characterize and have not generally been named. For this reason the use of the name Nant Ffrancon Formation is tentatively retained.

Mapping by the Geological Survey (Howells *et al.* 1985) shows the magnitude of the sub-Arenig unconformity to increase from north to south (see Fig. 1); the sandstone on the Bangor foreshore rests on the Cambrian Llanberis Slate Formation whilst the sequence exposed on the A5 rests on the Arvonian Minffordd Formation.

SEDIMENTOLOGY

Description of sedimentary sequences

Cutting on A5 near Caerhûn. (Loc. A)

A log through the sandstone unit is shown in Fig. 2.

The top of the underlying Minffordd Formation (Reedman *et al.* 1984) is dominated by gravel grade intraformational breccia associated with lithic sandstone, both composed entirely of Arvonian detritus. The base of the Maes y Geirchen Member, and hence of the Arenig, is marked by the first appearance of a medium grade micaceous quartzose sandstone with no evidence of any coarser quartzose material, though some angular fragments of the underlying Arvonian do occur. Coarser, gravel grade, quartz clasts come in about 5 m above the base, and even then are relatively sparse. Pebble grade extraformational clasts are absent from the entire sequence. The Maes y Geirchen Member may here be divided into three (see Fig. 2).

1: Lower Clean Sandstone Unit (Fig. 2, 0–27 m). This is approximately 27 m thick and is dominated by sandstone very similar to that seen at the base, i.e. although quartzose, it contains a very high proportion of mica. This sandstone is well-bedded, but monotonous, showing few sedimentary structures. It is hard and mostly grey in colour, though occasional rusty weathering is present. After the incoming of the first coarser material, about 5 m above the base, the sequence is somewhat more variable, though an area of poor exposure, 12 to 19 m above the base, is dominated by a lithology very similar to that which forms the basal 7 m, possibly with slightly greater rusty colouration. Just above this area are 5 m of slightly more muddy and rusty weathering sandstone, overlying a fairly massive coarse bed, which contain abundant fossil material. Most of the loose blocks from which fossils were collected probably came from this horizon. Scattered fossils do occur below this, as indicated on the section, but they are rare.

2: Muddy Sandstone Unit (Fig. 2, 27–41m). Though sandstone is still dominant, in this part of the sequence there is significantly more silty mudstone present than in the sandstone units above or below. The mud flasers are often very irregular in shape, and this has been increased by bioturbation, which for two reasons is also thought to be responsible for the more homogeneous muddy sandstone. First, occurring in the muddy sandstone are patches of cleaner sandstone within which mud flasers can be recognized, though they are apparently absent from the surrounding lithology. These patches probably represent regions of sediment which have escaped bioturbation. Second, two beds are present which show mud flasers in the cleaner sand of the lower half but are a more homogenous muddy sand in the upper. This would be compatible with biological reworking of the top of a single depositional package.

3: Upper Clean Sandstone Unit (Fig. 2, 41–55m). This differs from the Lower Clean Sandstone Unit in being paler, compositionally closer to quartzite and showing evidence of cross-bedding. The contact with the underlying muddy sandstone unit is somewhat gradational. The clearest examples of cross-bedding are tabular cosets of planar cross-bedding occupying the bed thickness, but trough cross-bedding may also be present. The combination of large scale cross-bedding with more mature sediment composition suggests a higher energy environment than that in which the lower part of the sequence was deposited. Other differences from the Lower Clean Sandstone Unit include a generally greater grain size, and the presence of mud clasts up to 8 cm in length. Some bioturbation is indicated by vertical muddy streaks but many of the beds are massive and featureless.

The transition into the overlying shale-dominated sequence is sharp and a rudaceous bed is associated with the junction. A gravel grade fraction, distinctly coarser than the lithologies below, is dominant, but the matrix is silty mudstone. The concentration of coarser material probably has a genetic association with the change in facies and may represent some form of lag deposit.

Foreshore section west of Bangor pier. (Loc. B)

A continuous section cannot be measured here because of dissection by faults, particularly those parallel to the cliff face (see Fig. 3). The only part of the section that can be accurately placed on the larger scale is that directly overlying the basal unconformity. However, this indicates that as little as 7 m of thick-bedded sandstone is present before argillaceaous, flaggy sandstone becomes prevalent. Thicker sandstone beds are present within this facies but there is no good evidence that they become dominant again.

The sandstone beds directly overlying the unconformity are different from those in the A5 section, with generally coarser lithologies and in having obvious lenticular units. There are two main types of coarse lithology present: fairly well sorted coarse quartzose sandstones occasionally grading towards gravel grade, and poorly sorted paraconglomerates.

It is these conglomerates that have yielded the small number of fossils found in this section. The matrix of these beds is a medium-grained micaceous and quartzose sandstone. The rudaceous component is polymict, angular to subrounded, and ranges up to small pebble grade. The dominant lithologies are quartzite and fragments of the underlying volcanics. The rudaceous component is generally fairly diffusely scattered in the beds, though not infrequently drapes low-angle foresets. Cross bedding is also apparent in the cleaner, well sorted sandstones beds.

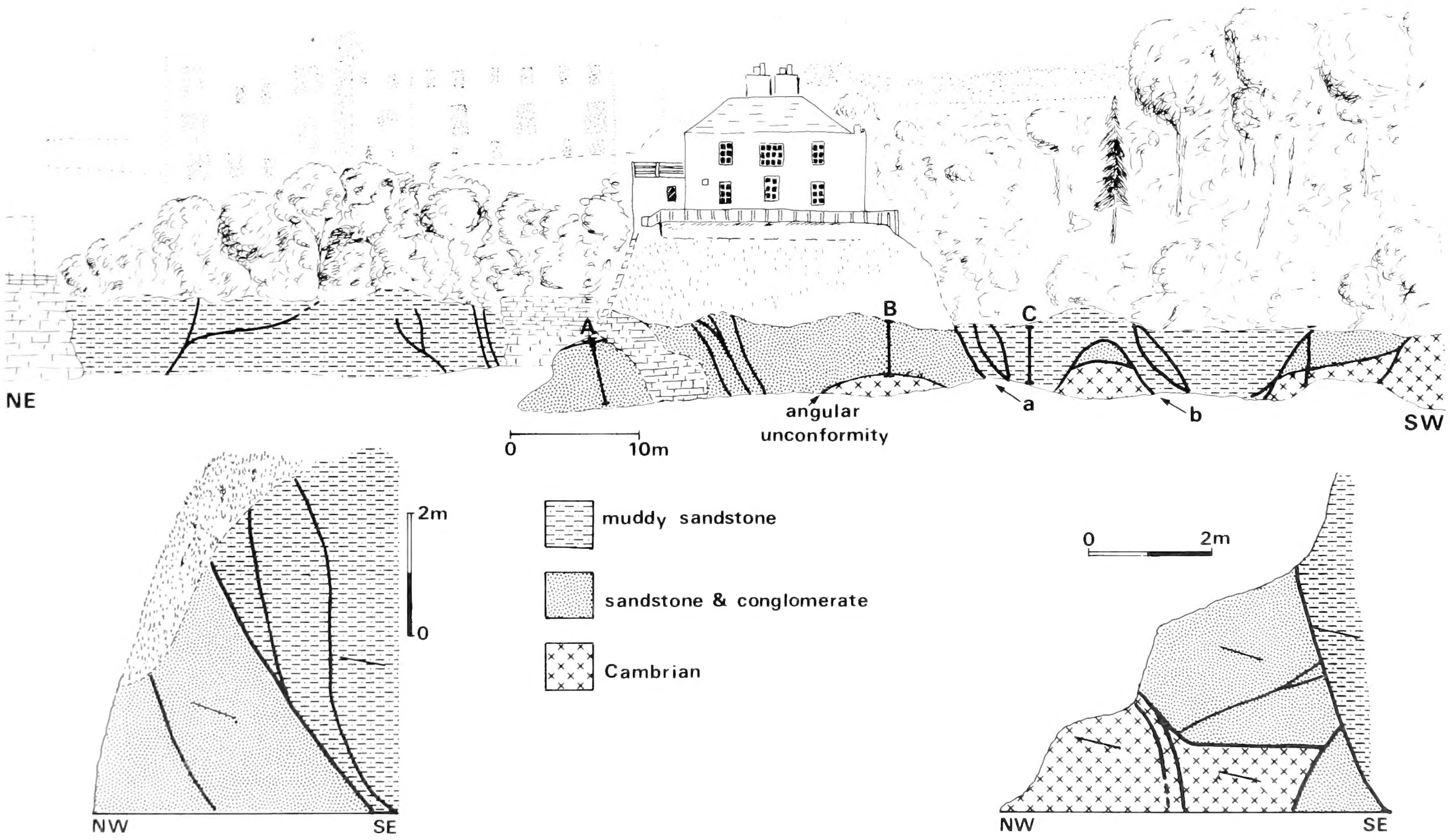

Fig. 3 Sketch of cliff section west of Bangor Pier.

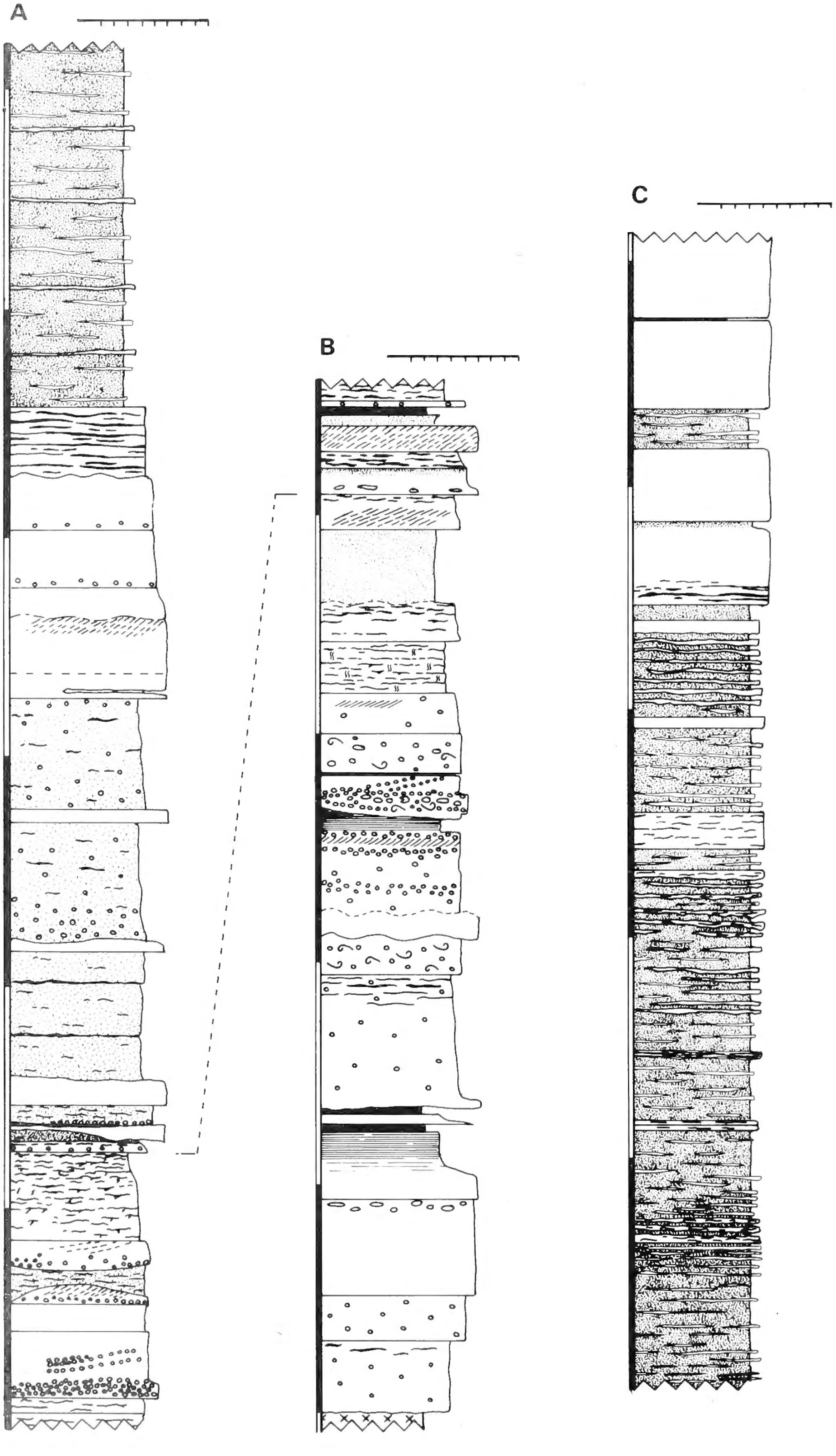

Fig. 4 Sedimentary logs of the Maes y Geirchen Sandstone Member west of Bangor Pier. Positions of sections are shown in Fig. 3. Possible correlation between sections A and B is indicated. Key given with Fig. 5, opposite.

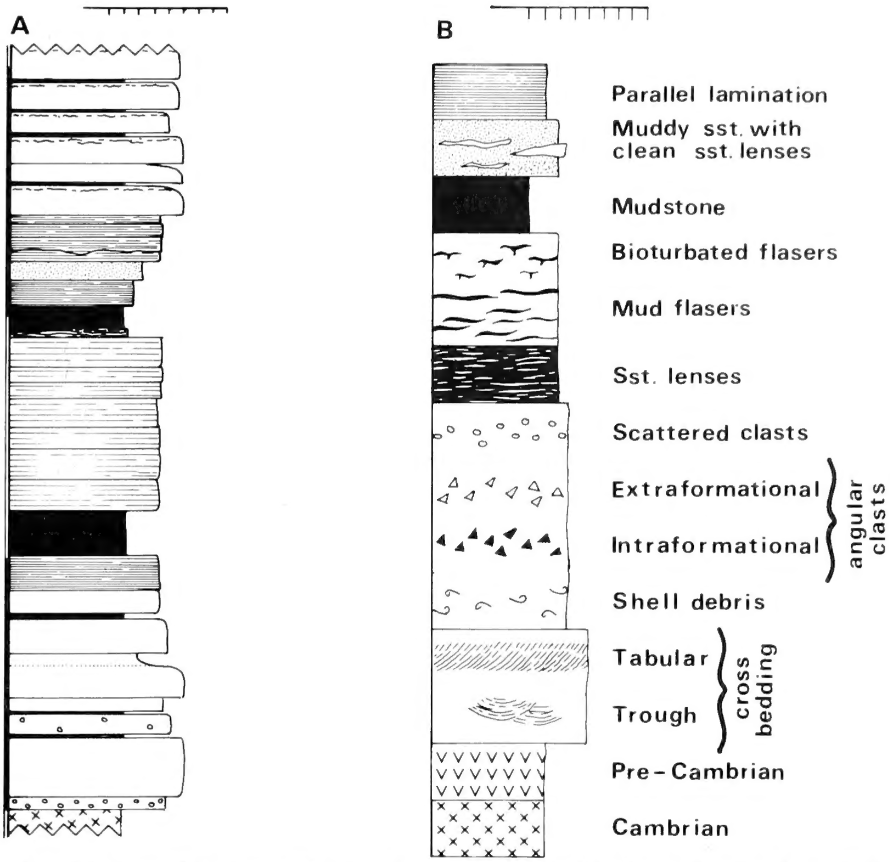

Fig. 5 A: Sedimentary log of the base of the Maes y Geirchen Sandstone Member inland from Penrhyn dock. B: Key to symbols used in sedimentary logs. Clean sandstones unshaded. At top, grain size scale from left to right: clay; silt; fine, medium, coarse sand; gravel; pebble; cobble; boulder. Vertical bars represent 1 m in all sections.

Inland from University College Cliff, Bangor. (Loc. C)

Only a very short section is exposed above the unconformity and this has not yielded any fossils. The coarse nature of the base is comparable to that west of Bangor Pier. This serves to confirm that the variation in the base is primarily north–south rather than influenced by the Bangor Fault.

Taphonomy

On the Bangor foreshore the few fossils that have been found appear to have become entrained with the rest of the coarse clastic fraction, and with it undergone relatively little sorting. This is in marked contrast to the section on the A5, where there is considerable sorting in the absence of any significant coarse clastic material.

Three main faunal elements are present in the A5 cutting: trilobites, brachiopods and bivalves. The first and last appear to be almost mutually exclusive with distinct modes of occurrence, whilst brachiopods occur with both and are occasionally dominant, usually when fossil material is relatively sparsely scattered.

The trilobite material is totally disarticulated. Though some fragments appear broken, there is no evidence of significant abrasion, e.g. genal spines still run to a point. The most common mode of occurrence is in beds that are very slightly graded from medium-coarse to medium sandstone which is of the typical quartz-mica type. Towards the tops of the beds there is some evidence of mud flasers. The trilobite material occurs in the top half of the beds predominantly parallel to bedding, its first appearance often marked by a concentrated band. Above this the fragments are generally more scattered, though concentrations can occur at virtually any point in the upper half, sometimes forming a nearly continuous surface of fragments. The absence of shell material from the lower half is fairly consistent.

Bivalves occur as distinct bands of both single and articulated valves within a sandstone bed and are often associated with gravel clasts of a comparable size. Such bands can be quite widely spaced or concentrated into a ‘roach’-like lithology. Occasional scattered specimens do occur between such bands but represent an insignificant proportion of the total number of specimens present.

Depositional Environment

In common with the sandstone units found at the local base of the Arenig in the rest of north Wales, the basal Arenig sandstone unit of the Caernarfon–Bangor area was deposited in a shallow-marine environment.

The presence of trilobites of the *Neseuretus* community suggests a shallow marine environment (Fortey & Morris 1982), and although this material is transported the presence of *Azygograptus* in the overlying ‘flaggy’ sandstones at Bangor (Beckly 1985) indicates that it has not been carried into a significantly deeper environment.

The lateral variation between the A5 section and the Bangor foreshore suggests shallowing, and a source area, to the north (see Fig. 6). The coarse units of the foreshore

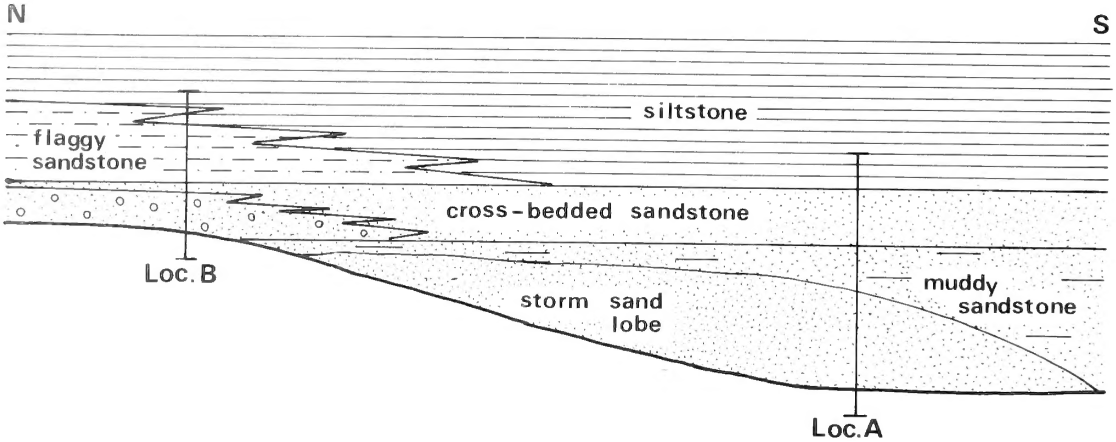

Fig. 6 Schematic depositional model for the Maes y Geirchen Sandstone Member in the Bangor area.

section are similar to the shallow-marine pebbly sandstones illustrated from the Lower Carboniferous of Morocco (Graham 1982). The poorly sorted nature of these deposits is not compatible with wave reworking and therefore it is likely that even these were deposited below normal wave-base.

As described, the A5 section broadly divides into three units. The absence of a basal coarse unit and the higher energy features of the Upper Clean Sandstone Unit suggests an overall shallowing during deposition, probably by gradual infilling of a basin. The Lower Clean Sandstone Unit of the A5 section is thought to represent a rapidly deposited sand lobe, probably storm-generated, with the muddy sandstone unit above indicating a quieter abandonment environment, with sandstone deposition more intermittent. The sandstone beds are comparable to, though thicker than, the type 1 sandstones recognized from the Caradocian of Shropshire (Brenchley & Newall 1982). The fossil material does not form basal coquinas (cf. Kreissa 1981) and this probably indicates that it has been transported rather than winnowed into a lag, the latter only being suggested by the bivalve bands. The concentration of the shell material within the top half of the beds suggests waning of a flow that was initially capable of moving the fragments. The concentrated bands probably reflect brief periods of winnowing in the later stages of a prolonged storm.

The features of the Upper Clean Sandstone Unit suggest relatively shallow water deposition, probably close to normal wave base. This represents a progradation of the basal facies seen at Bangor. The sharp transition between the top of this unit and the overlying shale-dominated sequence probably reflects a second, quite rapid, deepening of the basin.

SYSTEMATIC DESCRIPTIONS

Terminology follows that of the *Treatise on Invertebrate Paleontology,* O, Arthropoda 1 (Harrington, Moore & Stubblefield, *in* Moore 1959). 'Glabella' is usually understood to include the occipital ring. Systematic order is by family as they appear in the *Treatise* (Moore 1959).

Family **LEIOSTEGIIDAE** Bradley, 1925

Genus ***ANNAMITELLA*** Mansuy, 1920

TYPE SPECIES. *Annamitella asiatica* Mansuy, 1920.

DISCUSSION. In the review of this genus by Fortey & Shergold (1984: 323) a number of genera were considered to be junior synonyms. Though these included *Monella*, the type species of which is *A. perplexa* (Bates 1968) from Anglesey, it was suggested that this genus may be a junior synonym of a possibly separate genus *Proetiella* Harrington & Leanza (1957: fig. 59, 3–7), based on the presence of a 3P glabellar furrow.

The material described below is similar to *A. perplexa* in having a flat pygidial border, and anterior cranidial border not incorporated into the glabella. Neither of these characters is shared by *Proetiella* and therefore this grouping does not seem valid. *A. guizhousensis* Yin & Li (1978: pl. 183, figs 4–7) shares the cranidial characters of *A. perplexa* in having a 3P furrow and separate anterior border, but has a pygidium typical of other members of *Annamitella*. Therefore if *Monella* is to be recognized as a separate genus, the distinguishing characters must be those of the pygidium: flat border and less prominent development of axial rings and pleural furrows. However, for the present the two north Wales species are retained in *Annamitella*.

Annamitella sinesulcata sp. nov. Figs 7a–f; 8b

DIAGNOSIS. Effaced species of *Annamitella* with no evidence of lateral glabellar furrows. Weakly defined anterior border present. Pygidium with fairly broad, flat, sloping border.

HOLOTYPE. It19829, internal mould of solitary cranidium.

MATERIAL. Cranidia: It19803, It19818, It19829, It19858. Pygidia: It19817, It19837, It19840.

LOCALITY. Known only from A5 cutting at Caerhûn.

NAME. From the Latin *sine* (without); *sulcus* (furrow)

DESCRIPTION. Most material known from internal moulds.

Cranidium: Rectangular glabella defined by broad, deep axial furrows that are subparallel posteriorly but diverge anteriorly, giving glabellar sides a concave form. Transverse

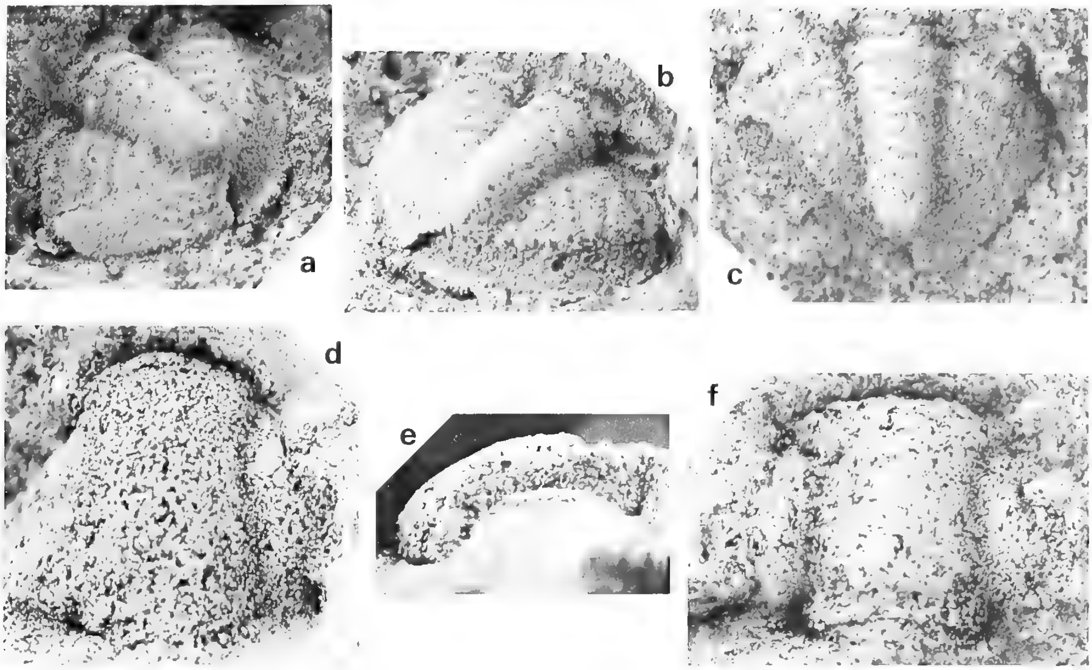

Fig. 7 *Annamitella sinesulcata* sp. nov. All material from Loc. A. a, b: It19840 (×3), oblique views of internal mould of pygidium. Note flat border and concave doublure. c: It19817a (×5), internal mould of pygidium. d: It19818 (×5), internal mould of cranidium. Note anterior border. e, f: **Holotype** It19829 (×5), internal mould of cranidium, lateral and dorsal views.

profile moderately convex, glabella standing well above fixed cheeks which are at approximately half total height of cranidium. Sagittal profile also convex, glabella curving steadily down from highest point immediately anterior to occipital furrow.

Occipital furrow broad and slightly concave posteriorly, causing axial widening of occipital ring. On exterior of exoskeleton this furrow would probably be narrower and more sharply defined (cf. Fortey & Shergold 1984: pl. 38, figs 3, 5); this is probably also true of the axial furrows.

Apart from the prominent occipital furrow and slight evidence of an anterior border, the glabella is totally effaced, with no indication of lateral glabellar furrows.

Fixed cheeks dominated by elongate, subparallel-sided inflated lobes about a quarter the width of glabella, but expanding inside palpebral lobe to about 0·45 times width of glabella. Some suggestion exists of depressed areas anterior and posterior to this major ridge on the fixed cheeks, but the form of these not clear.

Palpebral lobes prominent: slightly below level of fixed cheeks from which they are separated by shallow furrow; slightly curved and about a third of width of expanded cheek adaxial to them and about a third total length of cranidium, extending fom 0·25 – 0·6 of cranidial length (sag.).

Pygidium: Semicircular to slightly triangular in outline with prominent, slightly tapering, subparallel-sided axis and well rounded terminal axial piece. Axial furrows poorly developed, axis standing well above pleural fields and approximately semicircular in transverse section. Articulating half-ring not clear on any specimen. Three to four axial rings and pleural ribs developed, first axial ring much more obvious than others.

Moderately wide flat border of even width (approx. one

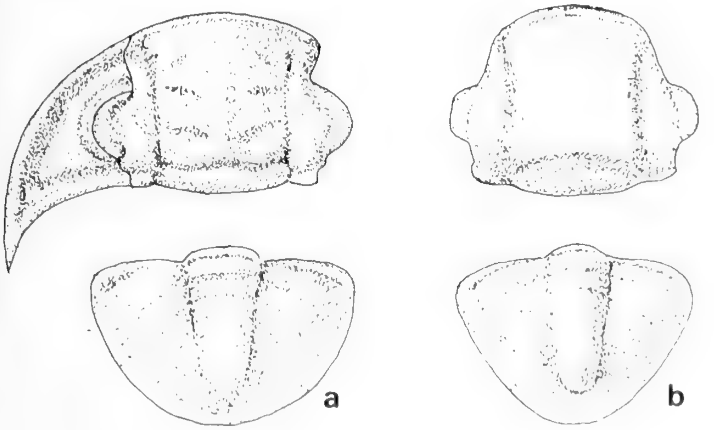

Fig. 8 a, *Annamitella perplexa* (Bates), with free cheek replaced. b, *Annamitella sinesulcata* sp. nov. (Both approx. ×3).

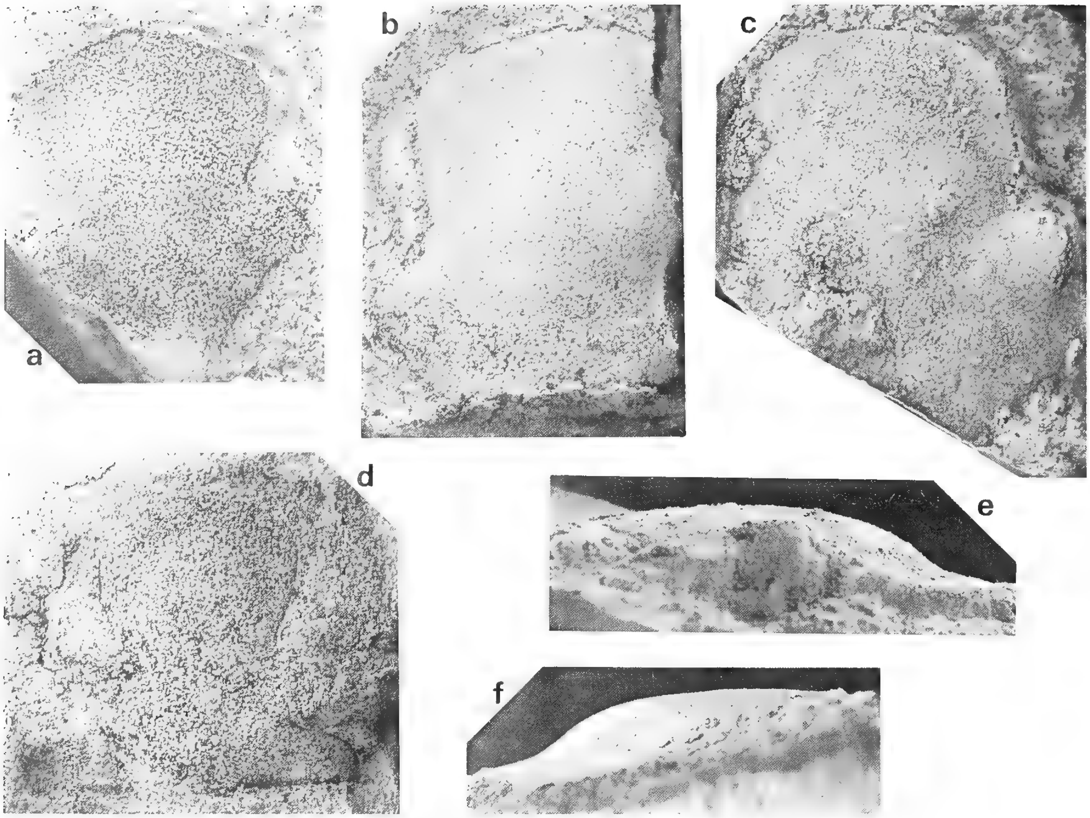

Fig. 9 *Asaphellus* cf. *graffi* (Thoral). All material from Loc.A. a: It19805 (×2). b, f: It19813d (×2). c, e: It19813c (×2). d: It19843 (×2). All are internal moulds of cranidia.

quarter length of axis) slopes fairly steeply: axis extends a short distance onto it. Doublure corresponds in position to border and is quite strongly concave on dorsal surface.

DISCUSSION. As noted in discussion of the genus, this species may be separated from all other members of the genus and grouped with *A. perplexa* (Bates) on the basis of the broad, flat pygidial border. It may easily be distinguished from *A. perplexa* by its effaced cranidium, a character also not seen in any other members of the genus.

Family **ASAPHIDAE** Burmeister, 1843
Subfamily **ISOTELINAE** Angelin, 1854

Genus ***ASAPHELLUS*** Callaway, 1877

TYPE SPECIES. *Asaphellus homfrayi* Salter 1866.

REMARKS. Usage follows diagnosis of Fortey & Owens (1987) and their proposed synonymy.

Asaphellus cf. ***graffi*** (Thoral) Figs 9a–f; 10a–j; 11a–d

cf. 1946 *Plesiomegalaspis graffi* Thoral: 61–68; pl. 6, figs 1 & 2; pl. 8, fig. 1; pl. 9, fig. 1; pl. 10; pl. 11, fig. 3; pl. 12; pl. 13, fig. 1; pl. 14, fig. 1a–b; pl. 15, fig. 4; pl. 16, fig. 4.

MATERIAL. Cranidia: It19805, It19810, It19813, It19834, It19843, It19848–9, It19857. Pygidia: It19824, It19827, It19842, It19847. Hypostomes: It19820, It19829, It19831, It19836, It19851. Free cheeks: It19803, It19823, It19833, It19838, It19850. Additional material in National Museum of Wales: 85.16G. 34–43, 85.16G.46.

LOCALITY. Cutting on A5 at Caerhûn.

DESCRIPTION. Species attaining moderate size: largest cranidium is 23 mm wide anteriorly, allowing estimate of cranidial length of *c*. 34 mm, whilst largest free cheek suggests cranidial length over 40 mm. Largest pygidium is 45 mm wide anteriorly.

Cranidium. Preocular sutures slightly divergent (range 49° to 22° enclosed angle), angle decreasing with size. Anterior of cranidium pointed, anterior sutures enclosing angle of 132° to 145°. Anterior sutures are intramarginal as confirmed by free cheeks (see below).

On one specimen (It19843), 2 cm long (sag.), the eye position can be seen clearly; it is placed well back in the posterior half, the palpebral lobe extending from 0·23 to 0·40 along the sagittal length of cranidium. Though not easy to judge exactly from free cheeks it appears that even in larger cranidia the length posterior to the eye would still be less than 1·5 times the length of the palpebral lobe. In the largest speciman (It19813) the post-palpebral length appears to be 1·35 times the length of palpebral lobe. Palpebral lobe semicircular in outline and only just below maximum elevation of glabella.

Glabella effaced, and slopes gently down on all sides: no axial or preglabellar furrows. Front of glabella slopes down into anterior border which is still slightly sloping but at a lower angle, producing a concave profile to the anterior of cranidium. Anterior border widest at anterolateral corners of

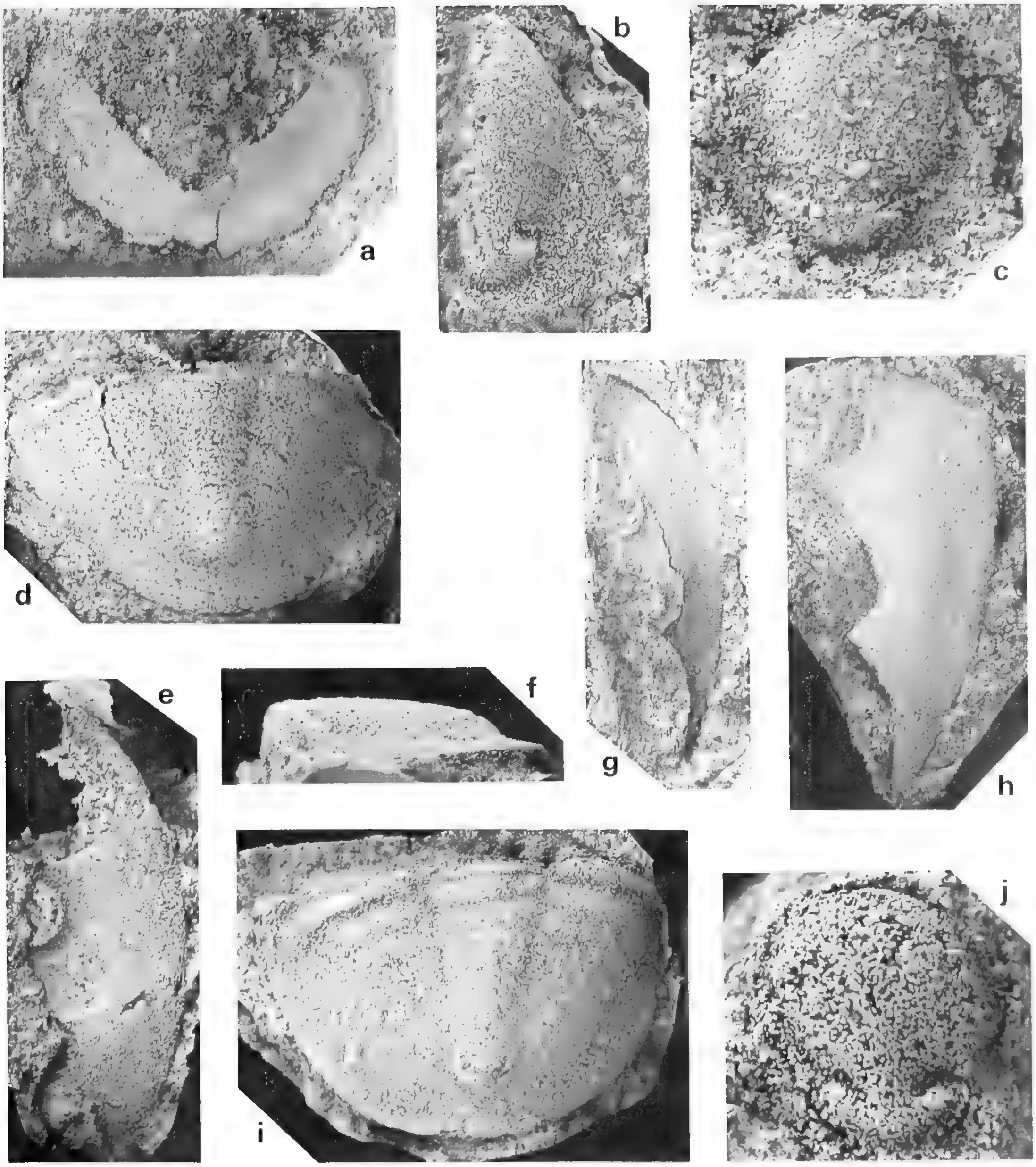

Fig. 10 *Asaphellus* cf. *graffi* (Thoral). All material from Loc. A. a: It19822 (×2), poor internal mould of pygidium showing doublure. b: It19829 (×3), latex cast of external mould of broken hypostome. c: It19831 (×7·5), internal mould of hypostome. d: It19827 (×1·25), latex cast of external mould of pygidium. e: It19803 (×1·18), latex cast of external mould of free cheek. f, i: It19824 (×1·25), latex cast of external mould of pygidium. g: It19838 (×1·25), internal mould of free cheek. h: It19833 (×1·25), latex cast of external mould of free cheek. j: It19820 (×7·5), internal mould of hypostome.

cranidium where it reaches one quarter of the maximum preocular width (tr.) of cranidium; it narrows towards the midline.

Though poorly preserved there is no evidence of any occipital furrow, and only slight evidence of a posterior border furrow.

Free Cheek. External margin gently curved and extending posteriorly into pronounced genal spine, which becomes broader and more truncate in larger specimens. Preocular and postocular sutures fairly straight for majority of length and strongly curved at their abocular ends. This curve turns the postocular suture through about 90°, to run perpendicular to the immediately adjacent part of genal spine, and thence to the posterior margin of cranidium. Preocular suture curves to become parallel with front margin of cranidium, with a thin extension of the dorsal exoskeleton continuing external curvature of the free cheek. The two sutures converge at an angle just less than 90° in plan view, and are of approximately equal length.

In plan view a broad concave border occupies just less than half the maximum width. Doublure is co-extensive and slightly more concave in profile. Terrace lines are faintly developed on the doublure.

A panderian opening is present on It19838 just interior to paradoublural line and close to posterior margin.

Hypostome. Oval in outline, with posterior broader.

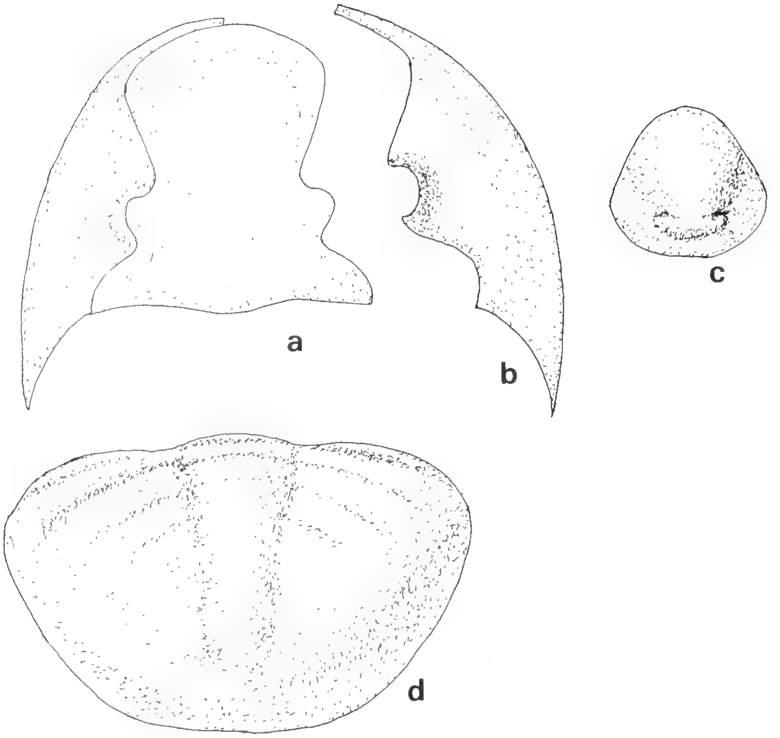

Fig. 11 *Asaphellus* cf. *graffi* (Thoral). a, cranidium with free cheek replaced. b, free cheek in plan view. c, hypostome. d, pygidium. (All approx. x1).

Anterior margin formed by median body; no anterior border preserved. Median body occupies about 0·9 of length (sag.), with posterior lobe one quarter of the length (sag.) of anterior lobe, and separated from it by a pair of prominent maculae. There is little evidence of a border furrow, but the maculae are joined by a slight furrow extending around the rear of the posterior lobe. Overall shape of median body is elliptical.

Prominent lateral border starts at approximately half the length of the anterior lobe, with margin initially straight and tangential to anterior curvature of lobe. Maximum width is opposite maculae. Posterior to this, the margin curves sharply inwards, the border narrowing into posterior border; posterior margin a smooth curve parallel to border furrow of posterior lobe.

Pygidium. Broadly semicircular in outline though slightly straightened postaxially. Length: breadth ratio 1:1·5–1·6 in largest pygidia. Transverse profile strongly convex. Border broad, about one third of the length (sag.) of axis at its widest, and steeply sloping, flat to slightly concave. Narrows postaxially with suggestion of increased concavity.

Axis only slightly inflated with faint axial furrows. Maximum width of axis less than 0·3 of maximum width (tr.) of pygidium, with posterior well rounded and extending a very short distance onto border. At most three axial rings are apparent and a similar number of pleural furrows: only the first of each is clearly defined. Narrow articulating half-ring.

Doublure approximately corresponds to border, and is more strongly concave than border. Narrows postaxially, giving distinct v-shape to interior doublural margin, though details of this are not well preserved.

DISCUSSION. The main problem in comparing the Welsh material with that of *A. graffi* (Thoral) is the generally larger size of the latter. If the larger specimens of the Welsh population are fully mature then this size difference may be a taxonomic difference in itself, but may alternatively reflect ecophenotypic variation. There is a small difference between the two populations in the development of the genal spines. These become blunter in larger specimens of both populations, but in the case of the type material of *graffi* the spine is still pointed in specimens with a cranidial length of 45 mm; Welsh specimens of this size already have blunt spines. There are a number of other minor differences that can be recognized.

(1) The eye in the Welsh specimens is more posterior in position. The eye in *A. graffi* is positioned at between about 0·3 and 0·5 of the cranidial length (sag.), whilst that of the Welsh specimens is between 0·2 and 0·4.

(2) The line of the postocular suture has a much sharper curvature in *A.* cf. *graffi*.

(3) The pygidial border appears to narrow postaxially in *A.* cf. *graffi* whilst of constant width in *A. graffi*. The ratio of the postaxial length against axial length is less than 0·25 in the Welsh specimens, and greater than this in the French specimens, but evidence is limited to two and three specimens respectively.

(4) The posterior margin of the posterior lobe of the hypostome is smoothly rounded in the Welsh specimens whilst there is a distinct pointed posterior axial extension to the lobe in *A. graffi*.

The asaphid described from the Carmel formation on Anglesey (Bates 1968: pl. 12, figs 1–6) has more divergent preocular sutures and a centrally placed eye. *A. whittardi* (Bates 1969) has a much more strongly furrowed pygidium (Whittard 1964: pl. 38, figs 10–13). The specimens figured as *A. graffi* by Gigout (1951: pl. 2, figs 1–5) from Morocco are probably better referred to *A. whittardi* than to *A. graffi*.

Family **CALYMENIDAE** Burmeister, 1843

Subfamily **REEDOCALYMENINAE** Hupé, 1955

Genus ***NESEURETUS*** Hicks, 1873

TYPE SPECIES. *Calymene parvifrons* var. *murchisoni* Salter, 1865.

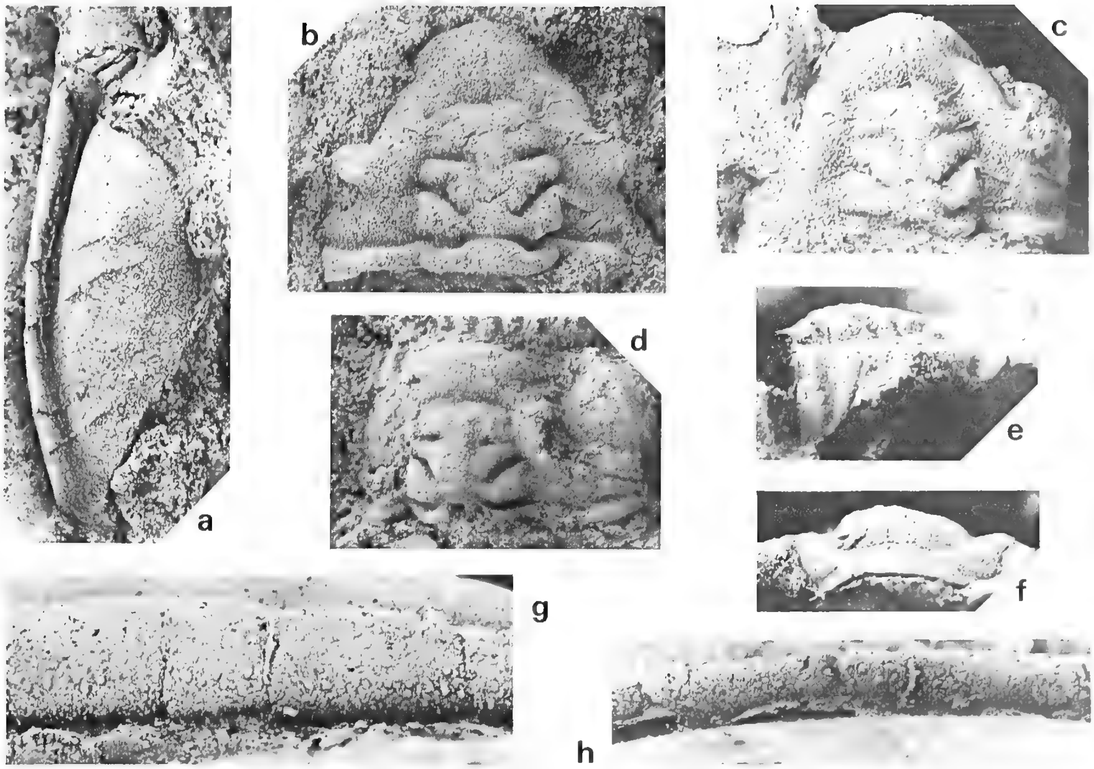

Fig. 12 *Neseuretus monensis* (Shirley). All material from Carmel Formation, central Anglesey; British Geological Survey colln. a; Af.831 (× 2·5), internal mould of free cheek. b: Af.832 (×2·5), holotype; latex cast of external mould of cranidium. c, e, f: Af.831 (×2·5), holotype; internal mould of cranidium. d: Af.830 (×3), internal mould of cranidium. g: Af.831 (×7·5), ornament on underside of doublure of free cheek. h: Af.831 (×7·5), ornament on border of free cheek.

Neseuretus monensis (Shirley 1936) Figs 12a–h

1919 *Neseuretus parvifrons* Salter; Greenly : 442, 446.
1936 *Synhomalonotus monensis* Shirley: 401–402; pl. 30, figs 1–4.
1968 *Neseuretus monensis* (Shirley) Bates : 193; pl. 14, figs 11, 16.

DIAGNOSIS. *Nesueretus* with oblique eye ridges, moderately long (sag.) anterior area 0·45 to 0·61 times preoccipital length (sag.) of glabella. No anterior furrow or border visible.

HOLOTYPE. British Geological Survey colln Af831–2. Internal and external moulds of isolated cranidium.

MATERIAL. Cranidia: Af830–2, Af1404, 56372. Free Cheek: Af831. All B.G.S. colln.

LOCALITY & OCCURRENCE. Carmel Formation, central Anglesey.

DESCRIPTION. **Cranidium**. Four specimens were examined, including the holotype and another specimen (Af830) figured by Shirley (1936). Apart from the holotype, only internal moulds are preserved. The holotype is probably deformed; it is extensively cracked and if complete the right free cheek would be completely obscured in plan view whilst the left would be well exposed. Hence the furrows are probably overdeepended. It was probably deformed by compression in the plane of the specimen, perpendicular to the axis. Specimen Af830 is probably the least deformed of the material examined.

Cranidium outline is trapezoidal, the triangular form noted by Shirley being based on the deformed holotype. Glabella has trapezoid outline, and stands well above palpebral lobes. Two prominent lateral furrows: 1P with typical posterior inclination, 2P perpendicular to axis. Faint 3P furrow present on Af830 and visible on left side of external mould of holotype. Occipital furrow curves forwards at the axis, causing a narrowing of the 1P lobe. Lateral furrows shallow, expanding into crescent-shaped depressed areas posteriorly, anterior margins of which are approximately level with 1P furrow. Preglabellar furrow moderately deep, with fossulae developed approximately at intersection with axial furrows. Eye ridges oblique; cross axial furrows just posterior to fossulae; enclose angle posteriorly of *c*.140°. Palpebral lobes posteriorly positioned. Line joining posterior edges crosses glabella at exterior end of 1P furrow, that for anterior at exterior end of 2P furrow. As noted by Shirley, this places the palpebral lobe opposite 2P lobe. Palpebral lobes separated from axial furrows by 0·4 of glabellar width, as measured between them.

Anterior area gently domed posteriorly, before curving down smoothly to anterior margin. No anterior border or furrow. Anterior margin curves under inflated fixed cheeks which cut into anterior area at approximately half its length (sag.). Ratio of length of anterior area (sag.) to preoccipital length of glabella (sag.) ranges 0·4–0·6.

Free Cheek. One deformed specimen known. Prominent border, exaggerated by deformation, separated by overdeepened furrow. Fine tuberculate ornament both on upper surface and on under doublural surface. Sutures intersect at approx 100°. Postocular suture 1·7 times as long as preocular.

Pygidium. No material additional to that described by Bates (1968) is available.

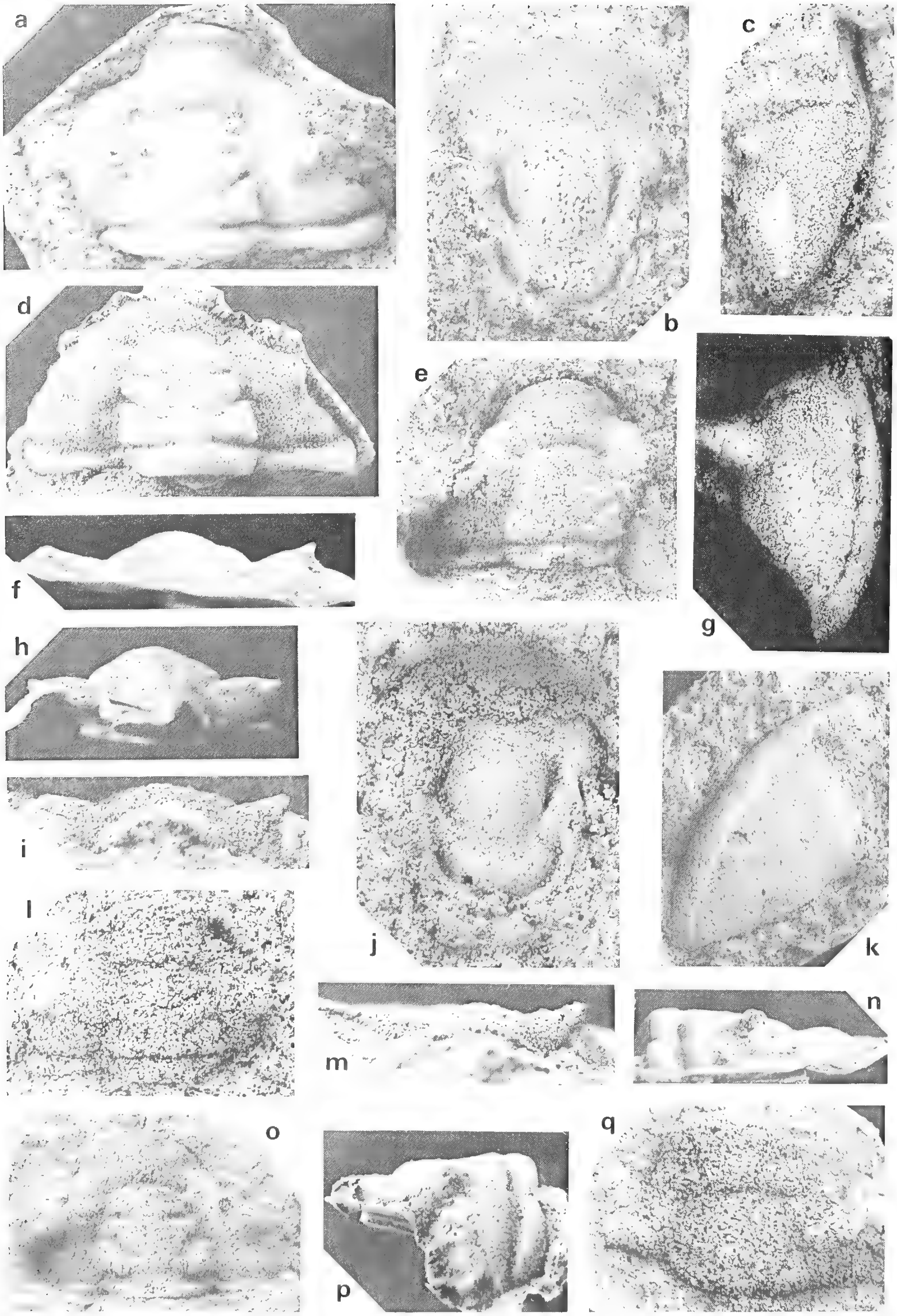

Fig. 13 *Neseuretus caerhunensis* sp. nov. All material from Loc. A. a, f, n: **Holotype** It19800 (×2), latex cast of external mould of cranidium. b: It19811 (×5), latex of external mould of hypostome. c: It19809 (×2), internal mould of free cheek. d, h, p: It19839 (×2), latex cast of external mould of cranidium. e: It19813 (×2), internal mould of cranidium. g: It19803 (×2·5), latex cast of external mould of free cheek. i, q: It19804 (×3), latex cast of external mould of cranidium. j: It19811 (×5), internal mould of hypostome. k: It19803 (×2·5), latex cast of external mould of free cheek. l, m: It19806 (×5), latex cast of external mould of free cheek. o: It19835 (×2), internal mould of cranidium.

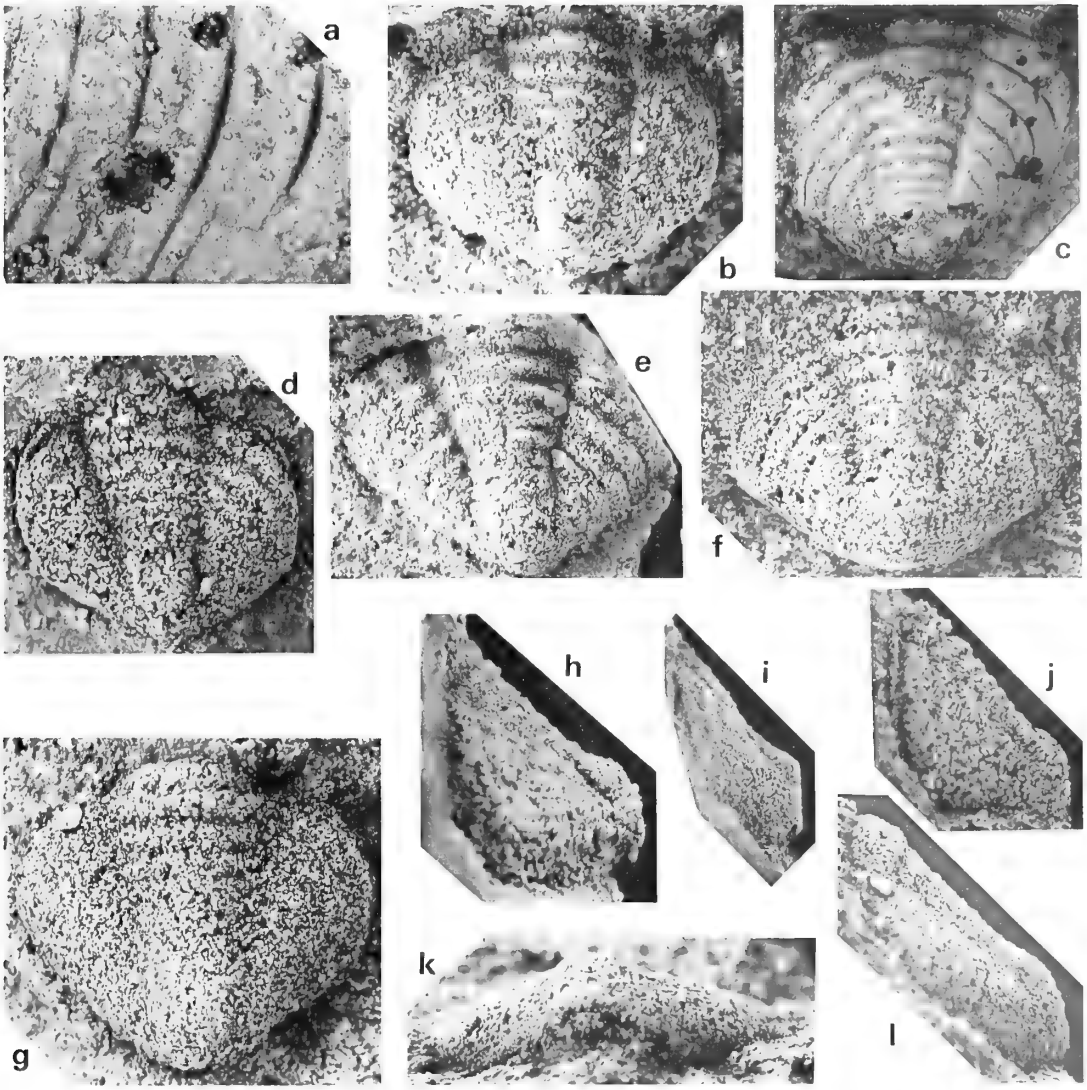

Fig. 14 *Neseuretus caerhunensis* sp. nov. All material from Loc. A. a: It19807 (×7·5), detail of ornament on internal mould of pygidium, lateral view. b, h: It19832 (×5), internal mould of pygidium. c: It19807 (×2·5), internal mould of pygidium. Note constrictions on lateral parts of axial rings. d, j; It19805 (×5), internal mould of pygidium. e: It19828 (×3), internal mould of pygidium. f, k: It19808 (×5), internal mould of pygidium. g, l: It19830 (×5), latex cast of external mould of pygidium. i: It19801 (×3), internal mould of pygidium.

Discussion. See under *Nesuretus caerhunensis*.

Neseuretus caerhunensis sp. nov. Figs 14a–l; 15a–d

Diagnosis. *Neseuretus* species with distinctly oblique trend of eye ridges and long (sag.) anterior area (more than 0·62 of preoccipital glabellar length (sag.)). Anterior border furrow slightly developed, marking off approximately horizontal border. Hypostome has distinct anterior and posterior lobes of the median body, the posterior lobe crossing the border furrow into an inflated anterior part of the lateral border. Posterior of hypostome smoothly rounded.

Holotype. It19800. Well-preserved cranidium.

Other material. Cranidia: It19804, It19806, It19813, It19819, It19835, It19839, It19842, It19845, It19854. Pygidia: It19801, It19805, It19807–8, It19828, It19830, It19832. Hypostomes: It19811, It19853. Free cheeks: It19803, It19809, It19816, It19825, It19852, It19856–7. Additional material in National Museum of Wales: 85.16G.51–63.

Locality & occurrence. Only known from type locality, the A5 cutting at Caerhûn. An indeterminable *Neseuretus* (N.M.W. 85.16G.47) from the Bangor foreshore is likely to be this species.

Name. After village near type locality.

Description. **Cranidium**. A number of cranidia are known, ranging in size up to 30 mm wide (tr.) and 18 mm long (sag.), the two best-preserved being of the maximum size: the description is based mainly on these. Cranidial shape is approximately sub-trapezoidal, with significantly rounded anterior, preocular sutures converging slightly, but anterior width (tr.) remaining greater than posterior width (tr.) of glabella.

Glabella is approximately trapezoidal and moderately inflated, well defined by axial and preglabellar furrows. Three

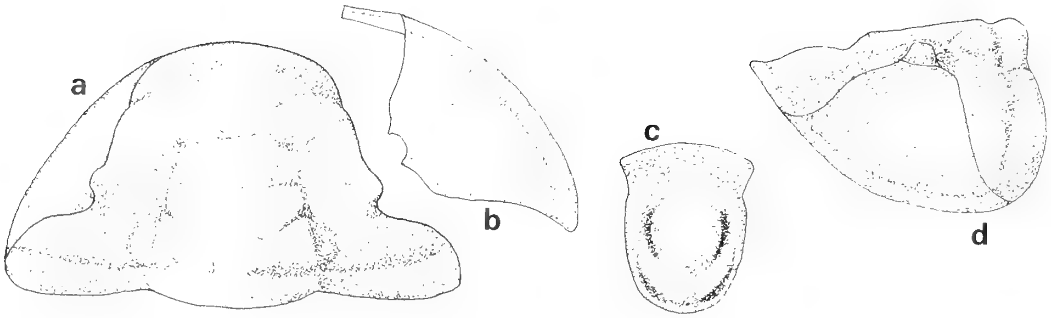

Fig. 15 *Neseuretus caerhunensis* sp. nov. a, cranidium with free cheek replaced. b, plan view of free cheek. c, hypostome. d, reconstruction of lateral view of cephalon. (All approx. ×2).

pairs of lateral glabellar furrows are present. The 1P furrow trends backwards towards the sagittal line and forms an angle of *c.* 50° with it. At its inner termination this furrow turns perpendicular to the sagittal line and may even be inclined slightly anteriorly in some cases. A fifth of glabellar width (tr.) is not cut by this pair of furrows. 2P furrow straight and approximately perpendicular to the sagittal line. On the holotype it is perched but this does not appear to be normal. The 3P furrow is very faint, but can be seen on the holotype and lies approximately midway between the 2P furrow and anterior of glabella. Axial ridge, apparent on well-preserved specimens, broadens and merges with anterior lobe. The 1P lobe narrows considerably adaxially, whilst the 2P expands adaxially by a compensating amount.

Occipital furrow is approximately straight and fairly evenly developed apart from slight fading over mid-axis. There appears to be a constriction of the furrow on either side of the glabella. In one specimen the axial part of furrow has a slight anterior curvature. Axial furrows expanded into a crescentic depressed area posterior to the palpebral lobe, and anterior to this area they are only slightly developed. Preglabellar furrow moderately well developed with fossulae present at its junction with axial furrows.

Palpebral lobes prominent: line joining their posterior margins crosses the glabella at, or just anterior to, the 1P furrow. They are separated from the glabella by half the glabellar width, as measured along the same line. Line joining anterior margins of palpebrebral lobes runs just posterior to 3P furrow. Eye ridges trend anteriorly from palpebral lobes, the pair enclosing an angle of 144°–154°, and cross the axial furrow just posterior to fossulae.

Anterior area (anterior border plus preglabellar field) large, ranging in length (sag.) from 0·6–0·8 of preoccipital length of glabella. Though posterior part of preglabellar field is somewhat domed, preocular fixed cheeks are more raised, producing appearance of slight furrows diverging anteriorly. Anterior border furrow moderately developed with anterior border horizontal in profile.

Free Cheek. In plan view the two sutures converge at about 90°, the preocular suture length being two-thirds of the postocular. A moderately inflated border is present, which occupies a quarter of the width opposite the eye. The border widens a little posteriorly whilst the doublure narrows, as it is turned to a higher angle relative to the plan view. No sculpture is seen on border, though this may reflect mode of preservation. A significant length of doublure extends from the front of the free cheek, confirming the wide separation of the anterior sutures.

Hypostome. Only one complete specimen is known, which is 9 mm long; it is represented by both internal and external moulds. A depressed anterior area, typical of the *Neseuretus* hypostome, is well developed, occupying just less than one third of the total length (sag.). The median body is divided into distinct anterior and posterior lobes, separated by a crescent-shaped depression. The anterior lobe is oval, narrower end posterior, with each end grading down into the depressed areas, and laterally bordered by deep furrows. Posterior lobe is crescent-shaped, its posterior edge steeper than anterior. This lobe extends across the line of the border furrow, dividing it in two and causing an inflated portion of the lateral border alongside the anterior lobe. Border furrow behind posterior lobe follows curvature of the latter, before it is truncated by extension of the posterior lobe. There is some suggestion of deepening at anterior ends, though depth of the posterior border furrow appears more even on the internal mould. Anterior part of border furrow becomes shallower posteriorly, grading into the depressed area separating the two lobes of median body. Posterior margin of hypostome smooth, and follows curvature of posterior border furrow. Posterior border narrow. Lateral border continuous with posterior border and merges with extension of posterior lobe into a broader and more elevated anterior portion, which curves down gently to the lateral margin.

Pygidium. Pygidia assigned to this species fall into two size groupings: greater and less than 10 mm in length (sag.). Two well-preserved specimens of the larger size have different outlines, one being distinctly triangular whilst the other is well rounded posteriorly. Both have a funnel-shaped axis, the axial furrows converging at 35° until just posterior of the fifth axial ring, and thereafter continuing subparallel. Nine axial rings are present on one specimen and show slight constrictions forming small tubercular inflations at their lateral terminations. On the other specimen only six axial furrows are apparent, with no evidence of the tubercular terminations; this may reflect coarser preservation. Posterior of axis inflated in sagittal profile. Six pleural furrows present on better-preserved specimen, short interpleural furrows being developed in the steeply down-turned sides of the pleural field. A fine tuberculate sculpture covers the pygidium.

The smaller pygidia are grouped with this species on the posterior inflation of the axis. However, they differ from the larger specimens in being somewhat effaced, with axial furrows only shallowly developed and fading posteriorly, and with three to four axial and pleural furrows indistinctly developed. A prominent articulating half ring which is longer (sag.) than first axial ring is present in two specimens.

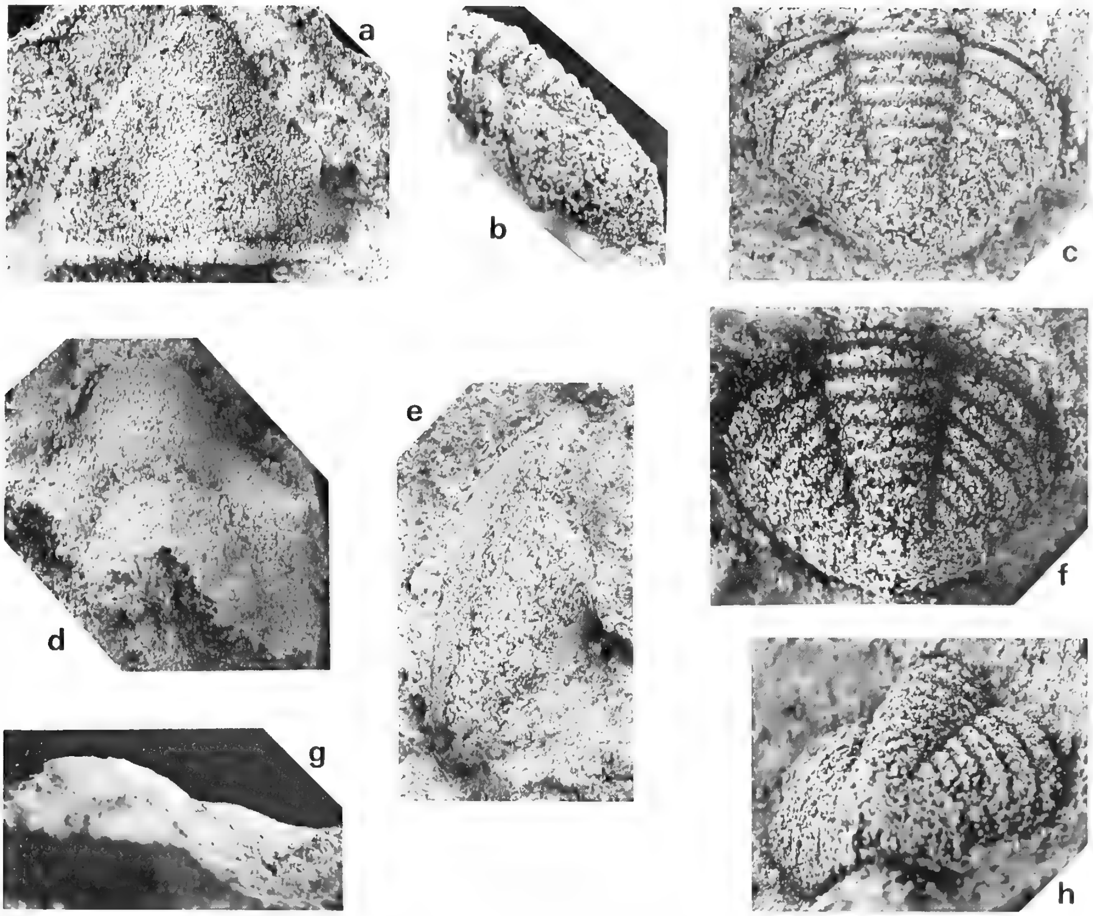

Fig. 16 *Calymenella preboiselli* sp. nov. All material from Loc. A except specimen It19844 (g) which comes from Loc. B. a: **Holotype** It19812 (×3), latex cast of external mould of cranidium. b, c: It19817 (×5), internal mould of pygidium. d, g: It19844 (×2.5), internal mould of cranidium. e: It19826 (×3), internal mould of free cheek. f, h: It19815 (×5), internal mould of pygidium.

This character is not preserved in either of the larger specimens.

Discussion. Since the various skeletal elements described under the above species are derived from an assemblage of disarticulated fragments, there is no direct evidence that they all belong to the same species. However, this is only questionable for the pygidia and these have been separated into two groups on the presence or absence of the posterior inflation of the axis, those not showing this being assigned to *Calymenella preboiselli* (p. 18). The development of a postaxial ridge, considered characteristic of *Neseuretus* (Hammann 1983: 40, fig. 17), is seen in two of the pygidia (e.g. his pl. 24, fig. 2) and the posterior inflation of the axis is also shown by other members of the genus (e.g. *N. parvifrons* (M^{c}Coy) Whittington 1966: pl. 4, fig. 12).

In only four other species of *Neseuretus* has the hypostome been described: *N. parvifrons* (M^{c}Coy) (Bates 1969 : 26; pl. 9, figs 4, 10; Whittington 1966: 501–2; pl. 5, figs 5, 8); *N. tristani* (Brongniart) (Henry 1980: pl. 10, figs 4a–b, pl. 11, figs 2, 5; Hammann 1983: pl. 6, figs 61, 64); *N. avus* Hammann (Hammann 1983: pl. 4, fig. 46) and *N. henkei* Hammann (Hammann 1983: pl. 7, fig. 74). Henry (1980) considers that there is considerable intraspecific variation in the form of the hypostome (1980: 71, fig. 25), but since each of his specimens comes from a different locality it seems more likely that the variation may be indicative of subspecies, as recognized by Hammann (1983). This would therefore suggest that the hypostome includes significant taxonomic features, limited in usefulness by its rare preservation.

The hypostome described above is quite distinct from those previously described in that the border furrow is not continuous. However, there is some similarity to that of *N. parvifrons*, in the form of the anterior and posterior lobes, and the hypostome of *Nesueretus caerhunensis* could easily be derived from this by the extension of the posterior lobe. There is no evidence of the maculae seen in *N. tristani*.

The form of the lateral glabellar furrows, in which there is a marked adaxial divergence of 1P and 2P, with the 2P furrow approximately perpendicular to the sagittal line, may be considered typical of *Neseuretus* as it is also seen in the type species *N. murchisoni* (Salter 1865). This, associated with the oblique form of the eye ridges, which are more normally perpendicular to the sagittal line (cf. Whittard 1960: pls 19, 20), separates the new species, along with *N. monensis* (Shirley 1936: 401–2; pl. 29, figs 1–4), from other members of the genus. The oblique form of the eye ridge results from the posterior position of the eye, approximately opposite the 2P lobe, a feature Shirley (1936: 402) noted as being diagnostic of *N. monensis*. The Bangor species is easily distinguished from *N. monensis* in having a longer anterior area and obvious anterior border.

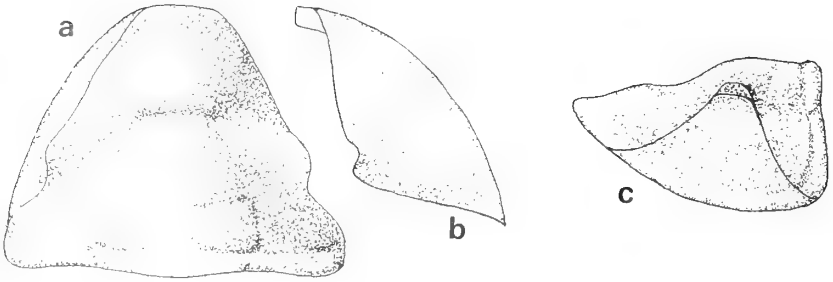

Fig. 17 *Calymenella preboiselli* sp. nov. a, cranidium with free cheek replaced. b, free cheek in plan view. c, lateral view of reconstructed cephalon. (All approx. ×3).

Genus *CALYMENELLA* Bergeron, 1890

TYPE SPECIES. *Calymenella boiselli* Bergeron, 1890.

Calymenella preboiselli sp. nov. Figs 16a–h; 17a–c

DIAGNOSIS. *Calymenella* very similar to type species in having elongate sub-triangular anterior area, but differing from this and other species in having less strongly developed lateral, preglabellar and occipital furrows. Glabella is of a rounded pentagonal form. Posterior part of pygidial axis is ill-defined.

HOLOTYPE. It19812. Cranidium.

MATERIAL. Cranidia: It19802, It19812, It19821, It19834, It19844. Pygidia: It19815, It19817. Free cheeks: It19803, It19826, It19832, It19837, It19855.

LOCALITY & OCCURRENCE . Cutting on A5 at Caerhûn, with a single specimen (It19844) from the foreshore at Bangor.

NAME. From close similarity to type species but occurring much earlier.

DESCRIPTION. **Cranidium.** Three well-preserved specimens known, all about 15 mm long. Poorly preserved specimens are difficult to distinguish reliably from the *Neseuretus* in the fauna. Cranidium strongly triangular, with slightly truncated, rounded anterior. Glabella occupies approximately three-fifths of preoccipital length (sag.) of cranidium and has rounded, sub-pentagonal outline. At least two pairs of shallow and broad, indistinctly developed lateral furrows are present, with 1P lobe moderately well defined. 1P furrow inclined gently backwards, causing 1P lobe to narrow adaxially. 1P furrow also slightly curved, being approximately perpendicular to axis at inner termination. Axial unfurrowed area present, of approximately same width as shallower portion of occipital furrow. 2P furrow very poorly defined and little more than a shallow depressed area, the orientation of which is unclear, but appears to be elongate perpendicular to axis. Axial and preglabellar furrows poorly developed. Absence of marked furrows means glabella is less well defined in plan view than is apparent from profile view. Palpebral lobes quite large, posterior margin approximately level with 1P furrow, and anterior margin only slightly behind anterior of glabella. Eye ridge present; inclined slightly forward towards sagittal line.

Preocular sutures straight in dorsal view and converge sharply towards anterior enclosing angle of 65°. Preglabellar field elevated just anterior to preglabellar furrow, and then sloping down with concave curvature into ill-defined anterior border, hardly apparent in dorsal view. Anterior of cranidium narrower than posterior width of glabella. Occipital furrow deepest at margins of glabella, fading over the axis and curving slightly forwards. Posterior border furrow well developed, curving slightly forwards abaxially. Occipital ring well-defined laterally but almost merges into preoccipital portion of glabella at axis. Posterior border widens laterally as result of anterior curvature of posterior border furrow.

Free Cheek. In plan view sutures converge at about 120°. Preocular suture slightly longer than postocular. Genal angle rounded. Doublure just under a quarter the width of free cheek opposite eye, and in plan view narrows towards genal angle apparently as result of being more steeply inclined to surface of free cheek. Slightly elevated border on dorsal surface approximately same width as doublure.

Pygidium. Both pygidia assigned to this species are known only from internal moulds, the external that exists for one being too poor to warrant description. Both are small, 6–7 mm long (sag.), approximately 1·25 times as wide as long and rounded posteriorly. Axis occupies one third of maximum width anteriorly and tapers posteriorly, margins defined by prominent axial furrows that converge to enclose angle of 20°. Six or seven axial rings present.

There are five or six pleural furrows; no interpleural furrows have been observed though this may result from coarse preservation. Posterior of axis ill-defined and appears to grade into the postaxial area: this is supported by the lateral profile which shows an almost continuous curvature between the two.

Articulating half-ring narrow.

DISCUSSION. The pygidia assigned to this species are distinguished from those of the *Neseuretus* by the absence of a posterior inflation of the axis and the more prominent axial and pleural furrows in specimens of equivalent size.

Calymenella has previously been considered restricted to the Caradoc and ?Ashgill (Hammann 1983 : 72) and therefore the material described here represents a significant extension of the range. In view of this it is remarkable that the north Wales species bears so close a resemblance to the type species of the genus, *C. boisseli* Bergeron, from which it differs mainly in its cephalic effacement.

The only other species that shows a comparable convergence of the preocular sutures is *C. alcantarae* Hammann & Henry 1978, but in both this and the type species the palpebral lobe is smaller than in the Welsh specimens, which accordingly have oblique eye ridges. In addition the furrows bounding the glabella tend to be more prominent in *C. alcantarae*.

The posterior of the pygidial axis is less clearly defined than is typical of the genus (see Hammann 1983: 38, fig. 16).

Calymenella sp. A Figs 18a–c

MATERIAL. It19814. External mould of cranidium.

LOCALITY. Cutting on A5 at Caerhûn.

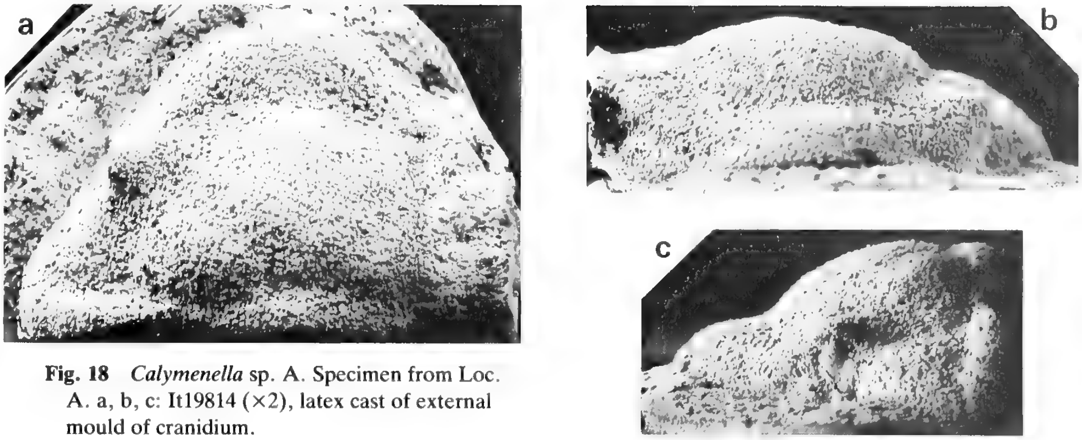

Fig. 18 *Calymenella* sp. A. Specimen from Loc. A. a, b, c: It19814 (×2), latex cast of external mould of cranidium.

DESCRIPTION. Dimensions of the single cranidium known: 22 mm long (sag.), 34 mm wide (tr.) and 13 mm high.

Outline of cranidium well rounded, semicircular to slightly triangular. Glabella outline similar to that of cranidium, highly domed; it occupies half the total height of the cranidium. Maximum elevation is just anterior to occipital furrow and in profile curves down smoothly to anterior. Glabella featureless except for occipital furrow and faint 1P furrow that forms an approximately straight depression from axial posterior of glabella to palpebral lobe, and separates off the somewhat inflated 1P lobe. Occipital ring widens axially and is poorly developed behind 1P lobes.

Preglabellar field 0·29 of total cranidial length (sag.) and approximately half preoccipital length (sag.) of glabella. Neither preglabellar nor axial furrows clearly developed, the margins of the glabella marked by sharp changes of slope. Posterior two-thirds of preglabellar field slopes gently downwards whilst anterior third is sharply curved down. The gently sloping area appears to narrow slightly as it curves towards the palpebral lobes, whilst the steeply sloping portion remains approximately the same width when viewed dorsally.

Palpebral lobe only slightly separated from glabella and in profile is approximately level with the base of glabella. It lies just over half way along the sagittal line of the cranidium, i.e. at between 0·49 and 0·59, and is only slightly elevated above the fixed cheeks. Posterior to palpebral lobe is a gently sloping area of the fixed cheek, widening posteriorly. Posterior border furrow only faintly developed though posterior border is quite strongly inflated and widens quite significantly abaxially.

In lateral view the facial sutures indicate a relatively small free cheek, the preocular suture not extending anterior of the glabella.

DISCUSSION. The generic placement of this specimen has proved difficult. It is included in *Calymenella* because, although a single cranidium is inadequate basis for the erection of a new genus, it bears a slight resemblance to *C. bayani* (Tromelin & Lebesconte) (cf. Hammann & Henry 1978 : 407, fig. 2). In plan view the specimen also bears some resemblance to *Platycorophe heberti* (Lebesconte) (see Henry 1980: pl. 15, fig. 1), but *Platycorophe* belongs to the Homalonotidae and there is no suggestion in the north Wales specimen of the concave lateral margin of the 1P lobe typical of this family.

AGE AND PALAEOGEOGRAPHIC IMPLICATIONS

The Bangor trilobite fauna provides no independent evidence on the exact age of the Maes y Geirchen Member within the Arenig Series. It is uncertain which Arenig Stage yielded the type material of *A. graffi* in the Montagne Noire, but it is reputed to be 'mid-Arenig'. Consequently *Azygograptus eivionicus* Elles, which occurs in the overlying 'flaggy' sandstone sequence on the Bangor foreshore (Elles 1922) provides the best control on the age. A review of this genus (Beckly 1985) has shown that *A. eivionicus* is characteristic of the Moridunian and may extend into the early Whitlandian. A *Neseuretus* community fauna of Moridunian age is known from the Henllan Ash Member of the Arennig area, north Wales (Whittington 1966), and contains species known also from south Wales (Fortey & Owens 1978). There seems no reason to suppose this fauna was incapable of colonizing the Bangor area, and age equivalence is perhaps unlikely. An early Whitlandian age is perhaps more probable.

An alternative argument could be that the Bangor fauna is Moridunian in age and the differences from the Henllan Member fauna are the result of 'provincial' isolation. Despite there being no species in common, there is clearly a close relationship between the fauna of the Bangor area and that from the Carmel Formation of Anglesey. The small differences that there are may be accounted for by an age difference, the Anglesey fauna probably being Fennian.

One result of the close similarity between the Bangor and Anglesey faunas is that Anglesey can no longer be viewed in isolation from the rest of north Wales, as has been the tendency in the past (Neuman 1984), and any provincial separation would have to be further east. Gibbons (1985) and Reedman *et al.* (1984) have summarized the geological evidence for an Anglesey-like 'terrane' having been near the Welsh Basin during the Lower Palaeozoic. The emphasis here will be on the faunal evidence that exists for the Arenig.

In the south-west of the Llŷn, around Aberdaron, rocks yielding a Moridunian fauna rest on the Mona Complex (Beckly 1985). The fauna includes *Merlinia selwynii* (Salter), an asaphid widespread throughout Wales (Fortey & Owens

1978), and the Gondwanan trinucleid *Hanchungolithus primitivus* (Born) recorded for the first time in the U.K. There is no evidence here of any isolation from the Welsh Basin, though the environment may have been slightly deeper than was typical of the *Neseuretus* community.

An alternative to 'provincial' separation is an environmental isolation, because the *Neseuretus* community environment may have been transient in a marginal setting. Such an environment existed at different places along the western margin of the Welsh Basin in all three stages of the Arenig. By the end of the Arenig the deep-water isograptid biofacies (Beckly 1987), typical of a marginal setting (Fortey & Cocks 1986), was present in the same area indicating the extremely rapid foundering that took place. Close facies association has already been noted in *Neseuretus* during the Arenig (Fortey & Owens 1987), and this is possibly the most likely explanation for the endemicity.

The extent of the endemicity of the Anglesey and Bangor faunas will be open to some question until faunas of the same facies and age have been reliably recognized elsewhere. However, the Bangor fauna is important in that Anglesey can no longer be considered in isolation from the Welsh mainland, and any major separation seems less likely.

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Lower and Upper Devonian brachiopods from the Budleigh Salterton Pebble Bed, Devon.

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CONTENTS

Synopsis. Since the mid nineteenth century, Devonian brachiopods have been identified from constituent pebbles in the Triassic at Budleigh Salterton. However, only now can they be recognized as coming from quartzite pebbles of two separate Devonian ages: (a) Lochkovian – Pragian, corresponding in facies and fauna to the Landévennec and Gahard Formations of France (previously termed the Grès à *Orthis monnieri*) and (b) Frasnian, with a fauna not corresponding directly with that from any other European quartzite. The brachiopod species originally described by Salter and Davidson are refigured and allotted to more modern genera, and fresh plate descriptions are presented to Davidson's 1881 Monograph on the Budleigh Salterton brachiopod fauna, including both Ordovician and Devonian species. The new species *Salopina adventita* is described, of lower Devonian age. Lectotypes are selected of the following nominal species of Davidson: *Crania transversa, Nucleospira vicaryi, Orthis vicaryi, Rhynchonella valpyana, R. vicaryi, R.? ovalis, Spirifera macroptera* var. *microptera, Strophomena edgelliana, S. etheridgii, S. rouaulti*; and of Salter *Spirifer antiquissimus* and *Leptaena vicaryi*.

INTRODUCTION

Since 1835, Palaeozoic faunas have been known in the Budleigh Salterton Pebble Bed of Triassic age, which outcrops along the cliffs for 2 km at Budleigh Salterton, Devon, and from which pebbles are found on the adjacent beach. The brachiopods were first described by Salter (1864), who recognized their central European affinities, but who failed to realise that more than a single geological age was represented. The fauna was subsequently described in more detail by T. Davidson in a series of publications (1866–71, 1870, 1880, 1881), who realised that three separate ages were involved; in modern terms Arenig, Llandeilo and Devonian. The Arenig and Llandeilo forms have been revised by Cocks & Lockley (1981). However, Davidson, although he correctly attributed some of the Devonian forms to French species, did not realise that at least two different Devonian ages were involved. Some of the brachiopod species can be attributed to the Lower Devonian, and can still be directly compared with some forms from France, for example the Landévennec and Gahard Formations (formerly known as the Grès à *Orthis monnieri*) of late Gedinnian or early Siegenian (Lochkovian–Pragian) age. The remainder of the fauna (including the spiriferides which Salter thought to be the oldest in the geological record) can be attributed to the Upper Devonian, specifically the Frasnian, although there are no quartzites of that age known from France, Belgium or Germany which carry the same fauna as that from Budleigh Salterton.

The British Museum (Natural History) is fortunate in possessing the most comprehensive collections of the Budleigh Salterton faunas, which were built up by two amateurs, W. Vicary and R.H. Valpy and bequeathed to the Museum in 1903 and 1905 respectively, and from which the bulk of Salter's and Davidson's species were described. The opportunity is taken here not only to refigure the Devonian forms and assign the older names to more modern genera, but also to present revised plate descriptions to Davidson's Palaeontographical Society Monograph of the Budleigh Salterton brachiopods (1881) in a similar way to those plate descriptions already presented for the Lower Palaeozoic of Britain (Cocks 1978).

AGE OF THE FAUNAS

The brachiopods which occur in the Budleigh Salterton pebbles can now be attributed to four different ages.

Ordovician

These faunas are described in Cocks & Lockley (1981), although revised plate descriptions to Davidson's monograph (1881) are presented in the Appendix here (p. 34). The brachiopods identified from the Middle Arenig are *Lingulobolus hawkei* (Rouault, 1850), *Lingulobolus brimonti* (Rouault, 1850), *Pseudobolus*? *salteri* (Davidson, 1866), *Ectenoglossa lesueuri* (Rouault, 1850) and possibly *Philhedrella*? *vicaryi* (Davidson, 1866), and from the late Llandeilo *Tafilaltia valpyana* (Davidson, 1869), *Salopia*? *pulvinata* (Salter, 1864), *Corineorthis erratica* (Davidson, 1869) and *Porambonites* sp. In addition, the species identified and illustrated by Davidson as '*Lingula*' *morieri* Tromelin, 1876 is almost certainly an Ordovician rather than a Devonian form.

Devonian

Davidson considered that all the Devonian faunas belonged to the Lower Devonian, although he was puzzled (1882:356) by the downward extension of the range of certain spiriferides. Now that more is known about Devonian brachiopods, it is clear that some of the Budleigh Salterton species are Lower Devonian, in particular from beds which must lie close to the Gedinnian–Siegenian boundary, including such well-known forms as *Platyorthis monnieri*, and that others, such as *Cyrtospirifer verneuili*, are of Upper Devonian, Frasnian, age. A close analysis of all the available pebbles confirms, not only that brachiopods of these two different ages do not co-occur on a single pebble, but also that virtually all of the varied Devonian fauna can be firmly attributed to one or other of these two ages. Some of the co-occurrences are documented in the systematic section below. The full list is as follows.

From the Gedinnian–Siegenian (Lockhovian–Pragian) pebbles came *Platyorthis monnieri* (Rouault, 1851), *Salopina adventita* sp. nov. (p. 24), *Leptostrophia etheridgii* (Davidson, 1870), *Shaleria vicaryi* (Davidson, 1870), *Mclearnites rouaulti* (Davidson, 1870), *Schuchertella*? sp., *Katunia*? *vicaryi* (Davidson, 1870), '*Camarotoechia*' *ovalis* (Davidson, 1870), *Nucleospira vicaryi* Davidson, 1870, *Athyris*? *incerta* Davidson, 1870, *Howellella cortazari* Carls, 1969 and *Mutationella*? *erratica* (Davidson, 1870), and possibly *Cryptonella*? cf. *rhenana* (Drevermann, 1902). From the Frasnian pebbles came *Petrocrania transversa* (Davidson, 1870), *Rhipidomella*? *budleighensis* (Davidson, 1870), *Douvillina edgelliana* (Davidson, 1870), *Douvillina*? *budleighensis* (Davidson, 1870), *Anoplia* sp., *Productella vicaryi* (Salter, 1864), uncinuliform sp. indet., '*Camarotoechia*' *valpyana* (Davidson, 1870), *Cyrtospirifer verneuili* (Murchison, 1840), *Cyrtospirifer*? *micropterus* (Davidson, 1870) and *Cryptonella*? sp.

In addition, there are various nominal species, '*Orthis hamoni* Rouault' of Davidson, '*Rhynchonella*' *winwoodiana* Davidson, 1870, '*Rhynchonella elliptica* Schnur' of Davidson and '*Rhynchonella thebaulti* Rouault' of Davidson, all of Devonian age and which remain unidentifiable for various reasons discussed below, and a small inarticulate, *Philhedrella*? *incerta* (Davidson, 1870), which could be of either Ordovician or Devonian age.

SYSTEMATIC PALAEONTOLOGY

All the species described from the Devonian pebbles in the Budleigh Salterton conglomerate are reviewed in turn below, and some hitherto undescribed forms, *Salopina adventita* sp. nov., *Schuchertella*? sp., *Anoplia* sp., and some terebratulides, are also illustrated for the first time. Those species described by Davidson and Salter are all ascribed to modern genera, apart from '*Orthis hamoni*', discussed under the Enteletacea and the Rhynchonellida below.

The specimen repositories are as follows: British Museum (Natural History), B, BB and BC; Sedgwick Museum, Cambridge, SM; British Geological Survey, GSM; Bristol City Museum, BRSMG; the Albert Memorial Museum, Exeter, Ex M; Royal Geological Society of Cornwall, RGSC; and the Royal Museum of Scotland, Edinburgh, RSM.

Class **INARTICULATA**
Order **ACROTRETIDA** Kuhn
Suborder **CRANIIDINA** Waagen
Superfamily **CRANIACEA** Menke
Family **CRANIIDAE** Menke

Genus ***PETROCRANIA*** Raymond, 1911

Petrocrania transversa (Davidson, 1870) Fig. 1

1870 *Crania transversa* Davidson: 78; pl. 4, figs 9, 10.
1881 *Crania transversa* Davidson; Davidson: 352; pl. 40, figs 9, 10.

LECTOTYPE (here selected) B 21544, the original of Davidson 1870: pl. 4, fig. 9 (and also of Davidson 1881: pl. 40, fig. 10).

DISCUSSION. The original specimen occurs on a slab with the common late Devonian rhynchonellide termed by Davidson *Rhynchonella inaurita* and so there is no doubt as to its age. Only a single valve is now in the Vicary Collection, although Davidson's original description speaks of two. The generic attribution is due to the fact that the anterior adductor scars are relatively smaller than the posterior scars and the apparent absence of ornament (although only the internal mould of the valve is known and so the possibility of a fine ornament cannot be entirely ruled out).

Class **ARTICULATA**
Order **ORTHIDA** Schuchert & Cooper
Suborder **ORTHIDINA** Schuchert & Cooper
Superfamily **ENTELETACEA** Waagen

The Budleigh Salterton enteletaceans of Devonian age consist of the three species described below, two from the Lower Devonian and one from the Upper Devonian. Not revised is the species described by Davidson (1881: 344, fig. 20) as *Orthis hamoni* Rouault. Rouault's original material from the Lower Devonian of Gahard, France has not been traced in the University of Rennes. Those specimens illustrated by Davidson are the only two known from Budleigh Salterton


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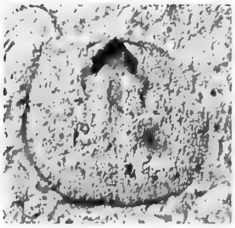
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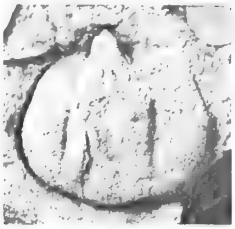
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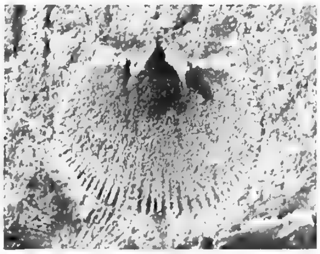
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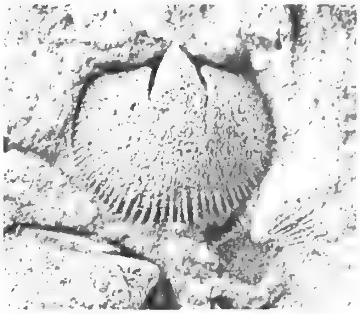
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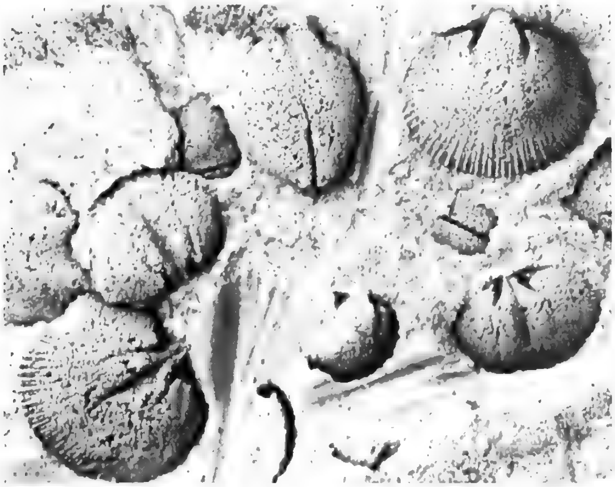
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Fig. 1 *Petrocrania transversa* (Davidson, 1870). **Lectotype** (here selected), B 21544, internal mould, × 2.

Figs 2–6 *Platyorthis monnieri* (Rouault, 1851). Fig. 2, B 21586, internal moulds of pedicle valves, × 1·5; Fig. 3, B 13283, internal mould of brachial valve, × 2; Fig. 4, BC 6573, internal mould of pedicle valve, × 2; Fig. 5, BC 6574, internal mould of brachial valve, × 2; Fig. 6, BB 70329, internal mould of pedicle valve, figured Davidson 1881: pl. 40, fig. 6, × 2.

Figs 7–9 *Salopina adventita* sp. nov. Fig. 7, BC 6577, internal mould of brachial valve, × 3; Fig. 8a, b, **holotype** BC 6576, latex cast and internal mould of pedicle valve, × 3; Fig. 9, BC 6575, internal moulds of a pedicle valve and several brachial valves, and a brachial valve of *Katunia? vicaryi*, × 4.

Fig. 10 *Rhipidomella? budleighensis* (Davidson, 1870). Holotype B 21412, internal mould of pedicle valve, the original of Davidson 1870: pl. 4, fig. 14, × 1·5.

(Davidson 1881: 345) and they are both on a single block. This block, which also includes the type of *Rhynchonella winwoodiana* Davidson, was in the Winwood collection, but it has not been traced in that collection in the Bristol City Museum. All that can be determined from Davidson's drawings is that the form is an enteletacean.

Family **DRABOVIIDAE** Havlíček

Genus ***SALOPINA*** Boucot, 1960

Salopina adventita sp. nov. Figs 7–9

DIAGNOSIS. *Salopina* with planoconvex brachial valve, subcircular outline, weak dorsal sulcus, fine costellae, and divergent brachiopores of medium length.

NAME. 'Coming from abroad.'

DESCRIPTION. *Exterior.* Pedicle valve convex, brachial valve planoconvex with weak dorsal sulcus and corresponding ventral fold; outline subcircular with relatively narrow hinge line. Small open delthyrium, and small curved apsacline pedicle interarea under uncurved umbo; brachial valve interarea very small, with umbo scarcely developed. Ornament of relatively fine costellae with characteristic salopinid branching and midline (Walmsley 1965: fig. 1). Occasional poorly developed growth lines seen.

Pedicle valve interior. Strong pair of teeth, supported by dental lamellae which merge with the floor posteriorly to the anterior end of the teeth. Relatively poorly developed impressions of the muscle field, which is unenclosed anteriorly. No trace of mantle canals and the valve interior is smooth except at the periphery where reflections of the external costellae may be seen.

Brachial valve interior. Small, linear to slightly pear-shaped cardinal process. Strong brachiophores which also act as the anterior part of the socket, the brachiophores of medium length for the genus and which are quadrilateral to spear-shaped at their bases and which extend anteriorly into raised muscle-bounding ridges in adult specimens (e.g. Fig. 9, lower left), which may extend for over half the valve length. The brachiophores diverge at angles from 65° to 90°. Central myophragm variably impressed, sometimes nearly strong enough to be called a weak septum. Adductor muscle field variably impressed, not usually separated posteriorly and anteriorly, and seldom with any trace of an anterior margin.

MATERIAL. Holotype BC 6576 (Fig. 8), the internal mould of a pedicle valve. Additional material: 12 other pedicle valves and 5 brachial valves on the same block as the holotype, including BC 6575 (Fig. 9), BC 6577 (Fig. 7); 2 pedicle valves and 7 brachial valves on the block registered B 21539, BC 6087–8 (including one broken brachial valve illustrated under *Leptostrophia etheridgii* in Fig. 19); and smaller numbers of both valves on other blocks.

DIMENSIONS (in mm)

		Length	Width
BC 6576	pedicle valve, holotype	6·1	6·6
BC 6575a	pedicle valve	6·5	6·2
BC 6577	pedicle valve	5·8	5·5
BC 6575b	brachial valve	5·5	7·4

DISCUSSION. Walmsley *et al.* (1969) have given a useful review of the ten species which had been described up to that time and which they ascribe to *Salopina*. Since then, other Silurian and later species have included *Salopina* sp. and *S. kosoviensis* described by Havlíček (1977) from the Motol Formation (Wenlock) and Kopanina formation (Ludlow) respectively of Bohemia; *S. brandi* described by Cocks (1979) from the Qarabil Formation (Wenlock) of Iran, *S. walmsleyi* described by Isaacson (1977) from the Lower Devonian of Bolivia; *S. boucoti* described by Sheehan (1976) from the Upper Silurian of Utah; *S. onukii*, *S. o. elongata* and *S. yamadai* described by Tachibana (1976, 1980) from the Silurian of Japan; *S. delta* and *S. submurifer* described by Johnson, Boucot & Murphy (1973, 1976) from the Upper Silurian and Lower Devonian of the Roberts Mountains, Nevada, U.S.A.; *S. kemezysi* Chatterton (1973) from the Lower Devonian of New South Wales; *S.? yichangensis* Rong & Yang (1981) from the Silurian of China; *S. kokbaitalensis* Ushatinskaya & Nilova (1975) from the Lower Devonian of Kazakhstan, U.S.S.R.; *S. aspera* Xu (1979) from the Tangxiang Formation (L. Devonian), Guangxi, China, and *S. mediocostata* Strusz (1982) from the Upper Silurian of Canberra, Australia. Thus *Salopina* now includes some 27 nominal species, although a complete review of the genus is outside the scope of the present work. Nevertheless, by the specific criteria nominated by Walmsley *et al.* (1969: table 2), *S. adventita* still differs from the other species by the combination of characters mentioned in the diagnosis.

Family **RHIPIDOMELLIDAE** Schuchert
Subfamily **RHIPIDOMELLINAE** Schuchert

Genus ***RHIPIDOMELLA*** Oehlert, 1890

Rhipidomella? budleighensis (Davidson, 1870) Fig. 10

1870 *Athyris? budleighensis* Davidson: 80; pl. 4, fig. 14.
1881 *Athyris budleighensis* Davidson; Davidson: 338; pl. 38, fig. 6.

HOLOTYPE (by monotypy). '. . . The internal cast of a ventral valve has alone been discovered . . . found by Mr Vicary along with *Spirifera Verneuilii* and *Rhynchonella inaurita*' (Davidson 1870: 80); B 21512, the original of Davidson 1870: pl. 4, fig. 14.

DISCUSSION. The holotype is poor, although it is certainly an enteletacean and not an athyrid, as thought by Davidson. It is a rhipidomellid; it may or may not be a *Rhipidomella, sensu stricto*, since the peripheral crenulations characteristic of the genus are not visible in the poor preservation. It is associated with an upper Devonian *Cyrtospirifer* and large rhynchonellide, and so its age is not in doubt – the only other rhipidomellids of middle and upper Devonian age (Boucot *et al.* 1965) are *Thiemella* and *Aulacella*, both of which have distinctive shell shapes. In addition to the holotype, there is another specimen in the Vicary Collection, B 21713, in which the muscle field can be seen more clearly.

Subfamily **PLATYORTHINAE** Harper, Boucot & Walmsley

Genus ***PLATYORTHIS*** Schuchert & Cooper, 1931

Platyorthis monnieri (Rouault, 1851) Figs 2–6

1851 *Orthis Monnieri* Rouault: 376.
1870 *Orthis Vicaryi* Davidson: 84; pl. 5, figs 20–22.
1881 *Orthis Monnieri* Rouault; Davidson: 345; pl. 4, figs 1–8.
1972 *Platyorthis monnieri* (Rouault) Renouf: 108; pl. 22, figs 7–15; pl. 23, figs 1–7.

TYPE SPECIMENS. Renouf (1972: 109) states that the types of *monnieri* have not yet been found in Rouault's collection at the University of Rennes. **Lectotype** of *vicaryi* (here selected) B 20940, the original of Davidson 1870: pl. 5, figs 20 (right-hand side), 21 and 22.

DISCUSSION. This distinctive species is by far the most common Lower Devonian brachiopod in the Budleigh Salterton Pebble Bed, and several hundred specimens have been obtained by a variety of collectors. The species has been extensively revised by Renouf (1972), and indeed he used some Budleigh Salterton material in his redescription of the Brittany material from the eponymous Grès à *Orthis monnieri* of Gedinnian or Siegenian age.

Order **STROPHOMENIDA** Öpik
Suborder **STROPHOMENIDINA** Öpik
Superfamily **STROPHOMENACEA** King
Family **STROPHEODONTIDAE** Caster
Subfamily **DOUVILLININAE** Caster

Genus ***DOUVILLINA*** Oehlert, 1887

Douvillina edgelliana (Davidson, 1870) Figs 21–22

1870 *Strophomena Edgelliana* Davidson: 86; pl. 6, figs 2–5.
1881 *Strophomena Edgelliana* Davidson; Davidson: 349; pl. 39, figs 5–7.
1978 *Douvillina edgelliana* (Davidson) Harper & Boucot: 151.

LECTOTYPE (here selected) B 21534, internal mould of a brachial valve, the original of Davidson 1870: pl. 6, figs 3, 4 and Davidson 1881: pl. 39, figs 7, 7a, and its counterpart, external mould of a brachial valve, the original of Davidson 1870: pl. 6, fig. 2 and Davidson 1881: pl. 39, fig. 6, refigured here as Fig. 21.

DISCUSSION. Three matching pieces survive of the pebble containing the lectotype and these contain the internal mould of a pedicle valve (Fig. 22), poorly preserved external and internal counterparts of another pedicle valve and external and internal counterparts of two brachial valves, one of which is the lectotype (Fig. 21). These stropheodontids are associated on the same pebble with numerous specimens of *Anoplia* sp., discussed below, and are, like all the species of *Douvillina, sensu stricto*, discussed by Harper & Boucot (1978: 150–1) of late Devonian (Frasnian) age. The species has a pedicle valve of medium to weak convexity and a brachial valve which is almost flat, excluding it from the resupinate *Douvillinoides* and the biconvex *Douvillinaria*. Although the type species of *Douvillina, D. dutertrii* (Murchison), has not been revised, the distinctive brachial valve structures of *edgelliana* are very close to the form illustrated by Harper & Boucot (1978: pl. 26, figs 17a, b) as *Douvillina* cf. *dutertrii* from the late Frasnian of the Spanish Sahara.

Douvillina? budleighensis (Davidson, 1870) Fig. 13

1870 *Strophomena budleighensis* Davidson: 86; pl. 6, fig. 1.
1881 *Strophomena Budleighensis* Davidson; Davidson: 349; pl. 39, figs 4, 4a, b.
1978 *Douvillina budleighensis* (Davidson) Harper & Boucot: 151.

HOLOTYPE (by monotypy). 'Of this species a remarkable internal cast of the ventral valve only has been found' (Davidson 1870: 86), B 21538, the original of Davidson 1870: pl. 6, fig. 1 and Davidson 1881: pl. 39, figs 4, 4a, b; refigured here as Fig. 13.

DISCUSSION. The holotype is still the only known specimen and consists of the internal mould of a pedicle valve. There is no counterpart, and so the nature of the ornament is unknown, which would be of systematic importance. The specimen is comparable with that illustrated as *Douvillina* cf. *cayuta* (Hall) by Harper & Boucot (1978: pl. 26, fig. 11) from the Chemung Group of Frasnian age in New York State, and so Davidson's species is assigned to *Douvillina* with a query. There are no other identifiable specimens on the type pebble, but the species is assigned here to the upper Devonian part of the Budleigh Salterton fauna on the basis of comparison with the New York form. *Douvillina, senso stricto*, has a range restricted to the Frasnian (Harper & Boucot 1978: 20). *D.? budleighensis* is much more convex and has a relatively larger muscle field than *Douvillina edgelliana* from Budleigh Salterton, and it seems most unlikely that they are conspecific.

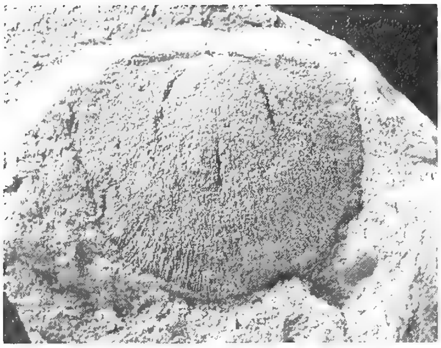
Genus ***MCLEARNITES*** Caster, 1945

Mclearnites rouaulti (Davidson, 1870) Figs 11–12

1870 *Strophomena Rouaulti* Davidson: 85; pl. 6, figs 8, 9.
1881 *Strophomena* sp. Davidson: pl. 39, figs 1a, b.
1881 *Strophomena Rouaulti* Davidson; Davidson: 348; pl. 39, fig. 9.
1972 *Douvillina (Mesodouvillina) lecaroensis* Renouf: 111; pl. 23, figs 8–16; pl. 24, figs 1, 7, 9.
1978 *Mclearnites (Mclearnitesella) lecaroensis* (Renouf) Harper & Boucot: 132.

LECTOTYPE of *rouaulti* (here selected), B 21540, internal mould of a brachial valve, figured Davidson 1870: pl. 6, fig. 8 (left) and also Davidson 1881: pl. 39, fig. 9c, refigured here as Fig. 12. There is also the internal mould of a pedicle valve on the same slab.

DISCUSSION. Only three pedicle valves and one brachial valve are known of this species from Budleigh Salterton; nevertheless it is distinctive and clearly attributable to *Mclearnites*. It is also the same form as that named *Douvillina (Mesodouvillina) lecaroensis* by Renouf (1972) from the Grès à *Orthis monnieri* of Brittany, which has already been attributed to *Mclearnites* by Harper & Boucot (1978: 132). The latter distinguish two subgenera based on minor ribbing differences and a third based on what they term a geniculation, but in my opinion the genus need not be subdivided above the species level.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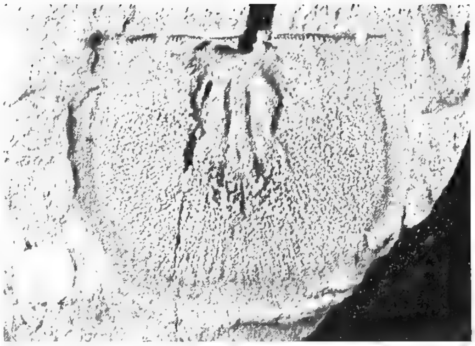
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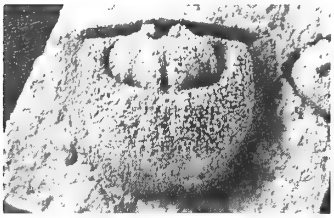
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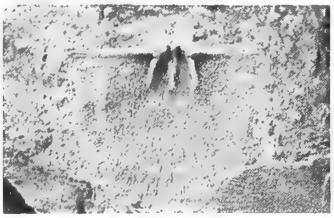
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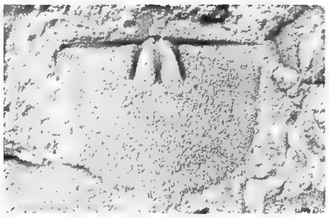
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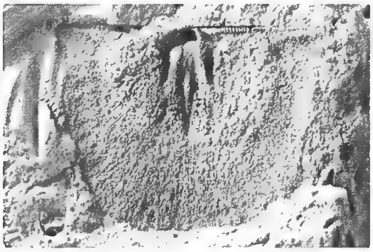
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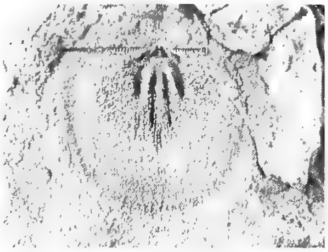
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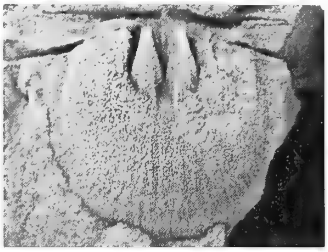
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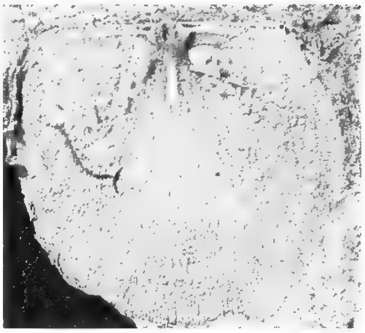
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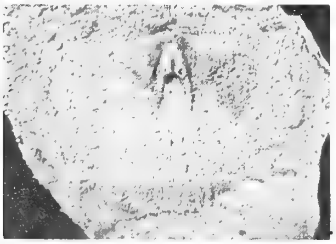
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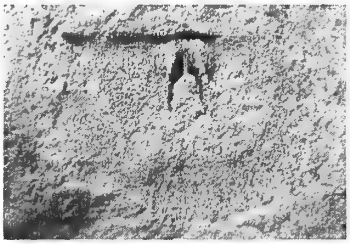
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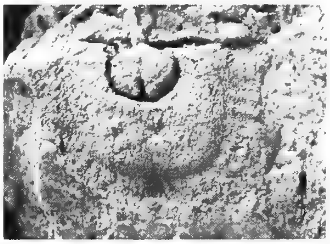
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Figs 11, 12 *Mclearnites rouaulti* (Davidson, 1870). Fig. 11, B 21600, internal mould of pedicle valve, × 1·5; Fig. 12, **lectotype** (here selected), B 21540, internal mould of brachial valve, figured in reverse by Davidson 1870: pl. 6, fig. 8 (left), × 1·8.

Fig. 13 *Douvillina? budleighensis* (Davidson, 1870). Holotype B 21538, internal mould of pedicle valve, figured Davidson 1870: pl. 6, fig. 1, × 2.

Figs 14–17 *Shaleria vicaryi* (Davidson, 1870). Fig. 14a, b, BC 6088, latex cast and internal mould of pedicle valve, × 2; Fig. 15, B 21637, internal mould of brachial valve, × 2; Fig. 16, B 21638, internal mould of brachial valve, × 2; Fig. 17, holotype B 21537, internal mould of pedicle valve, figured Davidson 1870: pl. 6, figs 6, 7, × 2.

Figs 18–20 *Leptostrophia etheridgii* (Davidson, 1870). Fig. 18, BC 6579, internal mould of brachial valve, × 1·5; Fig. 19, BC 6088, internal mould of pedicle valve, × 2; Fig. 20, **lectotype** (here selected), B 21539, latex cast of an internal mould of a brachial valve, figured Davidson 1870: pl. 6, figs 10 and 11, × 1·8.

Figs 21, 22 *Douvillina edgelliana* (Davidson, 1870). Fig. 21a, b, **lectotype** (here selected), B 21534, latex cast and internal mould of a brachial valve, figured Davidson 1870: pl. 6, figs 3 and 4, × 2. Fig. 22, B 21541, internal mould of pedicle valve, figure Davidson 1870: pl. 6, fig. 5, × 1·5.

Genus ***SHALERIA*** Caster, 1939

Shaleria vicaryi (Davidson, 1870) Figs 14–17

1870 *Strophomena Vicaryi* Davidson: 86; pl. 6, figs 6, 7.
1881 *Strophomena Vicaryi* Davidson; Davidson: 348; pl. 39, fig. 8.

HOLOTYPE (by monotypy). '. . . We are at present acquainted with one valve only' (Davidson 1870: 86); B 21537, the internal mould of a pedicle valve, the original of Davidson 1870: pl. 6, figs 6, 7, and Davidson 1881: pl. 39, fig. 8, refigured here as Fig. 17.

DISCUSSION. The holotype occurs on a piece of pebble without other fauna apart from the external impression of a flat strophomenide valve which may or may not be the same species. There are four other large pieces of pebble containing stropheodontids which are grouped here as being conspecific with the holotype, even though none of the pedicle valves on these slabs (e.g. Fig. 14) are quite as convex as the holotype (Fig. 17). The species is associated on the slabs with *Leptostrophia etheridgii* and *Salopina adventita* and is thus undoubtedly of lower Devonian age. The generic attribution is fairly certain, but the subgenus is less clear-cut – the three described by Harper & Boucot (1978: 161–4), *S.* (*Shaleria*), *S.* (*Janiomya*) and *S.* (*Protoshaleria*), all differ in some ways from *S. vicaryi* and thus no subgenus will at the moment be specified for the Budleigh Salterton form. None of the specimens has a definite counterpart, but from isolated impressions of shell fragments on the same pebbles, it seems probable that *S. vicaryi* lacks the interrupted ornament so widespread amongst species of *Shaleria*, for example the well-known *S. ornatella* from the late Silurian of the Welsh Borderland.

Subfamily **LEPTOSTROPHIINAE** Caster

Genus ***LEPTOSTROPHIA*** Hall & Clarke, 1892

Leptostrophia etheridgii (Davidson, 1870) Figs 18–20

1870 *Strophomena Etheridgii* Davidson: 85; pl. 6, figs 10–12.
1881 *Strophomena*? sp. Davidson: 350; pl. 39, fig. 2, *non* fig. 1.
1881 *Strophomena Etheridgii* Davidson; Davidson: 350; pl. 39, figs 10, 11.

LECTOTYPE (here selected), B 21539, internal mould of a large brachial valve, the original of Davidson 1870: pl. 6, figs 10, 11 and Davidson 1881: pl. 39, fig. 10 (refigured here as Fig. 20).

DISCUSSION. The species includes the largest strophomenide valves found at Budleigh Salterton (Fig. 20). One brachial valve interior and 8 pedicle valve interiors are present on the lectotype pebble, as well as specimens of *Shaleria vicaryi, Salopina adventita* and *'Camarotoechia' ovalis*; one pedicle valve interior, two brachial valve interiors (incl. Fig. 18) and many exteriors of both valves are preserved on another pebble, BC 6579, with the same associated fauna. The species is thus clearly of Lower Devonian age. The parvicostellae are of more or less equal size and thus the species can be attributed to *Leptostrophia* rather than *Mesoleptostrophia*, using the criteria of Harper & Boucot (1978), although I do not agree with those authors that these relatively minor ornamental changes should command subfamilial recognition in taxonomy.

Superfamily **DAVIDSONIACEA** King
Family **SCHUCHERTELLIDAE** Williams

Genus ***SCHUCHERTELLA*** Girty, 1904

Schuchertella? sp. Figs 23–24

?1870 *Streptorhynchus crenistria* Phillips; Davidson: 87; pl. 5, fig. 26.
?1881 *Orthis hipparionyx*? Vanuxem; Davidson: 347; pl. 39, *non* figs 1a, 1b.
?1881 *Streptorhynchus crenistria*? Phillips; Davidson: 351; pl. 39, fig. 3.

The original of Davidson's *'Streptorhynchus crenistria'* (1870: pl. 5, fig. 26 and 1881: pl. 39, fig. 3), B 20901, is merely a fragment of probable davidsoniacean shell. Whether or not this is conspecific with the other specimens figured here must remain for ever doubtful: it is certainly much larger. The original of Davidson's *'Orthis hipparionyx'* is an internal mould of a broken pedicle valve associated with a specimen of *Mclearnites rouaulti* and so is of early Devonian age; but it is doubtful whether that valve is of the same species as those illustrated here (Figs 23–24). Nevertheless, the brachial valve (Fig. 24) is associated on the same pebble with *Howellella cortazari* and is thus also of early Devonian age. It is undoubtedly a davidsoniacean, and very probably of the same species (it has the same ribbing style and general proportions) as the pedicle valve on another pebble (Fig. 23). The generic identification is more difficult, since early Devonian davidsoniaceans wait to be comprehensively reviewed, and thus the form is identified merely as *Schuchertella*? sp. for the present.

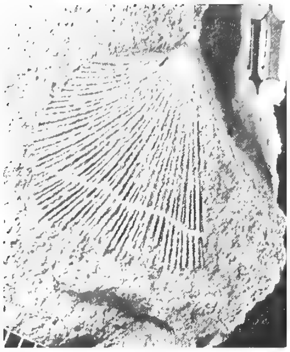
Suborder **CHONETIDINA** Muir-Wood
Superfamily **CHONETACEA** Bronn
Family **ANOPLIIDAE** Muir-Wood

Genus ***ANOPLIA*** Hall & Clarke, 1892

Anoplia sp. Figs 25–28

1870 *Chonetes* sp. Davidson: 87; pl. 6, fig. 13.
1881 *Chonetes* sp.? Davidson; 352; pl. 39, figs 12, 13.

It is unfortunate that the rock in which the specimens of *Anoplia* have been found is a relatively coarse quartzite, so that the finer details of morphology and possible ornamentation are not preserved, otherwise this chonetid would warrant formal description and the creation of a new specific name. There are quite a number of specimens available; eight pedicle valve internal moulds and three brachial valve internal moulds, plus several external moulds on one pebble (including BC 6580–83, Figs 25, 26, 28); twelve pedicle valves and three brachial valves on another (including B 14198, Fig. 27); four pedicle valves and two brachial valves on a third pebble, which also carries the type specimens of *Douvillina edgelliana* of undoubted Frasnian age; and also some other material. The species also co-occurs on pebbles with the large indeterminate uncinuliform (p. 31). This extends the age range of *Anoplia* upwards from the Emsian (Boucot & Harper 1968),



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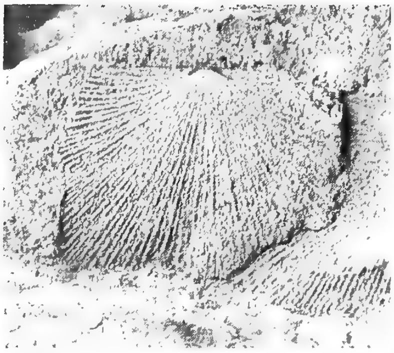

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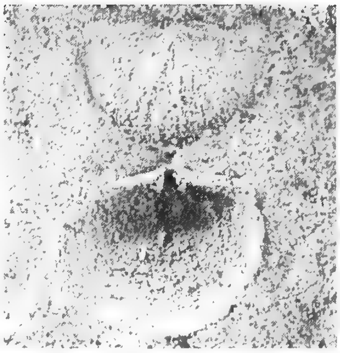

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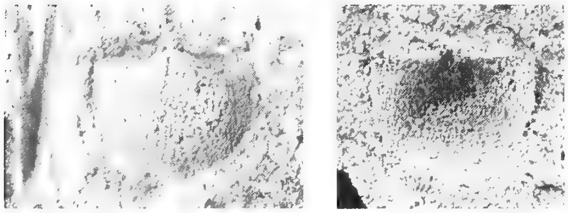

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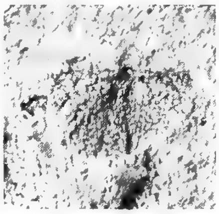

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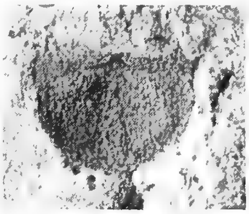

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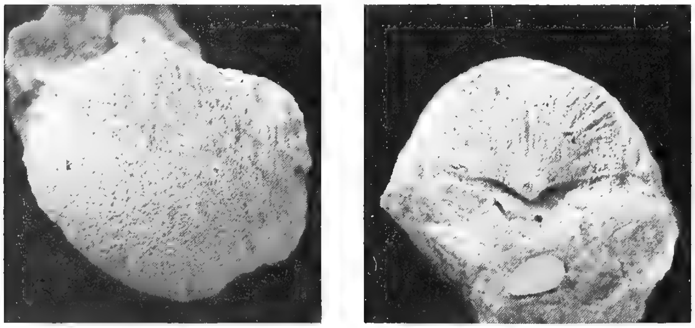

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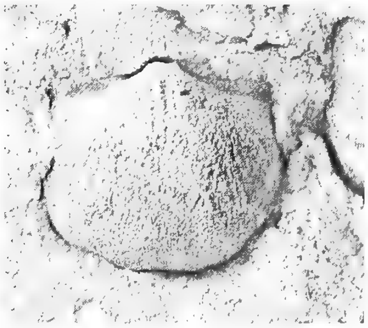

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Figs 23, 24 *Schuchertella*? sp. Fig. 23, B 21604, internal mould of pedicle valve, × 2; Fig. 24, B 21569, internal mould of brachial valve, × 2.

Figs 25–28 *Anoplia* sp. Fig. 25, BC 6580–1, latex casts of internal moulds of brachial valve (above) and pedicle valve, × 4; Fig. 26a, b, BC 6582, internal mould and latex cast of pedicle valve, × 3; Fig. 27, B 14198, internal mould of brachial valve, × 3; Fig. 28, BC 6583, internal mould of brachial valve, × 4.

Figs 29, 30 *Productella vicaryi* (Salter, 1864). Fig. 29a, b, **lectotype** (here selected), B 21550, internal mould of pedicle valve, figured Salter 1864: pl. 17, figs 16a, b, × 2; Fig. 30, B 21725, internal mould of pedicle valve, figured Davidson 1881: pl. 39, fig. 15, × 2.

but there is no doubt of its generic identification: the Budleigh Salterton species is very like the type species, *Anoplia nucleata* (Hall) and compares very well with specimens (e.g. BC 6629) from the Lower Devonian Camden Chert of Tennessee, U.S.A., except that the American species is relatively narrower and the brachial valve median septum is only rarely and weakly developed in the specimens from Budleigh Salterton.

Suborder **PRODUCTIDINA** Waagen
Superfamily **PRODUCTACEA** Gray

Salter (1864) and Davidson (1870) named one productoid species, *vicaryi*, which is reconsidered separately below, but it is probable that there is at least one further productoid present in the Budleigh Salterton pebbles. In particular, a distorted and crushed internal mould of a pedicle valve, B 21723, is not only large (width 37·2 mm, observed length 35·8 mm) but also appears to bear the internal reflection of external ribbing, unlike *Productella vicaryi* which is not ribbed.

Family **PRODUCTELLIDAE** Schuchert & Le Vene
Subfamily **PRODUCTELLINAE** Schuchert & Le Vene

Genus ***PRODUCTELLA*** Hall, 1867

Productella vicaryi (Salter, 1864) Figs 29–30

1864 *Leptaena Vicaryi* Salter: 296; pl. 17, figs 16, 17.
1870 *Productus Vicaryi* (Salter) Davidson: 87; pl. 6, fig. 14.
1881 *Productus Vicaryi* (Salter); Davidson:351; pl. 39, figs 14, 15.

LECTOTYPE (here selected), B 21550, the internal mould of a pedicle valve, the original of Salter 1864: pl. 17, figs 16a, b; W. Vicary Collection, refigured here as Fig. 29. There is no associated fauna on the pebble fragment. Salter also mentioned two brachial valves, one of which he figured, but their present whereabouts is unknown.

Discussion. There are twelve isolated pedicle valves, four isolated brachial valves and one badly damaged pair of conjoined valves (Ex M 4042, Wyatt-Edgell Collection) and some fragments of external moulds that can be attributed to this species. Some, e.g. B 21725 (Fig. 30), are associated on the same pebbles as *Cyrtospirifer verneuilli* and an indeterminate unicinuliform (p. 31), and like them *vicaryi* is thus undoubtedly of late Devonian (Frasnian) age. The species is of variable size, ranging up to Ex M 4042, which is broken, but seen to 34·2 mm in length. Salter's species is attributed here to *Productella* since it is smooth, the spines are scattered over all of the ventral valve exterior (in contrast to *Spinulicosta* Nalivkin in which the spines are largely restricted to the flanks and are associated with incipient ribbing), and the muscle fields in both valves are comparable with the type species, *P. subaculeata* (Murchison) from the Upper Devonian of France. The genus is widespread in Middle and Upper Devonian rocks in Europe, Asia and North America.

Order **RHYNCHONELLIDA** Kuhn

Rhynchonellides are common in the Devonian pebbles from Budleigh Salterton. However, of all the groups, they present the worst problems of identification since sometimes the preservation is poor, many specimens occur by themselves on single rock fragments, and there is a great deal of both homoeomorphy and also taxonomic division among Devonian rhynchonellides. Three of the species named by Davidson are briefly reviewed below, with illustrations of their type specimens, and the common Frasnian form, identified by Davidson as *Rhynchonella inaurita* Sandberger, is also illustrated. However, three other named forms are not properly reviewed, for various reasons as follows:

(a) '*Rhynchonella elliptica* Schnur?' of Davidson (1870: 81; pl. 5, fig. 4 and 1881: 342; pl. 38, figs 22–25). The illustrations consist of four rhynchonellide specimens, one not traced in the Winwood Collection at Bristol and the others still present in the British Museum (Natural History), Sedgwick Museum and British Geological Survey respectively. The missing Winwood specimen is associated with Upper Devonian spiriferides, but the others are all slightly different in aspect and remain indeterminate here, and of uncertain age.

(b) '*Rhynchonella thebaulti* Rouault' of Davidson (*Rhynchonella* sp. of Davidson 1870: 81; pl. 5, figs 5, 6, and *R. Thebaulti* of Davidson 1881: 342; pl. 38, figs 26–29). Again, three out of the four illustrated specimens survive today, but the ages of all are unknown and Davidson's (1881) figs 26 and 27 may represent a different species from his figs 28 and 29, to judge by the number of ribs on the fold; the specimens remain indeterminate here.

(c) '*Rhynchonella*' *winwoodiana* Davidson (1881: 340; pl. 38, fig. 19). Only a single specimen ever existed and this has not been traced in the Winwood Collection at Bristol City Museum. It was associated on a pebble with two enteletacean pedicle valves which Davidson termed *Orthis hamoni* Rouault: it is not clear whether this block was of Upper or Lower Devonian age, and, at least until the specimen again comes to light, *winwoodiana* must remain a *nomen dubium*.

Superfamily **RHYNCHONELLACEA** Gray

Genus ***CAMAROTOECHIA*** Hall & Clarke, 1893

'Camarotoechia' valpyana (Davidson, 1870) Fig. 33

1870 *Rhynchonella Valpyana* Davidson: 82; pl. 4, figs 26, 27.
1881 *Rhynchonella Valpyana* Davidson; Davidson: 343; pl. 38, figs 33, 34.

Lectotype (here selected), B 20984, the internal mould of conjoined valves, the original of Davidson 1870: pl. 4, fig. 26 and Davidson 1881: pl. 38, fig. 33; R.H. Valpy collection, figured here as Fig. 33.

Discussion. This small rhynchonellid is relatively rare, but, although the lectotype is a detached specimen and therefore intrinsically difficult to date, the species is to be found occasionally on slabs of late Devonian age. Its true generic attribution is uncertain, but it is referred here to '*Camarotoechia*' rather than '*Rhynchonella*'.

'Camarotoechia' ovalis (Davidson, 1870) Figs 34–35

1870 *Rhynchonella? ovalis* Davidson: 82; pl. 4, figs 24, 25.
1881 *Rhynchonella? ovalis* Davidson; Davidson: 344; pl. 38, figs 36, 37.

Lectotype (here selected), B 16359, internal mould of a brachial valve, the original of Davidson 1870: pl. 4, fig. 25 and also Davidson 1881: pl. 38, fig. 37; W. Vicary collection, refigured here as Fig. 34.

Discussion. This species is of Lower Devonian age, and occurs on slabs (e.g. BC 6578) together with *Salopina adventita* sp. nov. (p. 24) and *Leptostrophia etheridgii*. It has approximately 20 ribs and is without a strong fold or sulcus. Its true generic attribution is uncertain, although some features seem similar to *Cydimia* from the Lower Devonian of New South Wales (Chatterton 1973).

Genus ***KATUNIA*** Kulkov, 1963

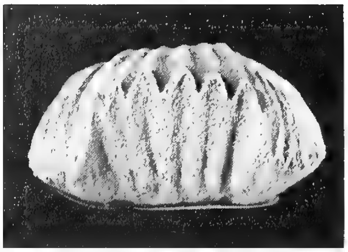
Katunia? vicaryi (Davidson, 1870) Figs 9, 36–38

1870 *Rhynchonella Vicaryi* Davidson: 82; pl. 7, figs 7, 8.
1881 *Rhynchonella Vicaryi* Davidson; Davidson: 343; pl. 38, figs 30, 31.

Lectotype (here selected), BB 70884, the internal mould of a pedicle valve, the original of Davidson, 1870: pl. 5, fig. 8, also Davidson, 1881: pl. 38, fig. 31; W. Vicary collection, figured here as Fig. 36.

Discussion. This species occurs commonly on the same slabs as *Salopina adventita* sp. nov. (e.g. Fig. 9), and is of Lower Devonian (Lockhovian–Pragian) age. It is referred with some hesitation to *Katunia*, whose type species comes from the Lower Devonian of the Altai Mountains, U.S.S.R.


31a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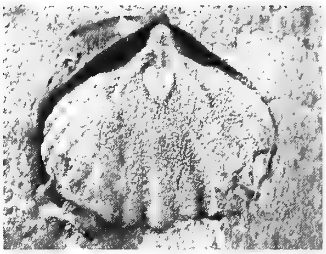
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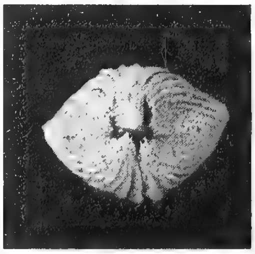
33a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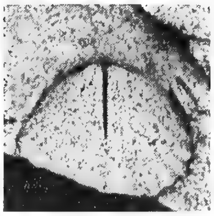
33c


33d


34a


34b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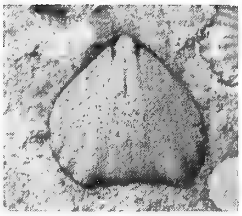
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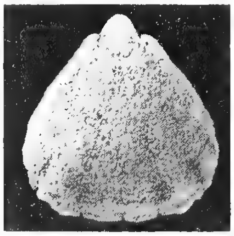
37a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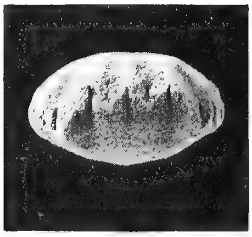
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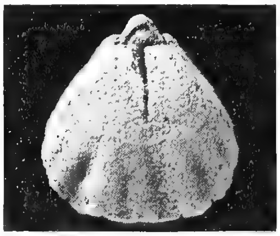
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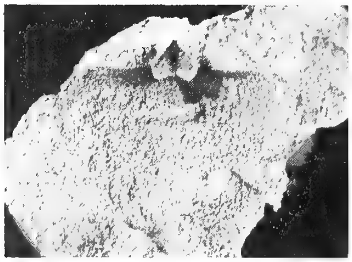
38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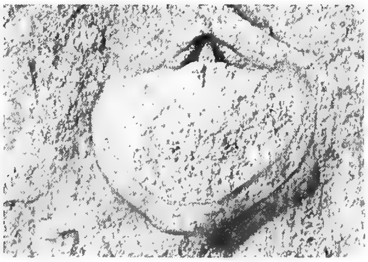

39b

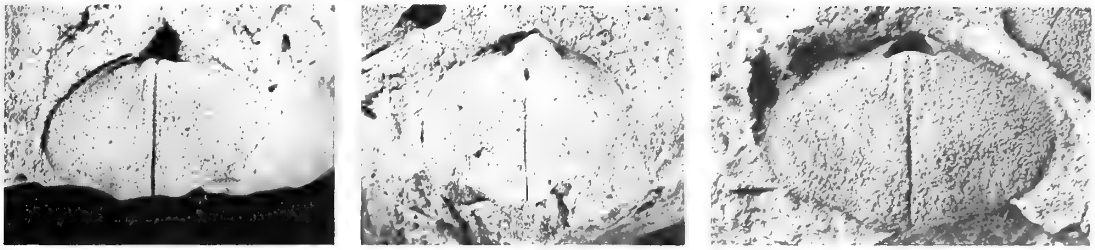
Figs 31, 32 Uncinuliform gen. et sp. indet. Fig. 31a, b, BC 6252, internal mould of conjoined valves, figured Davidson 1881: pl. 38, figs 35, 35a as *Rhynchonella inaurita*, × 2; Fig. 32, BC 21528, internal mould of pedicle valve, figured Davidson 1870: pl. 5, fig. 3 as *Rhynchonella inaurita*, × 1·5.

Fig. 33 '*Camarotoechia*' *valpyana* (Davidson, 1870). a–d, **lectotype** (here selected), B 20984, lateral, anterior, ventral and dorsal views of internal mould of conjoined valves, figured Davidson 1870: pl. 14, fig. 26, × 3.

Figs 34, 35 '*Camarotoechia*' *ovalis* (Davidson, 1870). Fig. 34a, b, **lectotype** (here selected), B 16359, internal mould of brachial valve, figured Davidson 1870: pl. 4, fig. 25, × 3; Fig. 35, BC 6578, internal mould of brachial valve, × 4.

Figs 36–38 *Katunia? vicaryi* (Davidson, 1870). Fig. 36, **lectotype** (here selected), BB 70884, internal mould of pedicle valve, figured Davidson 1870: pl. 5, fig. 8, × 2; Fig. 37a–d, B 21530, lateral, ventral, posterior and dorsal views of the internal mould of conjoined valves, × 3; Fig. 38, B 21641, latex cast of external mould of brachial valve, × 3.

Fig. 39 *Athyris? incerta* Davidson, 1870. a, b, **lectotype** (here selected), B 21711, latex cast and internal mould of a brachial valve, figured Davidson 1870: pl. 4, fig. 12, × 2.



Figs 40–42 *Nucleospira vicaryi* Davidson, 1870. Fig. 40, BC 6584, internal mould of brachial valve, × 1·5; Fig. 41, B 21716, internal mould of pedicle valve, × 1·5; Fig. 42, **lectotype** (here selected), B 21549, internal mould of brachial valve, figured Davidson 1870: pl. 4, figs 16, 17, × 2.

Indeterminate genus

Uncinuliform species, indet. Figs 31–32

1864 *Rhynchonella* sp. Salter: 296; pl. 17, fig. 15, ?fig. 14.
1870 *Rhynchonella inaurita* (Sandberger); Davidson: 80; pl. 5, figs 1–3.
1881 *Rhynchonella inaurita* Sandberger?; Davidson: 341; pl. 38, figs 35, 35a, b, ?fig. 21.

This is the most common rhynchonellide in the entire Budleigh Salterton fauna, with more than a hundred specimens in the British Museum (Natural History) and many more in other museums. It is undoubtedly of late Devonian age, since it often occurs on the same pebbles as *Cyrtospirifer verneuili*. Davidson referred the form to *Rhynchonella inaurita* Sandberger, apparently with confidence in 1870 but with a query in 1881. I consider the query more than justified, partly because Sandberger & Sandberger's species (1855) is recorded from an enormous range of horizons and localities from within the German Devonian, and partly because the only specimen which they figured (1855: pl. 33, fig. 5) has dental plates, which the Budleigh Salterton species lacks, and also has a much more exaggerated fold and sinus. The form is tentatively identified as an uncinulid here, but is not *Uncinulus* itself since the ribbing style at the commissure is different.

Order **ATRYPIDA** Moore
Superfamily **ATHYRIDACEA** M^{c}Coy
Family **ATHYRIDAE** M^{c}Coy

Genus ***ATHYRIS*** M^{c}Coy, 1844

Athyris? incerta Davidson, 1870 Fig. 39

1870 *Athyris incerta* Davidson: 80; pl. 4, fig. 12.
1881 *Athyris incerta* Davidson; Davidson: 338; pl. 38, fig. 5.

LECTOTYPE (here selected), B 21711, the original of Davidson, 1870: pl. 4, fig. 12, the internal mould of a brachial valve; W. Vicary collection, refigured here as Fig. 39.

DISCUSSION. Only one pebble containing *Athyris? incerta* is known, and it contains two well preserved brachial valves (including the lectotype), and one poorly preserved pedicle valve of *incerta* and a rather poorly preserved enteletacean which, however, can be identified as *Platyorthis monnieri*, thus putting the age of the athyrid as Lower Devonian. The generic attribution is uncertain: the type species of *Athyris* is *Terebratula concentrica* von Buch, which needs revision but which comes from the mid-Devonian of the Eifel region, Germany. The hinge plates of *incerta* are certainly of athyrid type, but not enough is known of the rest of the morphology to do otherwise than place it into *Athyris*?. Boucot *et al.* (1964: 819) show *Athyris* itself to range from the Siegenian to the Permian, and thus *incerta* would be among the earliest possibly attributable species, but the whole plexus requires both generic and specific re-evaluation.

Family **NUCLEOSPIRIDAE** Davidson

Genus ***NUCLEOSPIRA*** Hall, 1859

Nucleospira vicaryi Davidson, 1870 Figs 40–42, ?Fig. 51

1870 *Nucleospira Vicaryi* Davidson: 79; pl. 4, figs 15–18.
1881 *Nucleospira Vicaryi* Davidson; Davidson: 355; pl. 40, figs 29–31.
?1972 *Nucleospira* sp. Renouf: 122; pl. 26, fig. 10.

LECTOTYPE (here selected), B 21549, the internal mould of a brachial valve, the original of Davidson, 1870: pl. 4, figs 15 (upper right), 16 and 17, and also Davidson, 1881: pl. 40, figs 30 (upper left) and 31; W. Vicary collection, refigured here as Fig. 42.

DISCUSSION. The species is certainly of Lower Devonian age since pebble B 21714 contains both it and also *Salopina adventita* sp. nov. described on p. 24. It has the characteristic median septa in both pedicle and brachial valves and thus Davidson's original generic assignment is still valid.

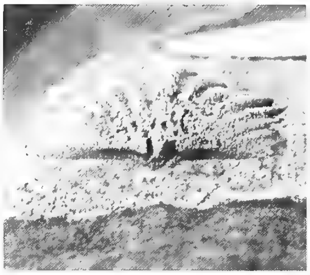
Order **SPIRIFERIDA** Waagen
Superfamily **SPIRIFERACEA** Waagen
Family **DELTHYRIDAE** Waagen
Subfamily **ACROSPIRIFERINAE** Termier & Termier

Genus ***HOWELLELLA*** Kozlowski, 1929

Howellella cortazari Carls, 1969 Figs 43a, b

1870 *Spirifera octoplicata* Sowerby?; Davidson: 79; pl. 4, fig. 23.
1881 *Spiriferina octoplicata* Sowerby; Davidson: 340; pl. 38, figs 7, 8.
1969 *Howellella cortazari* Carls: 343; pl. 4, figs 21–22.
1972 *Howellella* cf. *mercurii* (Gosselet); Renouf: 122; pl. 25, figs 7–9; pl. 26, fig. 1.
1985 *Howellella cortazari* Carls; Gourvennec: 158; pl. 2, figs 10–24.


43a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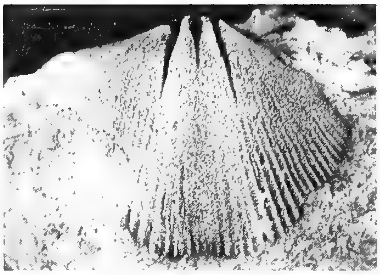
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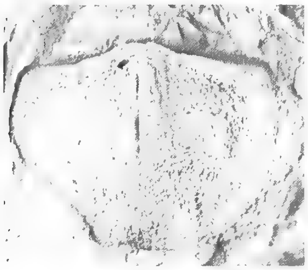
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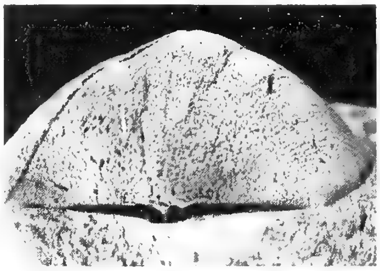
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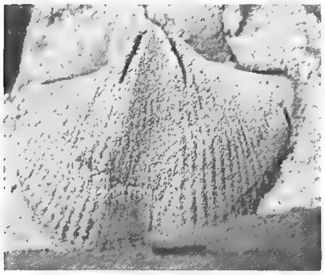
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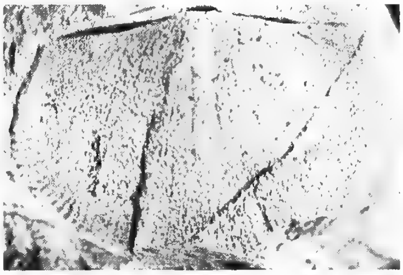
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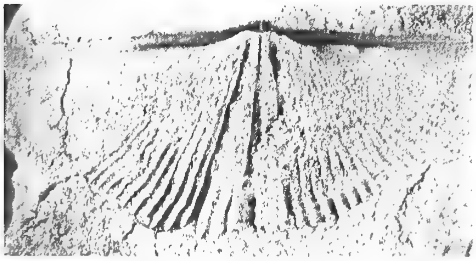
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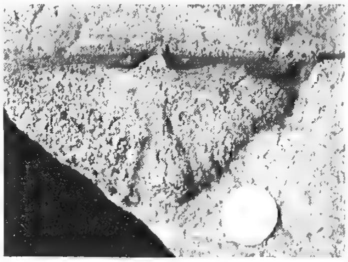
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Fig. 43 *Howellella cortazari* Carls, 1969. a, b, BB 70944, dorsal and posterior views of internal mould of brachial valve, × 3.

Figs 44–47 *Cyrtospirifer verneuili* (Murchison, 1840). Fig. 44, B 21542, internal mould of pedicle valve, × 1·5: fig. 45a, b, B 21521, dorsal and posterior views of internal mould of brachial valve, figured Salter 1864: pl. 17, fig. 11 as *Spirifer antiquissimus* (of which it is the **lectotype**, here selected), × 1·5; Fig. 46a–c, B 24470, posterior, lateral and dorsal views of brachial valve, × 1·5; Fig. 47, B 21526, internal mould of pedicle valve, figured Davidson 1870: pl. 4, fig. 20 (lower), × 2.

Figs 48–50 *Cyrtospirifer? micropterus* (Davidson, 1870). Fig. 48, BC 6090, internal mould of brachial valve, × 1·5; Fig. 49, B 21527, internal mould of central part of pedicle valve showing muscle field, the original of Davidson 1870: pl. 4, fig. 21, × 1·5; Fig. 50, **lectotype** (here selected), BB 70886, internal mould of brachial valve, figured Davidson 1870: pl. 4, fig. 22, × 2.

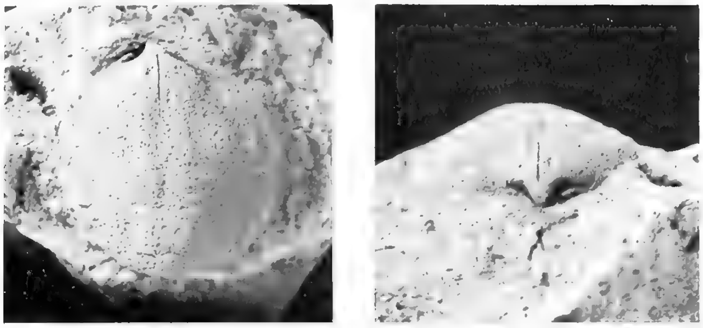
Gourvennec (1985) has revised Lower Devonian *Howellella* and concluded that the species are best differentiated both by the absolute size and by the numbers of costae. The Budleigh Salterton form never exceeds 13 mm in width (n=10) and has 6–9 costae per flank, indicating in Gourvennec's terms a transition between the large form of *H. mercurii* and *H. cortazari*. Since the type of *mercurii* is the smaller form (with type specimen from the Lower Gedinnian Mondrepuits Formation of the Ardennes), the Budleigh Salterton species is identified as *H. cortazari*, whose types come from the Lower Gedinnian Nogueras Formation of Aragon, Spain (Carls 1969).

Family **CYRTOSPIRIFERIDAE** Termier & Termier

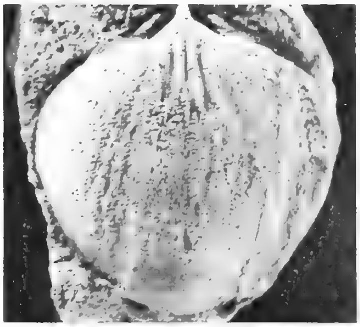
Genus ***CYRTOSPIRIFER*** Nalivkin, 1919

Cyrtospirifer verneuili (Murchison, 1840) Figs 44–47

1840 *Spirifer Verneuili* Murchison: 252; pl. 2, figs 3a–e.



51a 51b



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54a 54b 54c

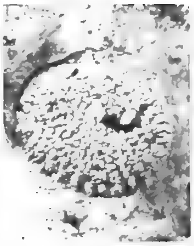

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Fig. 51 ?*Nucleospira vicaryi* Davidson, 1870. a, b, BC 6585, dorsal and posterior views of small brachial valve, × 3.
Fig. 52 *Cryptonella*? sp. BC 6435, internal mould of brachial valve, × 1·5.
Fig. 53 *Cryptonella*? cf. *rhenana* (Drevermann, 1902). B 21712, internal mould of small brachial valve, × 3.
Fig. 54 *Mutationella? erratica* (Davidson, 1870). a–c, Holotype, B 21543, dorsal, lateral and ventral view of internal mould of conjoined valves, × 3.
Fig. 55 *Mutationella* aff. *barroisi* (Asselberghs, 1930). B 20896, internal mould of brachial valve, × 3.

1864 *Spirifer antiquissimus* Salter: 295; pl. 17, figs 10–12.
1864 *Spirifer Davidis* Rouault?; Salter: 296; pl. 17, fig. 13.
1870 *Spirifera Verneuilii* (Murchison) Davidson: 78; pl. 4, figs 19–20
1881 *Spirifera Verneuilii* (Murchison); Davidson: 339; pl. 38, figs 9–14.
1882 *Spirifera verneuilii* (Murchison); Davidson: 35, ?pl. 2, fig. 1.
1942 *Spirifer (Cyrtospirifer) Verneuili* Murchison; Paeckelmann: 23; pl. 13, figs 2, 3.
1959 *Cyrtospirifer verneuili* (Murchison) Vandercammen: 114; pl. 4, figs 1–6.

LECTOTYPE of *antiquissimus* (here selected), B 21521, the internal mould of a brachial valve, the original of Salter, 1864: pl. 17, fig. 11; W. Vicary collection, refigured here as Fig. 45.

DISCUSSION. Murchison (1840) described *Spirifer verneuili* from the Ferques area in northern France from rocks of Upper Frasnian age (Wallace 1969). Davidson (1881, 1882) carefully compared the Budleigh Salterton specimens with the French forms, and came to the conclusion that they were conspecific. When Salter (1864) described *Spirifer antiquissimus*, he considered that all the Budleigh Salterton fauna was of Ordovician age and thus did not think to compare it directly with the French form from the late Devonian. *Cyrtospirifer* has been revised in a substantial monograph by Vandercammen (1959), who distinguished fifteen species of the genus and presented many measurements on a substantial number of specimens; however, these were almost entirely from Belgium, and Vandercammen did not revise any topotype specimens of *verneuili* from Ferques or discuss Murchison's original types except as they were illustrated. Paeckelmann (1942: pl. 3, fig. 2) had figured a young specimen from Ferques, but his systematics in general were discarded by Vandercammen. The whole species group, which occurs in great abundance in the late Devonian of Europe and possibly also elsewhere, is clearly rather complicated and its revision is outside the scope of this paper. Nevertheless, it is worth recording here that there are 11 specimens (registered B 19163–6) all from the 'Boulonnais' area, France (which includes the Ferques inlier), which were collected by Bouchard and were transferred from the Museum of Practical Geology to the British Museum (Natural History) with the rest of its foreign collections in 1905; these probably include at least some of the original specimens used by Murchison in 1840, although Murchison's figures appear rather generalized. Should the Budleigh Salterton form prove distinct from the true Ferques *verneuili*, then Salter's name *antiquissimus* would need to be revived.

Cyrtospirifer? micropterus (Davidson, 1870) Figs 48–50

1870 *Spirifera macroptera* Goldfuss? var. *microptera* Davidson: 79; pl. 4, figs 21, 22.
1881 *Spirifera speciosa* Schlotheim; Davidson: 340; pl. 38, figs 15–18.

LECTOTYPE of *micropterus* (here selected), BB 70886, the internal mould of a brachial valve, the original of Davidson, 1870: pl. 4, fig. 22 (not fig 22a); also figured by Davidson, 1881: pl. 38, fig. 15; W. Vicary collection, refigured here as Fig. 50.

DISCUSSION. Since Davidson's time more than one form of general cyrtospiriferid type has been identified from Budleigh

Salterton pebbles, but Davidson himself changed his mind on the identification. There do appear to be several specimens, including the type specimens of Davidson's variety *microptera*, which are relatively wider than the great bulk of *C. verneuili* specimens described above, and which are provisionally kept distinct here. The ventral interiors also seem different: the *microptera* specimens have a much weaker or even absent median septum, and relatively shorter dental plates; however, these features may be accentuated by the poor preservation (relatively coarse quartzite) of the *microptera* types.

Order **TEREBRATULIDA** Waagen

Occasional terebratulide specimens are found very rarely in Budleigh Salterton pebbles; Davidson (1870, 1881) illustrated some under the name *Terebratula sacculus* Martin and another single specimen under the new name of *Athyris? erratica*. The last specimen, since it was formally named by Davidson, is considered separately below, but the others consist simply of four separate specimens, none of which are worth full description. These are: BC 6435, a large (28·5 mm long) specimen with no ornament, found in the same pebble as late Devonian spiriferids and productids, and uncertainly identified as *Cryptonella?* sp. (Fig. 52); B 21712, a small (6·9 mm long) specimen (Fig. 53) which Dr A. J. Boucot has suggested may be identified as *Cryptonella?* cf. *rhenana* (Drevermann, 1902) of early Devonian age (although there are no internal age criteria from associated specimens); B 20896 (Fig. 55), another small specimen (4·9 mm long), associated with *Platyorthis monnieri* and therefore of definite early Devonian age, and which is very close to *Mutationella barroisi* (Asselberghs, 1930) as illustrated by Boucot (1960) from the Gedinnian of the Ardennes; and finally B 1759, not illustrated here, which is merely the external mould of a smooth pair of conjoined valves of general terebratuloid aspect, without associated fauna and thus of uncertain age; it is the original of Davidson, 1881: pl. 38, fig. 1.

Suborder **CENTRONELLIDINA** Stehli
Superfamily **STRINGOCEPHALACEA** King
Family **MUTATIONELLIDAE** Cloud

Genus ***MUTATIONELLA*** Kozlowski, 1929

Mutationella? erratica (Davidson, 1870) Fig. 54

1870 *Athyris? erratica* Davidson: 80; pl. 4, fig. 13.
1881 *Terebratula sacculus* Martin; Davidson: 337 (*pars*); pl. 38, fig. 3, ?fig. 2, *non* fig. 1.
1881 *Athyris? erratica* Davidson; Davidson: 338; pl. 38, fig. 4.
?1960 *Podolella* sp.; Boucot: 320.

HOLOTYPE (by monotypy).' ... The internal cast of one specimen was found by Mr Vicary' (Davidson 1870: 80), B 21543, the original of Davidson, 1870: pl. 4, fig. 13, the conjoined internal mould of both valves; W. Vicary Collection, refigured here as Fig. 54.

DISCUSSION. Davidson (1881: pl. 38, fig. 4a) is inaccurate in showing relatively strong ribs on the figured specimen; the internal mould has only faint ribs near the anterior margin. If the exterior were smooth, then the species would be assigned to *Podolella*; however, the faint ribs make an attribution to *Mutationella* rather more likely. Davidson obviously misinterpreted his own drawings when he later came to write the monograph (1881), since he in fact illustrated the same specimen (B 21543) under both *Terebratula sacculus* (pl. 38, fig. 3) and also *Athyris? erratica* (pl. 38, fig. 4), one drawing with and the other without ribs. The true *sacculus* is a Viséan form (Brunton 1982).

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APPENDIX — REVISED PLATE DESCRIPTIONS FOR DAVIDSON'S MONOGRAPH

In a previous work (1978), I presented revised plate descriptions for Davidson's 'Silurian' Monograph (1886–71) and its supplement (1882–83), which included all of the Lower Palaeozoic (and a very few Upper Palaeozoic) brachiopods dealt with by Thomas Davidson in his grand monograph, apart from those from Budleigh Salterton. These latter were not included partly because they formed a separate part of the Davidson monograph (1881) in which Lower and Upper Palaeozoic forms were mixed and partly because at the time of writing the 1978 work, the Budleigh Salterton species were badly in need of both taxonomic and stratigraphical revision. Since the latter has now been accomplished by Cocks & Lockley (1981) for the Ordovician species and in the present paper for the Devonian species, the opportunity is now taken to give revised plate descriptions for Davidson's 1881 Budleigh Salterton Monograph in a similar style to that of Cocks (1978). Because there is only a single plate (Davidson 1881: pl. 42) of Cornish species, these are also included, largely following the revision of Bassett (1981). Davidson's name for the species (transcribed exactly from his plate descriptions and thus often incorrect by modern standards in the use of brackets, abbreviations etc.) is set in *italic;* the modern identification of the specimens which Davidson drew is shown below in **bold** or ***bold italic***. A specimen number has been given where possible: where the specimen has not been traced the symbol 'nt' is used. In each case the Davidson Notebooks have been consulted to check the geological locality and original owner of the specimen, and corrections to the locality or collector or age as printed have been placed in square brackets.

PLATE XXXVIII

FIGS

1 *Terebratula sacculus*, Martin, sp.

indeterminate terebratulide

1, B 1759; Linford Collection. (Devonian, uncertain age), Budleigh Salterton.

2, 3 *Terebratula sacculus*, Martin, sp.
Mutationella? erratica (Davidson, 1870)
2, ?B 21543; Vicary Collection. 3, 3a, B 21543; Vicary Collection. (Probable Lower Devonian age), Budleigh Salterton.

4 *Athyris? erratica*, Dav.
Mutationella? erratica (Davidson, 1870)
4, 4a, B 21543; Vicary Collection. (Probable Lower Devonian age), Budleigh Salterton.

5 *Athyris incerta*, Dav. ***Athyris? incerta*** Davidson, 1870
5, 5a, B 21711 (Davidson errs in stating 'one specimen only' – there are two brachial valves and one pedicle valve on the slab), Vicary Collection. (Lower Devonian), Budleigh Salterton.

6 *Athyris Budleighensis*, Dav.
Rhipidomella? budleighensis (Davidson, 1870)
6, B 21512; Vicary Collection. (Upper Devonian), Budleigh Salterton.

7, 8 *Spiriferina octoplicata*, Sow.
Howellella cortazari Carls, 1969
7, BB 70944; Vicary Collection. 8, nt; Winwood Collection. (Lower Devonian), Budleigh Salterton.

9–14 *Spirifer Verneuilii*, Murch. = *disjunctus*, Phillips
Cyrtospirifer verneuili (Murchison, 1840)
9, BC 6253; T. Davidson Collection *ex* Vicary. 10, nt, Linford Collection. 11, BC 6254; T. Davidson Collection *ex* Vicary. 12, GSM 13617; Vicary Collection. 13, B 21526; Vicary Collection. 14, nt, Exeter Museum. All (Upper) Devonian, Budleigh Salterton.

15–18 *Spirifera speciosa*, Schlothe(i)m
Cyrtospirifer? micropterus (Davidson, 1870)
15, BB 70886; Vicary Collection. 16, B 21527; Vicary Collection. 17, BB 70887; Vicary Collection. 18, B 21574; Vicary Collection. (Upper) Devonian, Budleigh Salterton.

19 *Rhynchonella Winwoodiana*, Dav.
'Rhynchonella' winwoodiana Davidson, 1870
19, nt; Winwood Collection. (Probably Upper) Devonian, Budleigh Salterton.

20 *Orthis Hamoni*, Rouault **indeterminate enteletacean**
20, nt; Winwood collection, same pebble as Fig. 19. (Probably Upper) Devonian, Budleigh Salterton.

21 *Rhynchonella?* perhaps *Rh. inaurita?*
indeterminate rhynchonellide
21, GSM 13905; Winwood Collection. Devonian, Budleigh Salterton.

22–25 *Rhynchonella elliptica*, Schnur?
indeterminate rhynchonellides
22, nt; Winwood Collection. 23, SM X 1352; Wyatt-Edgell Collection. 24, B 21649; Vicary Collection. 25, GSM 13878; Vicary Collection. (Upper) Devonian, Budleigh Salterton.

26–29 *Rhynchonella Thebaulti*, Rouault
indeterminate rhynchonellides
26, B 20883; Valpy Collection. 27, nt; Valpy Collection. 28, GSM 13907; Wyatt-Edgell Collection. 29, GSM 13908; Wyatt-Edgell Collection. (Probably Upper) Devonian, Budleigh Salterton.

30, 31 *Rhynchonella Vicaryi*, Dav.
Katunia? vicaryi (Davidson, 1870)
30, BB 70883; Vicary Collection. 31, BB 70884; Vicary Collection. (Lower) Devonian, Budleigh Salterton.

32 *Rhynchonella*? Dav. **indeterminate rhynchonellide**
32, nt (notebook clearly states Winwood Collection, rather than Museum of Practical Geology as printed). Devonian, Budleigh Salterton.

33, 34 *Rhynchonella Valpyana*, Dav.
'Camarotoechia' valpyana (Davidson, 1870)
33, B 20984; Valpy Collection. 34, B 21644; Vicary Collection. (Upper) Devonian, Budleigh Salterton.

35 *Rhynchonella inaurita*, Sanb.?
uncinuliform gen. et sp. indet.
35, 35a, BC 6252; Vicary Collection. 35b, B 21528; Vicary Collection. (Upper) Devonian, Budleigh Salterton.

36, 37 *Rhynchonella ovalis*, Dav.
'Camarotoechia' ovalis (Davidson, 1870)
36, 36a, B 20975; Valpy Collection. 37, 37a, B 16359; Vicary Collection. (Lower) Devonian, Budleigh Salterton.

PLATE XXXIX

FIGS

1 *Orthis? hipparionyx*? ***Schuchertella?*** sp.
1, GSM 13509; Wyatt-Edgell Collection. (Lower) Devonian, Budleigh Salterton.

1 *Strophomena*, sp. ***Mclearnites rouaulti*** (Davidson, 1870)
1a, 1b (1a is the counterpart of 1b), GSM 13508; Wyatt-Edgell Collection (same slab as *Orthis? hipparionyx*? above). (Lower) Devonian, Budleigh Salterton.

2 *Strophomena*? sp.
Leptostrophia etheridgii (Davidson, 1870)
2, 2a, GSM 13904. (Lower) Devonian, Budleigh Salterton.

3 *Streptorhynchus crenistria*, Phillips
indeterminate davidsoniacean
3, B 20901; 'Vicary' Collection (should be Valpy). (Probably Lower) Devonian, Budleigh Salterton.

4 *Strophomena Budleighensis*, Dav.
Douvillina? budleighensis (Davidson, 1870)
4, 4a, 4b, B 21538; Vicary Collection. (Upper) Devonian, Budleigh Salterton.

5–7 *Strophomena Edgelliana*, Dav.
Douvillina edgelliana (Davidson, 1870)
5, B 21535; Vicary Collection. 6, 7, 7a, B 21534, lectotype; Vicary Collection. 7b, B 21541; Vicary Collection. (Upper) Devonian, Budleigh Salterton.

8 *Strophomena Vicaryi*, Dav.
Shaleria vicaryi (Davidson, 1870)
8a, 8b, 8c, 8d, B 21537, lectotype; Vicary Collection. (Lower) Devonian, Budleigh Salterton.

9 *Strophomena Rouaulti*, Dav.
Mclearnites rouaulti (Davidson, 1870)
9a, 9b, 9c, B 21540, lectotype; Vicary Collection. (Lower) Devonian, Budleigh Salterton.

10, 11 *Strophomena Etheridgii*, Dav.
Leptostrophia etheridgii (Davidson, 1870)
10, 10a, B 21539, lectotype; Vicary Collection. 11, BC 6087 (on same slab as lectotype); Vicary Collection. (Lower) Devonian, Budleigh Salterton.

12, 13 *Chonetes*, sp. ***Anoplia*** sp.
12, 13, nt; Davidson Collection *ex* Wyatt-Edgell. 13a, B 21546; Vicary Collection. (Upper) Devonian, Budleigh Salterton.

14, 15 *Productus Vicaryi*, Salter, sp.
Productella vicaryi (Salter, 1864)
14, B 14007; Davidson Collection *ex* Vicary. 15, B 21725; Vicary Collection. (Upper) Devonian, Budleigh Salterton.

PLATE XL

FIGS

1–8 *Orthis Monnieri*, Rouault.
Platyorthis monnieri (Rouault, 1851)
1a, 1b, 8 (left), B 20940 (the lectotype of *vicaryi*); Valpy Collection. 2, nt; Winwood Collection. 3, nt; Winwood Collection. 4, nt; Winwood Collection. 5, BC 6251; Valpy Collection (the same slab as Fig. 1). 6, nt; Winwood Collection. 7, reconstruction not based on specific specimens. 8 (right), B 13283; Davidson Collection *ex* Vicary. (Lower) Devonian, Budleigh Salterton.

9, 10 *Crania transversa*, Dav.
Petrocrania transversa (Davidson, 1870)
9, B 16360; Vicary Collection. 10, B 21544, lectotype; Vicary Collection. (Upper) Devonian, Budleigh Salterton.

11–13 *Discina Vicaryi*, Dav.
Philhedrella? vicaryi (Davidson, 1866)
11, B 21510, lectotype; Vicary Collection. 12, B 21584; Vicary Collection. 13, B 21491; Vicary Collection. (Probable Arenig age), Figs 11 and 12 from Budleigh Salterton, Fig. 13 from a pebble on Chesil Bank, Dorset.

14, 15 *Discina incerta*, Dav.
Philhedrella? incerta (Davidson, 1870)
14, B 21545, lectotype; Vicary Collection. 15, B 21580; Vicary Collection. (Ordovician or) Devonian, Budleigh Salterton.

16–20 *Lingula Lesueuri*, Rouault
Ectenoglossa lesueuri (Rouault, 1850)
16, B 21498; Vicary Collection. 17, SM X 1353; Vicary Collection. 18, nt; Winwood Collection. 19, SM X 1354; F.T.S. Houghton Collection. 20, Ex. M: F 2003; ‘purchased from a stonebreaker 1870’. (All Arenig), Fig. 19 from the glacial Drift of Ladypool Lane, near Birmingham, the remainder from Budleigh Salterton.

21 *Lingula Hawkei*, Rouault
Lingulobolus hawkei (Rouault, 1850)
21, Ex M: F 6066; T.B. Lear Collection. (Arenig), Woodbury Common [south-east of Exeter, Devon].

22, 23 *Dinobolus Brimonti*, Rouault, sp.
Lingulobolus brimonti (Rouault, 1850)
22, B 14321; Davidson Collection *ex* Vicary. 23, GSM 16629; Vicary Collection. (Arenig), Budleigh Salterton.

24 *Lingula? Salteri*, Dav.
Pseudobolus? salteri (Davidson, 1866)
24, B 14480; Davidson Collection *ex* Vicary. (Arenig), Budleigh Salterton.

25, 26 *Lingula Morierei*, Tromelin
‘Lingula’ morierei Tromelin, 1876
25, B 21581; Vicary Collection. 26, B 21583; Vicary Collection. (Arenig), Budleigh Salterton.

27 *Lingula*? ***?Lingulobolus hawkei*** (Rouault, 1850)
27, GSM 16628; Vicary Collection. (Arenig), Budleigh Salterton.

28 ? **?young specimen of *Lingulobolus brimonti*** (Rouault, 1850)
28, B 21578; Vicary Collection. (Arenig), Budleigh Salterton.

29–31 *Nucleospira Vicaryi*, Dav.
Nucleospira vicaryi Davidson, 1870
29, 30, reconstructed from B 7890 and B 21549; Vicary Collection. 31, B 21549; Vicary Collection. (Lower Devonian), Budleigh Salterton.

PLATE XLI

FIGS

1–9 *Orthis Bertho(i)si*, var. *erratica*, Dav.
Corineorthis erratica (Davidson, 1869)
1, nt; Winwood Collection: 2, nt; Winwood Collection. 3, BRSMG Cc 766.1; Winwood Collection. 4, GSM 13472; Vicary Collection. 5, BRSMG Cc 766.2; Winwood Collection. 6, B 20936; Valpy Collection. 7, GSM 13476; Winwood Collection. 8, GSM 5489. 9, GSM 13471, Wyatt-Edgell Collection. (Llandeilo), Budleigh Salterton.

10, 11 *Orthis pulvinata*, Salter, sp.
Salopia? pulvinata (Salter, 1864)
10, 11, B 21523, lectotype; Vicary Collection. (Llandeilo), Budleigh Salterton.

12–20 *Orthis Budleighensis*, Dav.
Tafilaltia valpyana (Davidson, 1869)
12, B 21616, including (centre left) the lectotype of *budleighensis*; Vicary Collection. 13, nt; Winwood Collection. 14, nt; Winwood Collection. 15, reconstructed from B 21611 and B 21626; Vicary Collection. 16, GSM 13480; Vicary Collection. 17, GSM 13496; Wyatt-Edgell Collection. 18, ?GSM 13483; Wyatt-Edgell Collection. 19, GSM 13496a; Winwood Collection. 20, nt in Cambridge. (Llandeilo), Budleigh Salterton.

21, 22 *Orthis Valpyana*, Dav.
Tafilaltia valpyana (Davidson, 1869)
21, reconstructed from B 21533 and B 21524; Vicary Collection. 22, B 21533; Vicary Collection. (Llandeilo), Budleigh Salterton.

23 *Terebratula?* sp.
monoplacophoran, perhaps *Vallatotheca* sp.
23, B 21531; Vicary Collection. (Llandeilo), Budleigh Salterton.

PLATE XLII

FIGS

1–6 *Strophomena grandis*, Sow.
Corineorthis cornubiensis (Davidson, 1881)
1, RGSC 633; Peach Collection. 2, nt RGSC but Davidson cast within B 13657; Peach Collection. 3, nt RGSC, but Davidson cast within B 13657; Peach Collection. 4, composite reconstruction from Peach Collection specimens. 5, nt RGSC but Davidson cast within B 13657; Peach Collection. 6, nt RGSC; Peach Collection. (Llandeilo), Carn (Rocks), Gorran (Haven), Cornwall.

7–10 *Orthis calligramma*, var.
Schalidomorthis stubblefieldi Bassett, 1981
7, RGSC 1044; Peach Collection. 8, 9, GSM 10378; Peach Collection. 10, nt RGSC but Davidson cast B 13065; Peach Collection. (Llandeilo), Carn (Rocks), Gorran (Haven), Cornwall.

11, 12 *Orthis scotica*? M^{c}Coy, sp.
?Schalidomorthis stubblefieldi Bassett, 1981
11, RGSC 661; Peach Collection. 12, nt Truro Museum. (Llandeilo), Gorran Haven, Cornwall.

13 *Orthis* sp.? **indeterminate orthide**
13, nt RSM but Davidson cast B 13306; Peach Collection. (Llandeilo), Carn (Rocks), Gorran Haven, Cornwall.

14, 15 *Orthis Berthoisi*, var. *cornubiensis*, Tromelin.
Corineorthis cornubiensis (Davidson, 1881)
14, 15, BB 73794, lectotype, *ex* Truro Museum; Peach Collection. (Llandeilo), Caerhayes, Cornwall.

16–25 *Orthis Budleighensis*. ***Heterorthina*** sp.
16, 18, 19, RSM 1951.5; Peach Collection. 17, nt RGSC; Peach Collection. 20, nt RGSC; Peach Collection. 21, nt RGSC; Peach Collection. 22, RGSC 943; Peach Collection. 23, GSM 10374; Wyatt-Edgell Collection. 24, nt GSM; Etheridge Collection. 25, GSM 10334; Wyatt-Edgell Collection. (Llandeilo), Figs 16–19 from Carn rocks, Gorran Haven, Figs 21, 22 from Gerrans Bay, and Figs 20 and 23–25 only labelled Gorran Haven, Cornwall.

26 *Orthis testudinaria*, Dalman type.
Dalmanella testudinaria (Dalman, 1828)
26, Naturhistoriska Riksmuseet, Stockholm, one of a type lot of over 70 specimens; Dalman Collection. (Ashgill), Borenshult, Ostergötland, Sweden.

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Supposed Triassic bryozoans in the Klipstein Collection from the Italian Dolomites redescribed as calcified demosponges

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SYNOPSIS. Type and other specimens of supposed bryozoans described by Klipstein (1843–5) from the Triassic Cassian Formation (Carnian) of the Italian Dolomites are redescribed. All of Klipstein's figured specimens are shown to be calcified demosponges ('sclerosponges') and not bryozoans. *Ceriopora alpina* Klipstein is referred to *Leiospongia* d'Orbigny and a valid type species (*Achilleum verrucosum* Münster) is selected for this genus to replace a previous invalid selection. Probable spicules are identified in *L. alpina* and an un-named congeneric species. *Catenipora orbignyana* Klipstein and *Calamopora ? gnemidium* Klipstein are both assigned to the new genus *Cassianochaetetes*, the former as the type species. *Achilleum polymorphum* Klipstein is also revised and placed in *Leiospongia*. Non-type material in the Klipstein Collection includes further calcified demosponge specimens identified as *Leiospongia* sp., ?*Cassianochaetetes milleporatus* (Münster, 1841), *Cassianochaetetes* sp., and *Atrochaetetes lagaaiji* (Bizzarini & Braga, 1978). Whereas a high diversity of calcified demosponges is evident in the Cassian Formation, only one true bryozoan, identified as the trepostome *Dyscritella zardinii* Schäfer & Fois, has been recognized among Klipstein's material. It is probable that several other Triassic calcified demosponges have been misidentified as bryozoans, usually as cerioporine cyclostomes. Morphological criteria for distinguishing bryozoans from calcified demosponges are given.

INTRODUCTION

Knowledge of the 'sclerosponges' (a polyphyletic grouping of demosponges with a calcareous basal skeleton, henceforth referred to as 'calcified demosponges') from the Cassian Formation (Lowermost Carnian) of the Dolomites (northern Italy) is very poor in spite of their abundance as fossils. Several species have been misidentified in the past as bryozoans and their descriptions are therefore to be found in the bryozoan literature. Other problems arise from insufficiently detailed descriptions of species and misinterpretations of earlier works.

Most of the type material of Münster (1841) and the entire Klipstein Collection (Klipstein 1843–45) of 'calcified demosponges' from the Cassian Formation have never been restudied. Recently, one of us (PDT) rediscovered type material of Klipstein (1843–45) in the Bryozoa collection of the BM(NH). More of Klipstein's material was found subsequently in the sponge collection. Among these finds are four figured syntypes. The purpose of this paper is to redescribe these syntypes and additional associated material from the Klipstein Collection, and to establish the status of these species as calcified demosponges and not bryozoans. Opportunity is taken to outline some of the differences between Triassic calcified demosponges and the bryozoans with which they are frequently confused.

History of the Klipstein Collection in the British Museum (Natural History)

At the time of publication of his 'Beiträge zur geologischen Kenntnis der östlichen Alpen', August von Klipstein was a professor of geology at the University of Giessen (now in West Germany). In 1851 he sold his entire fossil collection (6147 specimens) from the Alps, which consisted mainly of fossils from the Cassian Formation (5362 specimens), for the then enormous sum of £250 to the British Museum (according to correspondence kept in the MS collections of the Department of Palaeontology Library). The significance of some of Klipstein's specimens as types seems not to have been appreciated following incorporation of the specimens into the BM(NH) collections, and the existence of these important specimens in the BM(NH) has been widely overlooked by palaeontologists. For example, Flügel (1963) reported that the type specimens of Klipstein's 'bryozoan' species were missing.

The Klipstein Collection of Triassic calcified demosponges

Klipstein (1843–45) described 19 new species of calcareous sponges (including supposed bryozoans) from the Cassian Formation of St Cassian (Italy). Figured specimens belonging to 16 of these species have been recognized in the collections of the BM(NH):

'Calamopora' gnemidium (S10464, S10466, S10467, each a different species)
'Catenipora' orbignyana (S10465)
'Ceriopora' alpina (S10463)
'Achilleum' poraceum (S9541)
'Achilleum' polymorphum (S9540)
'Manon' pertusum (S9550)
'Manon' poraceum (S9545)
'Tragos' acute-marginatus (S9544)
'Tragos' sulcatum (S9542)
'Tragos' spongiosum (S9543)
'Scyphia' hieroglypha (S9551)
'Scyphia' polymorpha (S9548 – pl.19, fig.12a only)
'Scyphia' ? armata (S9549 – pl.19, fig.13 only)
'Gnemidium' stellaris (S9546)
'Gnemidium' concinnum (S9547)

The holotypes/syntypes of four Klipstein species are probably lost. These are:
'Tragos' involutum (1 specimen)
'Tragos' ramosum (both specimens figured under this name)
'Catenipora' spongiosa (1 specimen)
'Gnemidium' pyriforme (1 specimen)

The sponge nature of *'Stromatopora' porosa* (90014) is very questionable.

Locality and Stratigraphy

Klipstein's specimens came from the Cassian Formation, near St Cassian (Dolomites, northern Italy) according to both his publication and the original handwritten labels which survive with some of the specimens. However, Klipstein did not mention any specific locality in the St Cassian area. Most likely, his specimens are from the classical fossil localities of the 'Stuores-Wiesen' or 'Seeland-Alpe' near St Cassian. The stratigraphical age of these sections in the Cassian Formation has been studied by Urlichs (1974), who regarded them as lowermost Carnian (*aon* Subzone and *aonoides* Subzone).

Methods of study, sponge morphology and measurements

Before sectioning, external morphology was studied and photographed. The uncoated specimens were examined and micrographs prepared using back-scattered electrons with an ISI 60A SEM (see Taylor 1986).

Thin sections were prepared from all the important specimens to show details of internal morphology which are essential in discriminating between species.

The St Cassian calcified demosponges described here range in external morphology from dome-shaped to columnar or pedunculate (mushroom-shaped). Internally, the sponge is constructed of a mass of tubes or calicles. These calicles open onto the upper surface (or theca) of the sponge as a series of polygonal apertures. During life the theca would have been enveloped by the soft living tissue of the sponge. A system of shallow, radiating grooves (astrorhizae) may be visible on well-preserved thecal surfaces. Skeletal walls exterior to the living tissue are relatively smooth and form an epitheca which occurs at the base of the sponge but can also extend upwards around the stalk of pedunculate sponges. Multiple epithecae may occur in sponges which have regenerated.

New calicles are added to the growing sponge either by fissipar or intraparietal budding. In fissipar budding the lumen of the parent calicle is continuous with that of the daughter calicle, whereas in intraparietal budding this is not so and the daughter calicle arises entirely from the splitting of a calicle wall. Calicles are usually crossed at intervals by tabulae. The microstructure of the calicle walls and tabulae is similar and is either spherulitic or elongate spherulitic. Both fabrics consist of aragonite fibres arranged radially in spheres, but elongate spherulitic fabrics have preferential development of fibres orientated in the growth direction of the sponge (see Wood 1987: text-fig. 2). In some sponges, portions of calicles at varying distances beneath the theca become back-filled by aragonite fibres which may partly or completely block the lumen of the calicle. Rarely, spicules are incorporated in the calicle walls; these can be distinguished from superficially similar microborings by their straightness.

Measurements of calicle diameter, wall thickness and spherule diameter were made from thin sections using an eyepiece graticule fitted to a petrographical microscope. Whenever possible, measurements of the former two parameters were made from sections cutting calicles transversely. The minimum internal diameter of calicles was measured because this is less affected by section obliquity and wall thickness than is maximum external diameter (centre of wall to centre of wall).

SYSTEMATIC DESCRIPTIONS

An attempt has been made to describe fully the important specimens in the Klipstein Collection, utilizing characters visible externally as well as internal characters and skeletal microstructure. Because the systematics of 'coralline' sponges, 'sclerosponges', 'stromatoporoid' and 'sphinctozoan' sponges is currently under review by several workers (e.g. Vacelet 1985, Wood 1987), the higher level classification employed below must be regarded as tentative.

Klipstein's calcified demosponge species are re-assigned as follows:
Achilleum polymorphum Klipstein = *Leiospongia polymorpha* (Klipstein)
Ceriopora alpina Klipstein = *Leiospongia alpina* (Klipstein)
Catenipora orbignyana Klipstein = *Cassianochaetetes orbignyanus* (Klipstein)
Calamopora ? gnemidium Klipstein = *Cassianochaetetes gnemidius* (Klipstein)

Phylum **PORIFERA**
Class **DEMOSPONGIAE** Sollas, 1875
? Subclass **TETRACTINOMORPHA** Levi, 1956
? Order **AXINELLIDA** Bergquist, 1978
Family **incertae sedis**

Genus *LEIOSPONGIA* d'Orbigny, 1849

[= *Achilleum* Münster, 1834 (partim) (non ? *Achilleum* Goldfuss, 1826; non *Achilleum* Oken, 1815); *Ceriopora* Goldfuss, 1826 (partim); *Leiofungia* Fromentel, 1859 (obj. syn.); *Hartmanina* Dieci, Russo & Russo, 1975 (obj. syn.)].

DIAGNOSIS. Hemispherical sponges with almost straight calicles which are divided at irregular intervals by tabulae. Calicle walls and tabulae consist of spherules of aragonite. Spicules (style, acanthostyle or fusiform) are occasionally

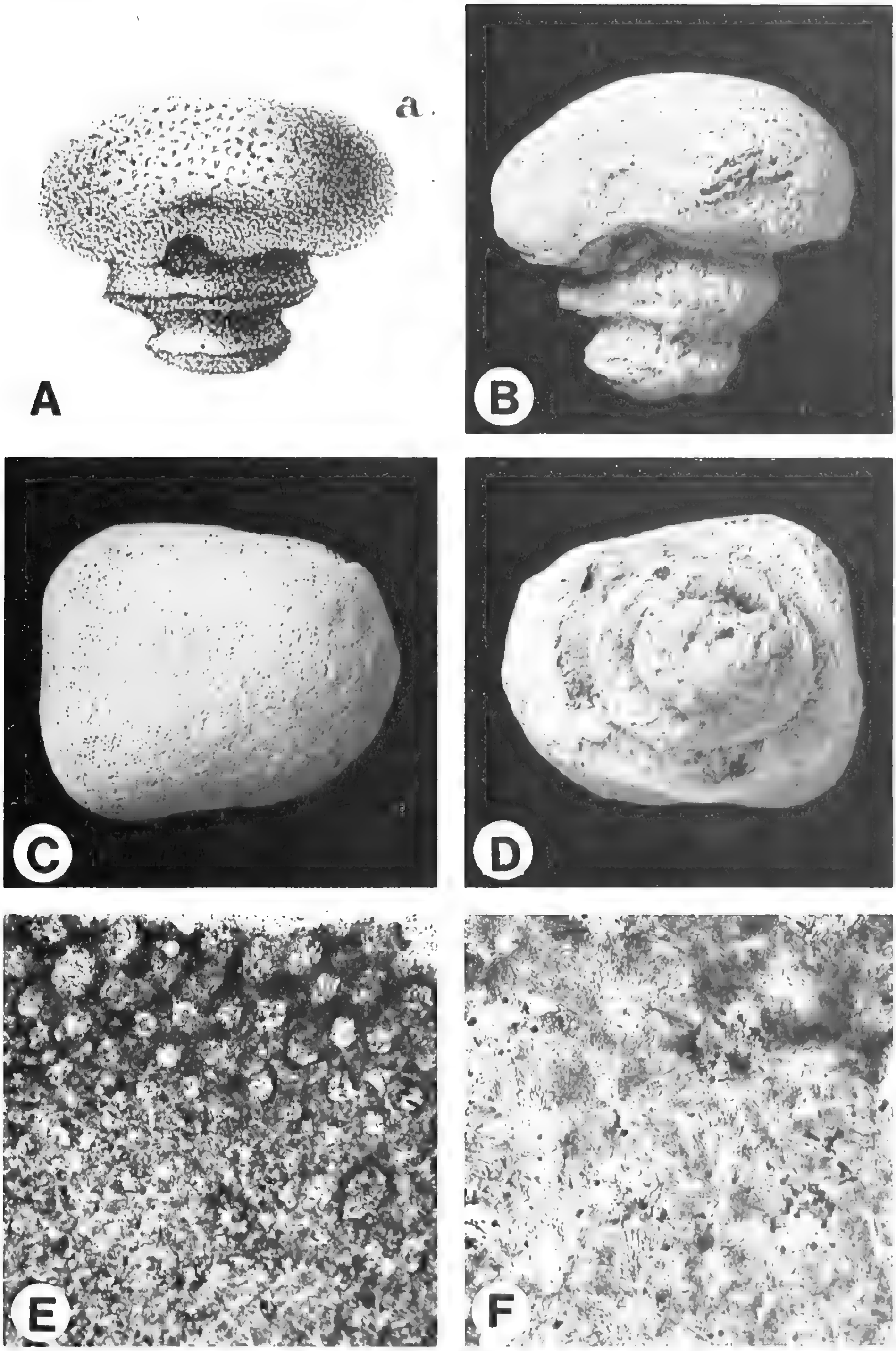

Fig. 1 *Leiospongia alpina* (Klipstein). Cassian Fm., St Cassian. Holotype, S10462. A, reproduction of pl.19, fig.17a of Klipstein (1845). B, side view, × 3·9. C, top view, × 3·9. D, underside showing epitheca, × 3·9. E, transverse sections of calicles, × 35. F, spherulitic wall structure, × 130.

incorporated into the walls and arranged parallel to growth direction. New calicles are added by fissipar division or intraparietal budding.

TYPE SPECIES. *Achilleum verrucosum* Münster, 1841, herein designated.

ATTRIBUTED SPECIES. *Leiospongia verrucosa* (Münster, 1841), *Leiospongia alpina* (Klipstein, 1845), *Leiospongia polymorpha* (Klipstein, 1845), '*Leiospongia*' sp.

REMARKS. The subsequent designation of '*Achilleum*' *milleporatum* Münster, 1841 as the type species of *Leiospongia* d'Orbigny, 1849 by de Laubenfels (1955: E100) is invalid and a new type species has to be chosen. This is necessary because the *International Code of Zoological Nomenclature* stipulates that the type species of a genus has to be chosen from species included in the original description of the genus; *Achilleum milleporatum* is not among the species listed in the original description of *Leiospongia*.

The reason why de Laubenfels (1955) chose an inappropriate type species of *Leiospongia* apparently stems from the fact that Alcide d'Orbigny published his new genus in two publications which appeared almost simultaneously. These publications are: 'Note sur la classe de Amorphozoaires' (in *Revue et Magasin de Zoologie*, (2 ser.) **1**: 545–550); and *Prodrôme de paléontologie*, etc. (**1**: 240). The latter is the far better known publication, whereas the former is seldom cited. It is important to establish which was published first. The cover date of the relevant issue of *Revue et Magasin*, given as November, 1849, is quite probably incorrect as session reports from various societies up to 26 November 1849 are included in this issue of the journal. However, the *Revue et Magasin* was a monthly journal and the deadlines given for subscriptions in the January issue make it quite plausible that the journal was published during the month following that given on the cover. Furthermore, all catalogues that we consulted (e.g. Royal Society of London 1870, Neave 1939) give the publication date of the November issue as 1849. In the absence of contrary evidence, the date of publication of d'Orbigny's ' Note sur la classe de Amorphozoaires' is therefore interpreted as 31 December 1849, and we refer to it as d'Orbigny (1849).

The date of publication of d'Orbigny's *Prodrôme de paléontologie* etc., **1**, in which he attributed further species to *Leiospongia* including *Achilleum milleporatum* Münster, 1841, can be determined fairly precisely. D'Orbigny presented a copy of the work as a gift to the Société géologique de France during the session of the society on 21 January 1850 (see *Bull. Soc. géol. Fr.*, Paris, (2) **7**: 98–99). Earlier sessions of this society had taken place on 4 January and 14 January but, although d'Orbigny attended these sessions, he did not present his work. Therefore, publication is likely to have been sometime between 14 and 21 January, and we interpret the year of publication as 1850.

Only species-group names included in d'Orbigny's first description (d'Orbigny 1849) of *Leiospongia* d'Orbigny, 1849 can qualify as potential type species. These are: *Achilleum verrucosum* Münster, 1841 and *Achilleum granulosum* Münster, 1841. Since the type specimen of *Achilleum granulosum* Münster, 1841 is still not redescribed, we herein designate *A. verrucosum* as the type species of the genus *Leiospongia* d'Orbigny, 1849. The holotype of this species has been redescribed by Dieci *et al.* (1975). Unaware of the above mentioned problems, they have chosen *A. verrucosum* Münster, 1841 as the type species of their new genus *Hartmanina*, which is, *ipso facto*, an objective junior synonym of *Leiospongia* d'Orbigny, 1849.

Leiofungia Fromentel, 1859 is an intended but unjustified emendation of *Leiospongia* d'Orbigny, 1849.

Zittel (1878) regarded *Leiospongia* as 'related to certain calcareous hydrozoans (*Millepora*)'.

Leiospongia alpina (Klipstein, 1845) Fig. 1

1845 *Ceriopora alpina* Klipstein: 286; pl. 19, figs 17a, b.
1963 *Ceriopora alpina* Klipstein; Flügel: 228.

DIAGNOSIS. The calicles are straight and are occasionally backfilled with aragonite. Possible monaxon megascleres may be embedded in the walls, orientated parallel to growth direction. Calicle diameter about 0·10 mm.

HOLOTYPE. BM(NH) S10462 (specimen and 1 thin section); figd Klipstein 1845: pl. 19, figs 17a, b. This is the only unequivocal syntype and is therefore taken to be the holotype. Fig. 1A–F.

OTHER MATERIAL. BM(NH) S10463 (specimen and 1 thin section), Klipstein Colln.

LOCALITY AND HORIZON. St Cassian, Italy, Cassian Formation, lowermost Carnian.

DESCRIPTION. The holotype shows a growth-form with multiple epithecae. The calicles are almost straight and are occluded at intervals by tabulae or an irregular backfill. The walls are formed of aragonite spherulites which are beginning to recrystallize in the holotype. Tabulae mostly consist of a single row of spherulites. Apparent spicules (visible in S10463) are occasionally embedded in the calicle walls and are simple monaxon megascleres, orientated roughly parallel to growth direction (suggesting that spicule embedment occurred by chance), about 0·002 mm thick and at least 0·08 mm long; no microscleres have been found.

MEASUREMENTS (in mm)		S10462	S10463
calicle diameter:	mean	0·10	0·10
	S.D.	0·019	0·016
	range	0·07–0·15	0·08–0·12
	N	20	10
wall thickness		0·04–0·07	0·05–0·09
spherulite diameter		0·06–0·12	0·06–0·12

REMARKS. There are some doubts about the attribution of this species to the genus *Leiospongia* d'Orbigny, 1849 because the type species of *Leiospongia*, *L. verrucosa* (Münster, 1841), was redescribed in insufficient detail by Dieci *et al.* (1975), who gave no details of the spicules, calicle diameter or tabulae.

Leiospongia polymorpha (Klipstein, 1845) Fig. 2

? 1841 *Achilleum radiciformis* Münster: 25; pl. 2, fig. 20.
1845 *Achilleum polymorphum* Klipstein: 281; pl. 19, fig. 3.
? 1975 *Hartmanina radiciformis* (Münster) Dieci *et al.*: 143; pl. 51, figs 7, 8; pl. 52, fig. 2.

DIAGNOSIS. *Leiospongia* with straight calicles, mean calicle diameter about 0·15 mm, and thick walls.

HOLOTYPE. BMNH S9540, specimen and 1 thin section, Klipstein Colln. Fig. 2A–C.

LOCALITY AND HORIZON. St Cassian, Italy; Cassian Formation, lowermost Carnian.

DESCRIPTION. The specimen is 35 mm high and has a maximum width of 11 mm. The base of a broken-off branch is present. There is no visible epitheca and the astrorhizal system is very faint. The calicles are comparatively straight and partitioned by rare tabulae. The calicle walls, formed of large aragonitic spherules, are irregular and incomplete. Recrystallization, however, has obliterated other diagnostic features (e.g. presence or absence of spicules).

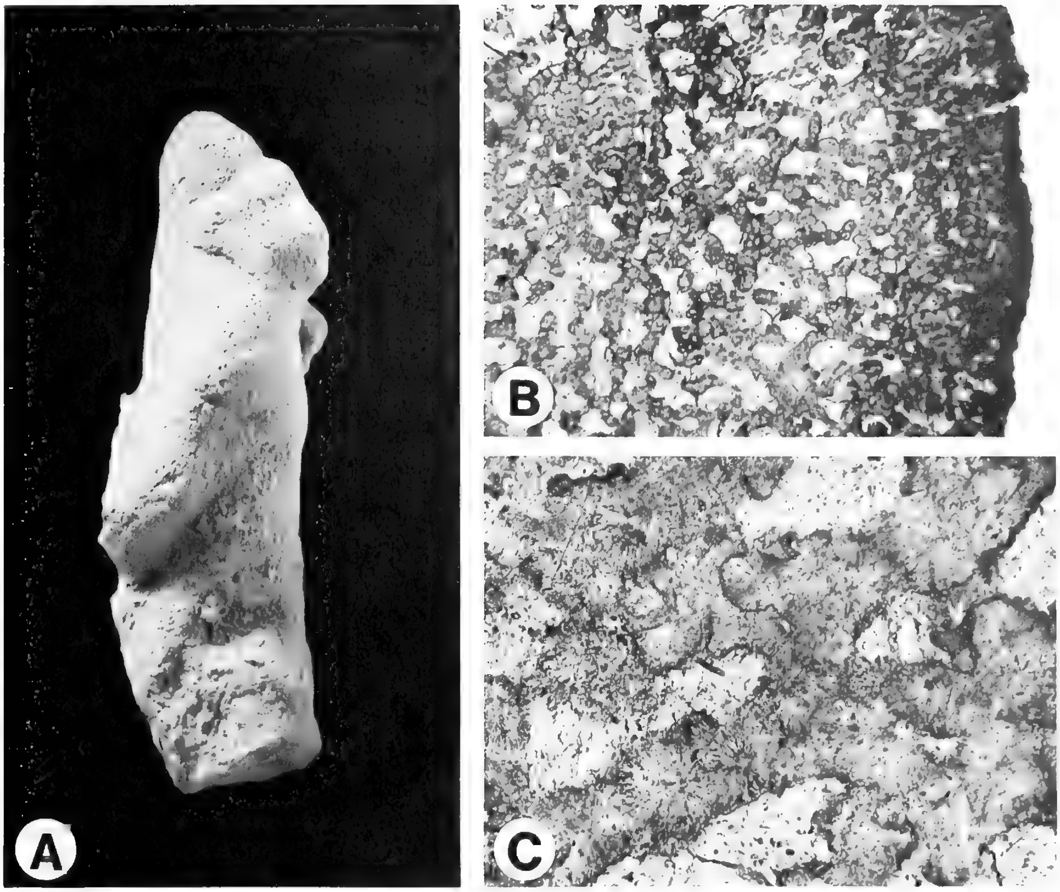

Fig. 2 *Leiospongia polymorpha* (Klipstein). Cassian Fm., St Cassian. Holotype, S9540. A, side view, × 2·5. B, transverse section, showing incomplete calicle walls, × 21. C, spherulitic wall structure, × 190.

MEASUREMENTS (in mm)	S9540
calicle diameter	0·09–0·20
wall thickness	0·04–0·15
spherulite diameter	0·05–0·15

REMARKS. The outer shape of *Leiospongia polymorpha* (Klipstein, 1845) resembles very much *'Hartmanina' radiciformis* (Münster, 1841) from the same locality. However, in their redescription of *'Hartmanina' radiciformis*, Dieci *et al.* (1975) give no details of such important diagnostic features as calicle diameter, tabulae shape, and wall thickness. Therefore, a more certain synonymy between *Leiospongia polymorpha* (Klipstein, 1845) and *'Hartmanina' radiciformis* (Münster, 1841) is impossible at the present time.

Leiospongia sp. Fig. 3

1845 *Calamopora* (?) *gnemidium* Klipstein: 285 (partim); pl. 19, fig.15b only (*non* pl. 19, figs 15a, 16a, b).

1963 *Ceriopora cnemidium* (Klipstein); Flügel: 228 (partim).

MATERIAL. BMNH S10464, Klipstein Colln. Fig. 3A–G.

LOCALITY AND HORIZON. St Cassian, Italy; Cassian Formation, lowermost Carnian.

DESCRIPTION. The sponge overgrows a coral fragment. Calicles are ill-defined; in the outer parts of the sponge they are divided by tabulae, whereas those in the basal parts are almost completely backfilled with aragonite. The tabulae consist of a single row of spherulites. Spicules, occasionally incorporated in calicle walls, are monaxon megascleres orientated parallel to growth direction, about 0·005 mm thick and up to 0·15 mm long.

MEASUREMENTS (in mm)	S10464
calicle diameter	0·12–0·18
wall thickness	0·06–0·10
spherulite diameter	0·04

REMARKS. This is the only calcified demosponge with an encrusting growth-form among the Klipstein material from St Cassian. The systematic value of the growth-form is unclear. The calicle measurements are slightly larger than those of *Leiospongia alpina* (Klipstein, 1845), and the spherulites of the basal skeleton are significantly smaller than those in both *Leiospongia alpina* and *L. polymorpha*. Therefore, there is some doubt about the assignment of this species to the genus *Leiospongia*.

Subclass **TETRACTINOMORPHA** Levi, 1956
Order **AXINELLIDA** Bergquist, 1978
Family **CERATOPORELLIDAE** Hartman & Goreau, 1972

Genus ***CASSIANOCHAETETES*** nov.

[= *Catenipora* Lamarck, 1816 (partim); *Ceriopora* Goldfuss, 1826 (partim); *Polytrema* Risso, 1826 (partim) (non *Polytrema*

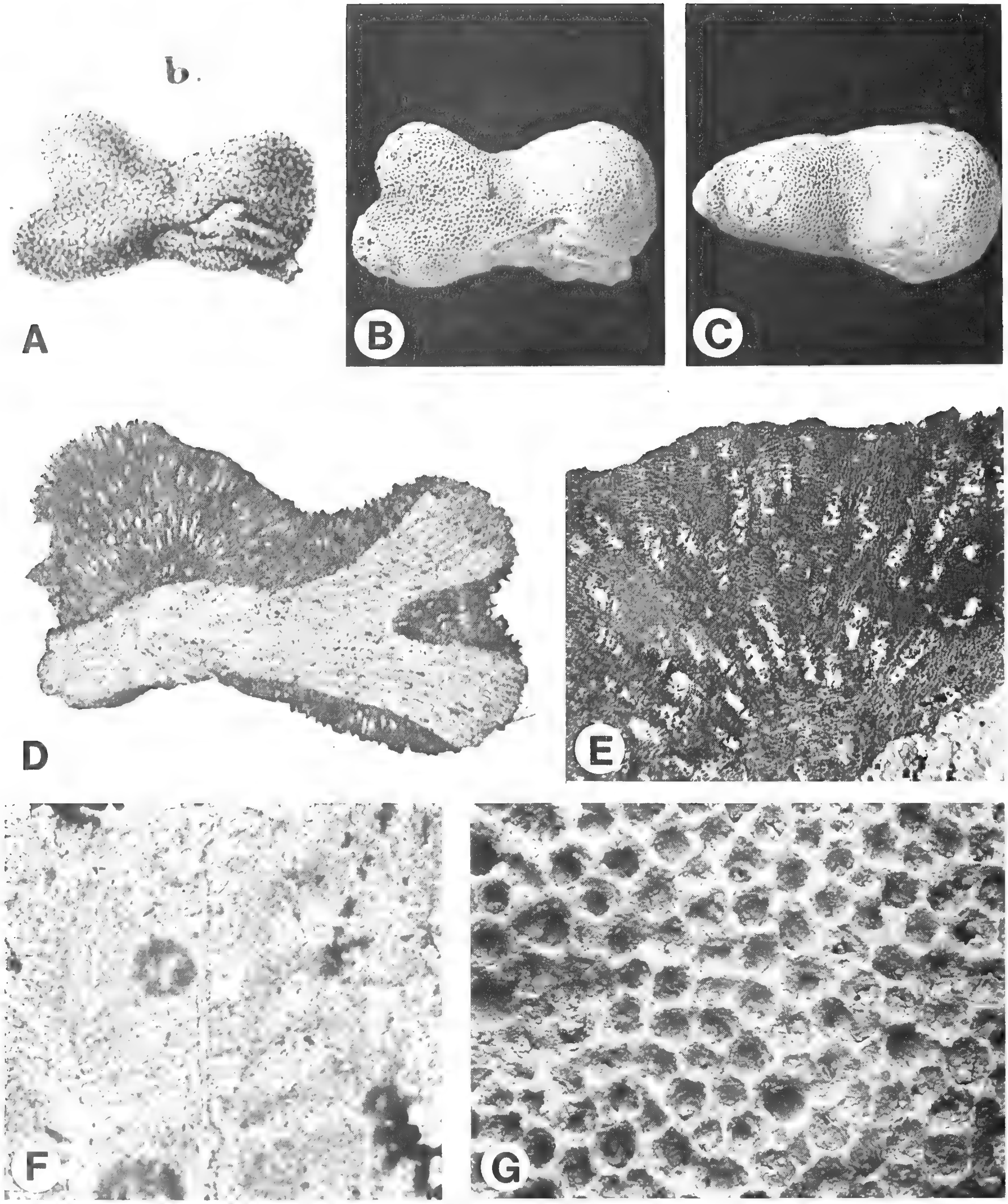

Fig. 3 *Leiospongia* sp. Cassian Fm., St Cassian. Specimen figured as *Calamopora* (?) *gnemidium* by Klipstein (1845: pl. 19, fig. 15b), S10464. A, reproduction of Klipstein's original figure. B, side view, × 4·2. C, top view, × 4·2. D, section showing dark-coloured *Leiospongia* sp. encrusting pale-coloured coral, × 7·6. E, oblique longitudinal section of calicles, × 21. F, spicule (centre) embedded in wall, × 375. G, scanning electron micrograph of thecal surface showing calicles, × 38.

Rafinesque, 1819); *Calamopora* Goldfuss, 1829 (partim); *Tragos* Münster, 1834 (partim) (non ? *Tragos* Goldfuss, 1826; non *Tragos* Schweigger, 1819); *Achilleum* Münster, 1834 (partim) (non ? *Achilleum* Goldfuss, 1826; non *Achilleum* Oken, 1815); *Leiospongia* d'Orbigny, 1849 (partim); *Actinospongia* d'Orbigny, 1849 (partim); *Leiofungia* Fromentel, 1859; *Actinofungia* Fromentel, 1859 (partim); *Leiospongia* de Laubenfels, 1955].

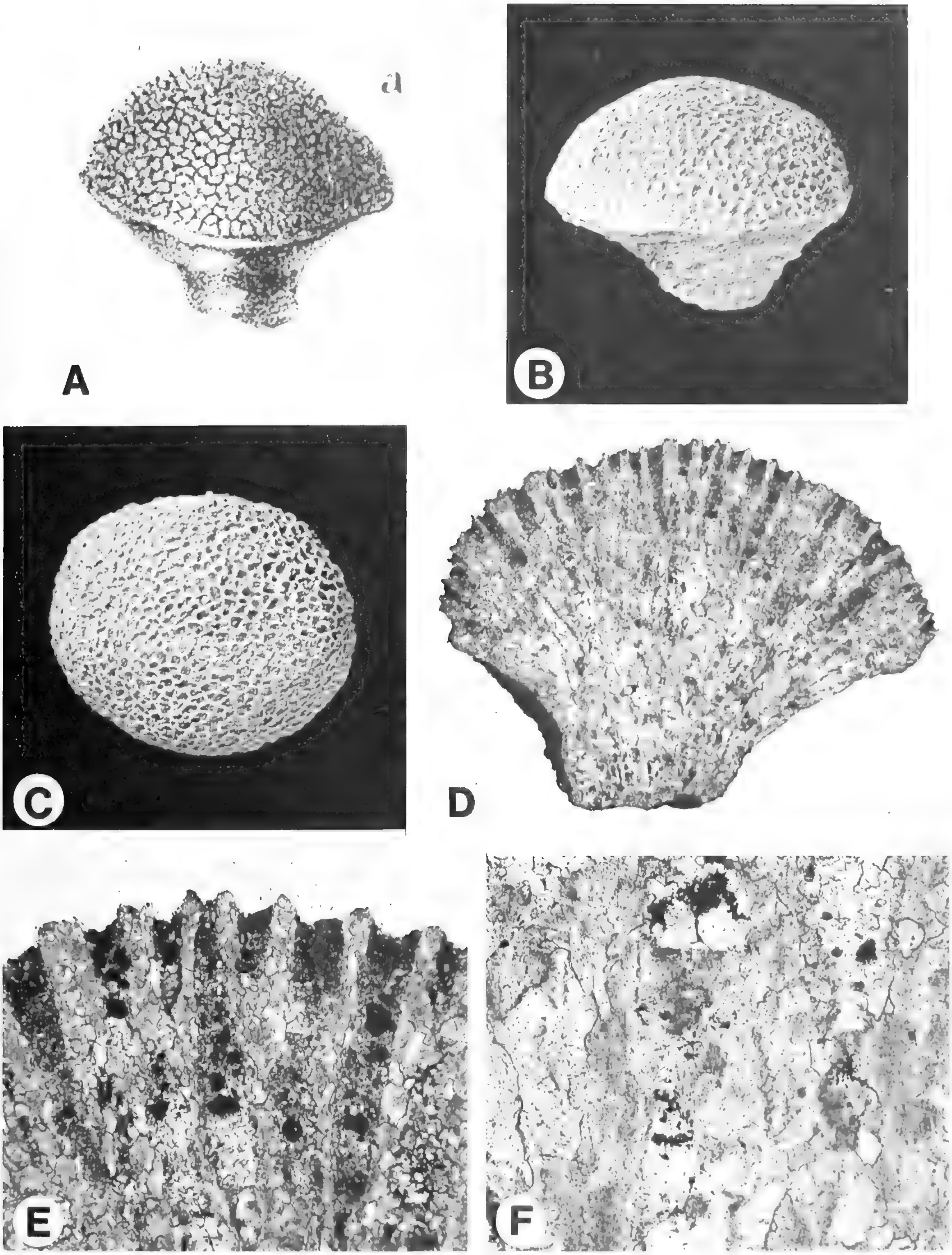

Fig. 4 *Cassianochaetetes orbignyanus* (Klipstein). Cassian Fm., St Cassian. Holotype, S10465. A, reproduction of pl. 19, fig. 20a of Klipstein (1845). B, side view showing basal epitheca, × 4·4. C, top view of thecal surface, × 4·4. D, longitudinal section, × 7·3. E, longitudinal section of calicles, × 20. F, tabulum with straight upper edge, × 55.

Diagnosis. A ceratoporellid sponge with elongate spherulitic wall structure and tabulae in the calicles which consist of tufts of aragonite crystals. The horizontal elements may be developed as calicle narrowings, or as tabulae with a flat upper side and tufted lower surface, or as irregular calicle occlusions. The calicles are always bent. Incorporation of spicules into the skeleton has not been observed.

NAME. From the Cassian Formation. Masculine.

TYPE SPECIES. *Catenipora orbignyana* Klipstein, 1845.

REMARKS. *Cassianochaetetes* n. gen. differs from *Atrochaetetes* by the tabulae which have flat upper surfaces and tufted lower surfaces, and in the bent calicles. The Recent genus *Ceratoporella* differs in always having backfilled calicles.

The new genus *Cassianochaetetes* may be the same as *Leiospongia*, *sensu* de Laubenfels, 1955 and Dieci *et al.*, 1975 (non *Leiospongia* d'Orbigny, 1849). However, this opinion depends on the correct identification of a specimen from the Klipstein Collection as *Cassianochaetetes milleporatus* (see below, p. 48).

Species of this new genus have been previously assigned to ten different genera, all incorrectly. *Catenipora* Lamarck, 1816, *Ceriopora* Goldfuss, 1826 (revised by Nye, 1976) and *Polytrema* Risso, 1826 non Rafinesque, 1819 are all known or probable bryozoan genera. *Calamopora* Goldfuss, 1829 is a tabulate genus which has been suppressed by the plenary power of the ICZN (ICZN 1976). *Achilleum*, *sensu* Münster, 1834 and *Tragos*, *sensu* Münster, 1834 are not congeneric with the two available genera *Achilleum* Oken, 1815 and *Tragos* Schweigger, 1819, and are therefore inappropriate names for the sponges from St Cassian. *Actinospongia* d'Orbigny, 1849 (and *Actinofungia* Fromentel, 1859) is a calcareous sponge (Boule, 1923), while *Leiospongia* d'Orbigny, 1849 (and *Leiofungia* Fromentel, 1859) is a calcified demosponge with a conventional spherulitic wall structure (see above, p. 40).

ATTRIBUTED SPECIES. *Catenipora orbignyanus* Klipstein, 1845, *Calamopora ? gnemidium* Klipstein, 1845, *Achilleum milleporatum* Münster, 1841 and *Cassianochaetetes* sp. (p. 48), all from the Cassian Formation (lowermost Carnian) of the Italian Dolomites.

'Achilleum' reticulare Münster, 1841 and *'Achilleum' subcariosum* Münster, 1841, both from the St Cassian Formation of northern Italy, were attributed to *Leiospongia*, *sensu* de Laubenfels, 1955, by Dieci *et al.* (1975). However, they appear to be sufficiently different from *Cassianochaetetes* to justify separation at generic level. They are expressly excluded herein from *Leiospongia* d'Orbigny, 1849.

Cassianochaetetes orbignyanus (Klipstein, 1845) Fig. 4

1845 *Catenipora orbignyana* Klipstein: 288; pl. 19, figs 20a, b.
1850 *Leiospongia reticularis* d'Orb.; d'Orbigny: 209 (partim).
? 1865 *Leiofungia orbignyana* Klipstein; Laube: 243; pl. 2, fig. 15.
? 1911 *Leiospongia* cfr. *Orbignyiana* Klipstein sp.; Vinassa de Regny: 9.
? 1933 *Leiospongia* cfr. *orbignyana* Klipst.; Venzo, *in* Migliorini & Venzo: 148.
1963 *Catenipora orbignyana* Klipstein; Flügel: 228.
? 1975 *Leiospongia orbignyana* (Klipstein); Dieci *et al.*: 139; pl. 51, fig. 2.

DIAGNOSIS. The calicles are slightly curved and large, about 0·4–0·5 mm in diameter. The epitheca shows well-developed growth lines.

HOLOTYPE. BMNH S10465 (specimen and 2 thin sections), figd Klipstein 1845: pl. 19, figs 20a, b. This is the only recognizable syntype and is therefore taken as the holotype. Fig. 4A–F.

LOCALITY AND HORIZON. St Cassian, Italy; Cassian Formation, lowermost Carnian.

DESCRIPTION. The sponge is fungiform with a convex theca, and is 9 mm high and 11 mm in maximum diameter. The epitheca is well-developed and displays growth lines. The calicles are strongly curved and are partitioned rarely by tabulae consisting of irregular tufts of aragonite crystals or by tabulae with flat upper sides and irregular tufts of aragonite crystals on their lower sides. There are no spicules incorporated in the walls. The wall structure consists of elongate spherules of aragonite crystals.

MEASUREMENTS (in mm)		S10465	
calicle diameter	*c.*	0·44	
wall thickness		0·09	(or greater)

REMARKS. D'Orbigny (1850: 209) regarded this species as a junior synonym of *'Achilleum' reticulare* Münster, 1841, an opinion not shared, however, by Dieci *et al.* (1975). Detailed re-examination of the holotype of *'Achilleum' reticulare* Münster, 1841 is required to settle the problem.

Most references to this species in the literature are doubtful (Laube 1865, Vinassa de Regny 1911, Venzo *in* Migliorini & Venzo 1933 and Dieci *et al.* 1975). However, confident reassignment of the specimens studied by these authors is precluded by the inadequacy of their descriptions and the small size of their figures.

Cassianochaetetes gnemidius (Klipstein, 1845) Fig. 5

1845 *Calamopora ? Gnemidium* Klipstein: 285; pl. 19, fig. 15a (*non* pl. 19, figs 15b, 16a, b).
1850 *Polytrema gnemidium* d'Orb.; d'Orbigny: 208.
? 1865 *Actinofungia astroites* Münster; Laube: 243 (*non* pl. 12, figs 6a, b).
1878 *Calamopora Cnemidium* Kl.; Quenstedt: 548; pl.140, fig.46.
non 1889 *Ceriopora Cnemidium* Klipstein sp.; v. Woehrmann: 196, pl. 5, figs 21, 21a.
?? 1911 *Ceriopora Gnemidium* (Klipstein); Vinassa de Regny: 16; pl. 2, fig. 12.
?? 1936 *Ceriopora* cfr. *cnemidium* (Klipstein); Woehrmann; Kühn: 127.
1963 *Ceriopora cnemidium* Klipstein; Flügel: 228.
non 1978 *'Ceriopora' gnemidium* (Klipstein, 1843); Bizzarini & Braga: 33; pl.1, figs 1–3.

LECTOTYPE. S10466 (specimen and 2 thin sections), figd Klipstein, 1845: pl. 19, fig. 15a. Each of Klipstein's three figured specimens of *Calamopora ? Gnemidium* is here regarded as a different species; selection herein of one of these figured specimens as the lectotype therefore leaves no remaining conspecific specimens which could be accorded the status of paralectotypes. Fig. 5A–F.

LOCALITY AND HORIZON. St Cassian, Italy; Cassian Formation, lowermost Carnian.

DESCRIPTION. Growth-form is semiglobular with a hidden epitheca, the incomplete sponge measuring over 35 mm in size. The astrorhizal system consists of very shallow furrows radiating from several dome-shaped mamelons. The calicles are bent and tabulae are rare and when present are formed of

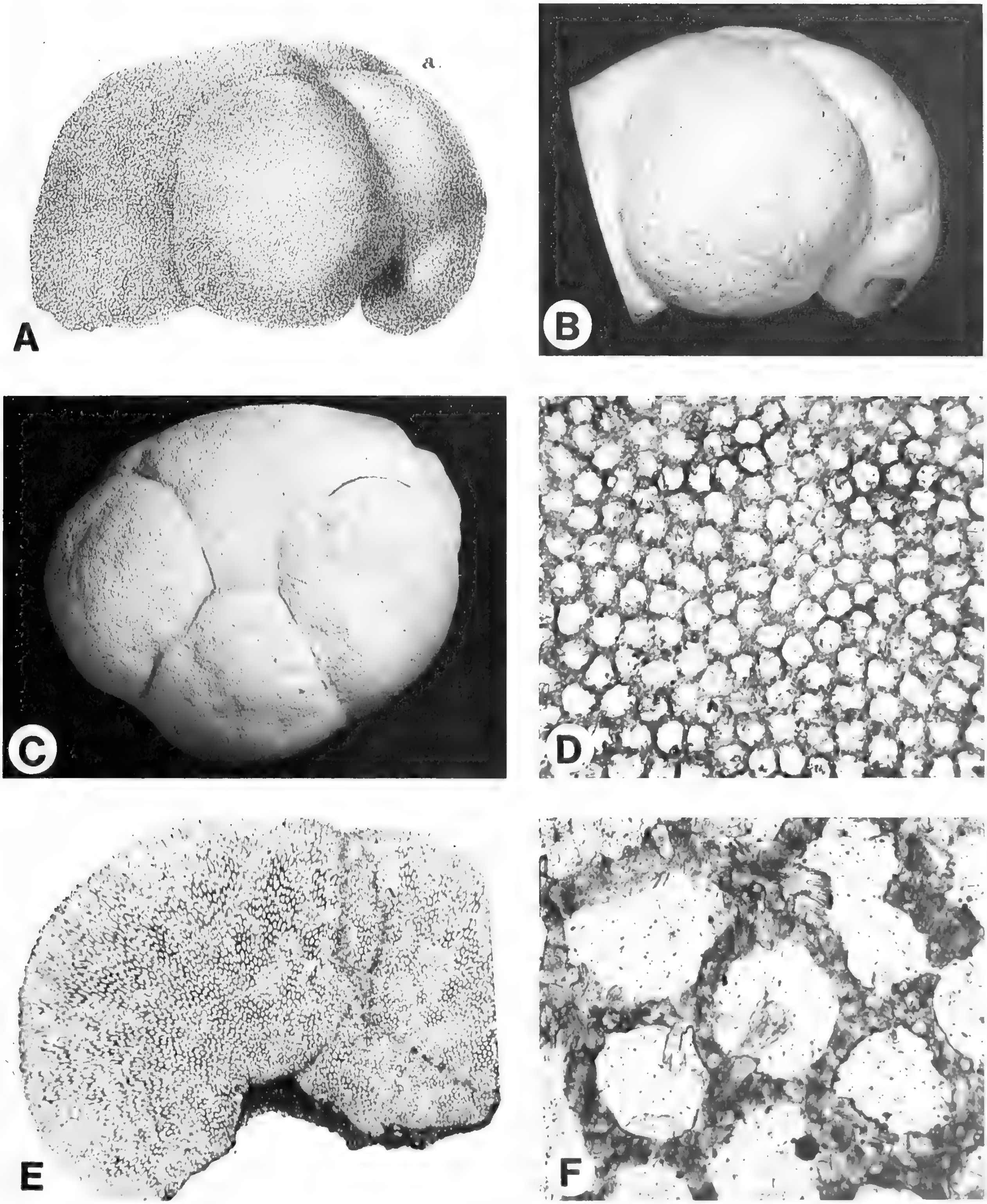

Fig. 5 *Cassianochaetetes gnemidius* (Klipstein). Cassian Fm., St Cassian. **Lectotype,** selected herein, S10466. A, reproduction of pl. 19, fig. 15a of Klipstein (1845). B, side view (bottom left corner of specimen has been cut off since Klipstein's figure was drawn), × 1·7. C, top view, × 1·6. D, transverse sections of calicles, × 21. E, section, × 2·9. F, tufts of aragonite crystals growing from calicle walls with elongate spherulitic microstructure, × 92.

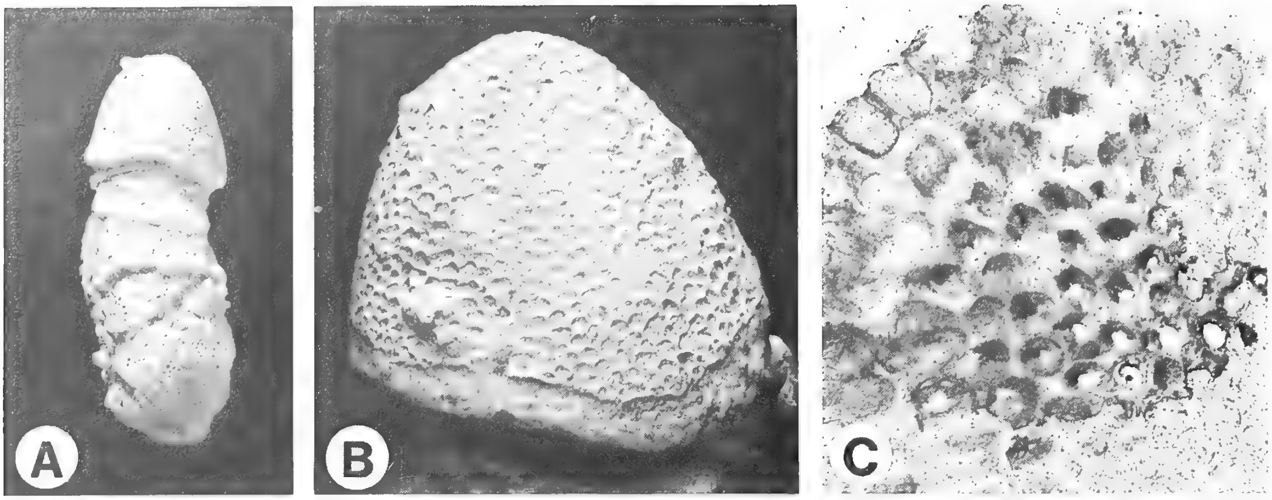

Fig. 6 ?*Cassianochaetetes milleporatus* (Münster). Cassian Fm., St Cassian. S10468. A, side view showing columnar form and multiple epithecae, × 3·8. B, scanning electron micrograph of thecal surface, × 16. C, section, × 32.

irregular tufts of aragonite crystals. Wall structure is elongate spherulitic. There are no spicules incorporated in the walls.

MEASUREMENTS (in mm)		S10466
calicle diameter:	mean	0·18
	S.D.	0·026
	range	0·12–0·24
	N	20
wall thickness		0·03–0·06

REMARKS. The species *'Calamopora'* ? *gnemidium* Klipstein, 1845 has very often been misinterpreted. This is partly because Klipstein (1845) figured under this name three different specimens, each a different species, and the species-group name *gnemidium* has never been restricted to any single one of these specimens. However, Woehrmann (1889) restricted *'Calamopora' gnemidium* to the two specimens figured by Klipstein (1845) as pl. 19, figs 15a and 15b (BMNH S10466 and S10464 respectively). Since the specimen figured on pl. 19, fig. 15b is a coral overgrown by a calcified demosponge (= *Leiospongia* sp., p. 43), the specimen figured on pl. 19, fig. 15a is here chosen as the lectotype of *'Calamopora' gnemidium* Klipstein, 1845.

Two different spellings of the species name appear in the literature, *gnemidium* and *cnemidium*. It is evident from Klipstein's paper that *gnemidium* is the original spelling; *cnemidium* is therefore an incorrect secondary spelling without nomenclatorial validity.

Most other references to this species cannot be verified because of the insufficiently detailed descriptions given. An exception is the reference to *'Ceriopora gnemidium'* in Bizzarini & Braga (1978) who described the species as showing '.. a structure made of granular calcitic laminae'. Their material certainly does not belong to *Cassianochaetetes gnemidius* (Klipstein).

? ***Cassianochaetetes milleporatus*** (Münster, 1841) Fig. 6

1841 *Achilleum milleporatum* Münster: 26; pl. 1, fig. 5.
1850 *Leiospongia milleporata* d'Orb.; d'Orbigny: 240.
1859 *Leiofungia milleporata*; Fromentel: 49.
1865 *Leiofungia milleporata* Münster; Laube: 241; pl. 2, fig. 12.
1878 *Achilleum milleporatum* Quenstedt: 541; pl. 140, figs 33–40, 48.
1879 *Leiospongia milleporata*; Zittel: 47.
1975 *Leiospongia milleporata* (Münster); Dieci *et al.*: 139; pl. 51, fig. 1; pl. 53, fig. 1.

MATERIAL. BMNH S10468 (specimen and 2 thin sections), Klipstein Colln. Fig. 6A–C.

LOCALITY AND HORIZON. St Cassian, Italy; Cassian Formation, lowermost Carnian.

DESCRIPTION. The specimen has a slender, columnar growth-form with multiple epithecae indicating regeneration. Each epitheca is short and the theca is strongly convex. The calicles appear to be curved. Tabulae and spicules have not been observed. The wall structure is elongate spherulitic, but the aragonite crystal bundles are strongly altered by the beginnings of sparitization.

MEASUREMENTS (in mm)	S10468
calicle diameter	0·10–0·15
wall thickness	*c.* 0·03

REMARKS. This description is included because *C. milleporatus* (Münster, 1841) is the type species of *Leiospongia* de Laubenfels, 1955 (non *Leiospongia* d'Orbigny, 1849). However, it is not absolutely certain that the specimen from the Klipstein Collection belongs to this species. The growth-form and the wall structure correspond with Münster's holotype, which has been redescribed by Dieci *et al.* (1975), but the dimensions and details of tabulae shape and calicle form have not been published.

Cassianochaetetes sp. Fig. 7

1845 *Calamopora* ? *gnemidium*; Klipstein: 285; pl. 19, figs 16a, b (*non* pl. 19, figs 15a, b).

MATERIAL. BMNH S10467 (specimen and 2 thin sections), figd Klipstein 1845: pl. 19, figs 16a, b. Fig. 7A–E.

LOCALITY AND HORIZON. St Cassian, Italy; Cassian Formation, lowermost Carnian.

DESCRIPTION. The specimen is fungiform, 8 mm high and has a maximum diameter of 9 mm. The epitheca is well-developed

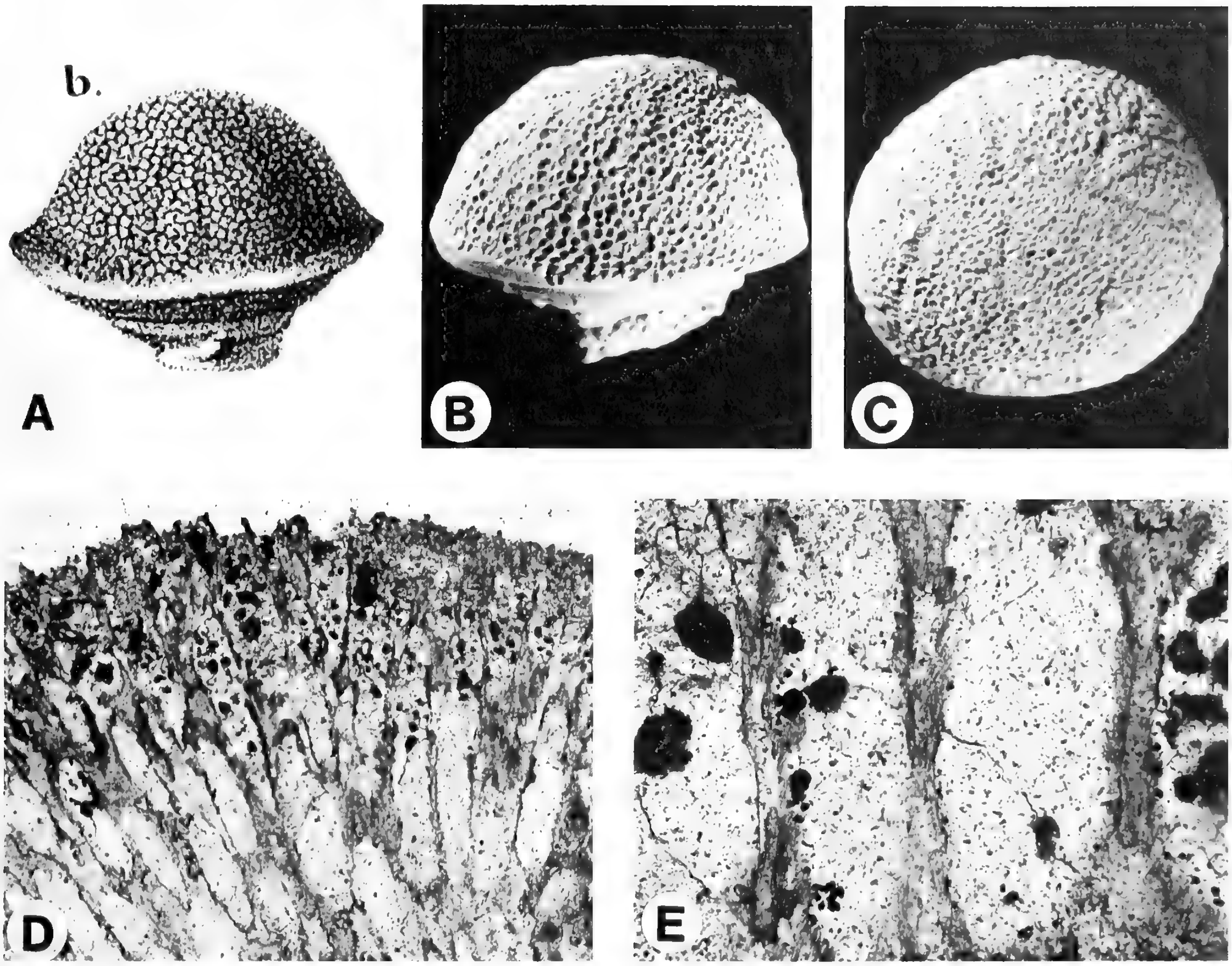

Fig. 7 *Cassianochaetetes* sp. Cassian Fm., St Cassian. Specimen figured as *Calamopora* (?) *gnemidium* by Klipstein (1845: pl. 19, figs 16a, b), S10467. A, reproduction of Klipstein's fig. 16b. B, side view, × 5·9. C, top view showing astrorhizae, × 5·9. D, oblique longitudinal section, × 21. E, calicle walls, × 89.

and shows growth lines. There is one astrorhizal system, radiating from the centre of the convex theca, consisting of shallow grooves which may bifurcate. The calicles are strongly bent and tabulae are very rare. Wall structure is elongate spherulitic. There are no spicules.

Measurements (in mm)	S10467
calicle diameter	0·19–0·28
wall thickness	0·03–0·06

Remarks. The general shape of the specimen most closely resembles *Cassianochaetetes orbignyanus*, but the calicles are much smaller, and the presence of an astrorhizal system is a further distinguishing feature. Although this probably represents a new species, it would be unwise to propose a new name on the basis of the single available specimen.

Some other Triassic calcified demosponges described as bryozoan genera

The bryozoan literature includes several other examples of Triassic fossils which are more likely to be calcified demosponges. For example, Schäfer & Fois (1987) list eight so-called cerioporine cyclostomes from the U. Triassic whose microstructures suggest that they may not be bryozoans. The Klipstein Collection contains material which permits a detailed description and reinterpretation of one such supposed bryozoan genus. In two other cases, we indicate possible synonymies and incorrect attributions. However, definite reassignments of many of these fossils must await detailed redescriptions of the type material.

1. *Seelandia* Bizzarini & Braga, 1978

Family **CERATOPORELLIDAE** Hartman & Goreau, 1972

Genus ***ATROCHAETETES*** Cuif & Fischer, 1974

[=*Seelandia* Bizzarini & Braga, 1978.]

Revised diagnosis. Ceratoporellidae with horizontal elements in the tubes which consist of bundles of radiating crystals. The horizontal elements can be developed either as calicle constrictions, as tabulae with flat undersides, or as almost complete infillings of a segment of a calicle. New calicles arise by intraparietal budding (very common) or by fissipar division (very rare). An astrorhizal system may be present.

TYPE SPECIES. *Atrochaetetes tamnifer* Cuif & Fischer, 1974.

REMARKS. Bizzarini & Braga (1978) regarded *Seelandia* as a cyclostome bryozoan. However, *Seelandia* displays the same wall structure (elongate spherulitic, with no central wall axis) and tabulae shape (crystal bundles with straight undersides) as the 'chaetetid' *Atrochaetetes* Cuif & Fischer, 1974. Even though Bizzarini & Braga (1978) recognized these obvious similarities between *Seelandia* and *Atrochaetetes*, they were convinced of the bryozoan affinities of *Seelandia* and chose to propose a new genus rather than transfer the firmly-established 'chaetetid' *Atrochaetetes* to the Bryozoa. We regard *Seelandia* and *Atrochaetetes* as identical and therefore *Seelandia* Bizzarini & Braga, 1978 as a junior subjective synonym of *Atrochaetetes* Cuif & Fischer, 1974. The microstructure of the skeleton, its aragonitic composition (see below, p. 53), the shape of the tabulae, and the presence of an astrorhizal system in some species of *Atrochaetetes* such as *A. annoscai* (Bizzarini & Braga, 1978), indicate unequivocally that *Atrochaetetes* is a calcified demosponge.

Although well-preserved, our material of *Atrochaetetes* does not display any spicules. It is probable that the 'spicules' described by Dieci *et al.* (1977) in *Atrochaetetes 'medius'* Cuif & Fischer, 1974 [= *Atrochaetetes lagaaiji* (Bizzarini & Braga, 1978)] are borings made by thallophyte algae. Similar borings in our material may resemble spicules. By contrast, the spicules of *Meandripetra zardinii* Dieci, Russo, Russo & Marchi, 1977 are genuine; note the differences in general shape and size between the spicules of *Meandripetra* and the so-called 'spicules' of *Atrochaetetes* (Dieci *et al.* 1977: pl. 7, figs 3a–b; pl. 3, fig. 1).

ATTRIBUTED SPECIES. *Atrochaetetes tamnifer* Cuif & Fischer, 1974, *A. medius* Cuif & Fischer, 1974, and *A. alakirensis* Cuif & Fischer, 1974, all from the Carnian of Alakir Çay (Lycia, Turkey); *A. lagaaiji* (Bizzarini & Braga, 1978) and *A. annoscai* (Bizzarini & Braga, 1978), both species from the lowermost Carnian of the Cassian Formation; and *A. 'tamnifer'* Cuif & Fischer, 1974 of Cuffey *et al.* (1979), probably an undescribed species, from the Jurassic/Cretaceous Limestone near Orhaneli, northwestern Turkey.

Atrochaetetes lagaaiji (Bizzarini & Braga, 1978) Fig. 8

non 1974 *Atrochaetetes medius* n. sp.; Cuif & Fischer: 8; pl. 2, figs 2, 3.
1977 *Atrochaetetes medius* Cuif & Fischer; Dieci *et al.*: 236; pl.1, figs 6a, b; pl. 2, figs 4a, b; pl. 3, figs 3a–d.
1978 *Seelandia lagaaiji* n.sp.; Bizzarini & Braga: 40; pl. 5, figs 1–6.

MATERIAL. BMNH S10469 (specimen and 2 thin sections), Klipstein Colln. Fig. 8A–F.

LOCALITY AND HORIZON. St Cassian, Italy; Cassian Formation, lowermost Carnian.

DESCRIPTION. The specimen is 18 mm high and has a diameter of 12 mm. The epitheca is well developed and displays growth lines. The calicles are straight and intercepted by tabulae which have flat undersides and upward-pointing tufts of aragonite crystals on their upper sides. Tabulae are comparatively rare, there are large distances between successive tabulae in a calicle, their thickness varies and some incomplete tabulae have been observed ('tube narrowings'). Wall structure is elongate spherulitic. Spicules have not been found.

MEASUREMENTS (in mm)		S10469
calicle diameter:	mean	0·20
	S.D.	0·046
	range	0·10–0·27
	N	20
wall thickness		0·04–0·09

REMARKS. The measurements of the Klipstein specimen correspond comparatively well with *'Seelandia' lagaaiji* Bizzarini & Braga, 1978 but the external growth-form with the well-developed epitheca is different. However, the potential range of variation in growth-form is not known in this species.

The measurements of *Atrochaetetes 'medius'* given in Dieci *et al.* (1977) do not correspond with the measurements of *Atrochaetetes medius* mentioned in Cuif & Fischer (1974), but match well with the measurements of *Atrochaetetes lagaaiji* (Bizzarini & Braga, 1978).

2. *Cassianopora* Bizzarini & Braga, 1978

[= *Tubuloparietes* Schnorf, 1960.]

Cassianopora Bizzarini & Braga, 1978 is identical with the 'hydrozoan' genus *Tubuloparietes* Schnorf, 1960. Both show slightly irregular calicles with tabulae and the same granular-vacuolar microstructure of the skeleton. The systematic position of the genus *Tubuloparietes*, however, is unclear. Schnorf (1960) placed it within the family Milleporidiidae of the Hydrozoa. Since a great many putative fossil Hydrozoa are calcified demosponges, this too might be a sponge, though the granular-vacuolar wall structure is not yet known from any genuine calcified demosponge.

3. *Zlambachella* Flügel, 1961

From the Austrian Rhaetian, Flügel (1961) described *Zlambachella alpina* as the only species of a new monotypic genus of trepostome bryozoans. Schäfer & Fois (1987) questioned the bryozoan affinities of this species, and inspection of Flügel's figures suggest that this *Z. alpina* may be a calcified demosponge. Growth-form resembles that of the Triassic calcified demosponges described above, boundaries of the tube walls are diffuse, walls do not appear to thicken distally, and the putative acanthostyles are dissimilar from most bryozoan acanthostyles and may be borings.

Bryozoan specimen in the Klipstein Collection

Phylum **BRYOZOA** Ehrenberg, 1831
Class **STENOLAEMATA** Borg, 1926
Order **TREPOSTOMATA** Ulrich, 1882
Suborder **AMPLEXOPOROIDEA** Astrova, 1965
Family **DYSCRITELLIDAE** Duneava & Morozova, 1967

Genus ***DYSCRITELLA*** Girty, 1911

Dyscritella zardinii Schäfer & Fois, 1987 Fig. 9

1984 *Arcticopora* sp.; Boardman: 22; figs 4A–C.
1987 *Dyscritella zardinii* Schäfer & Fois: 179; pl. 2, figs 1–5.

MATERIAL. BMNH D54220 (specimen and oblique longitudinal and transverse acetate peels), Klipstein Colln. Fig. 9A–D.

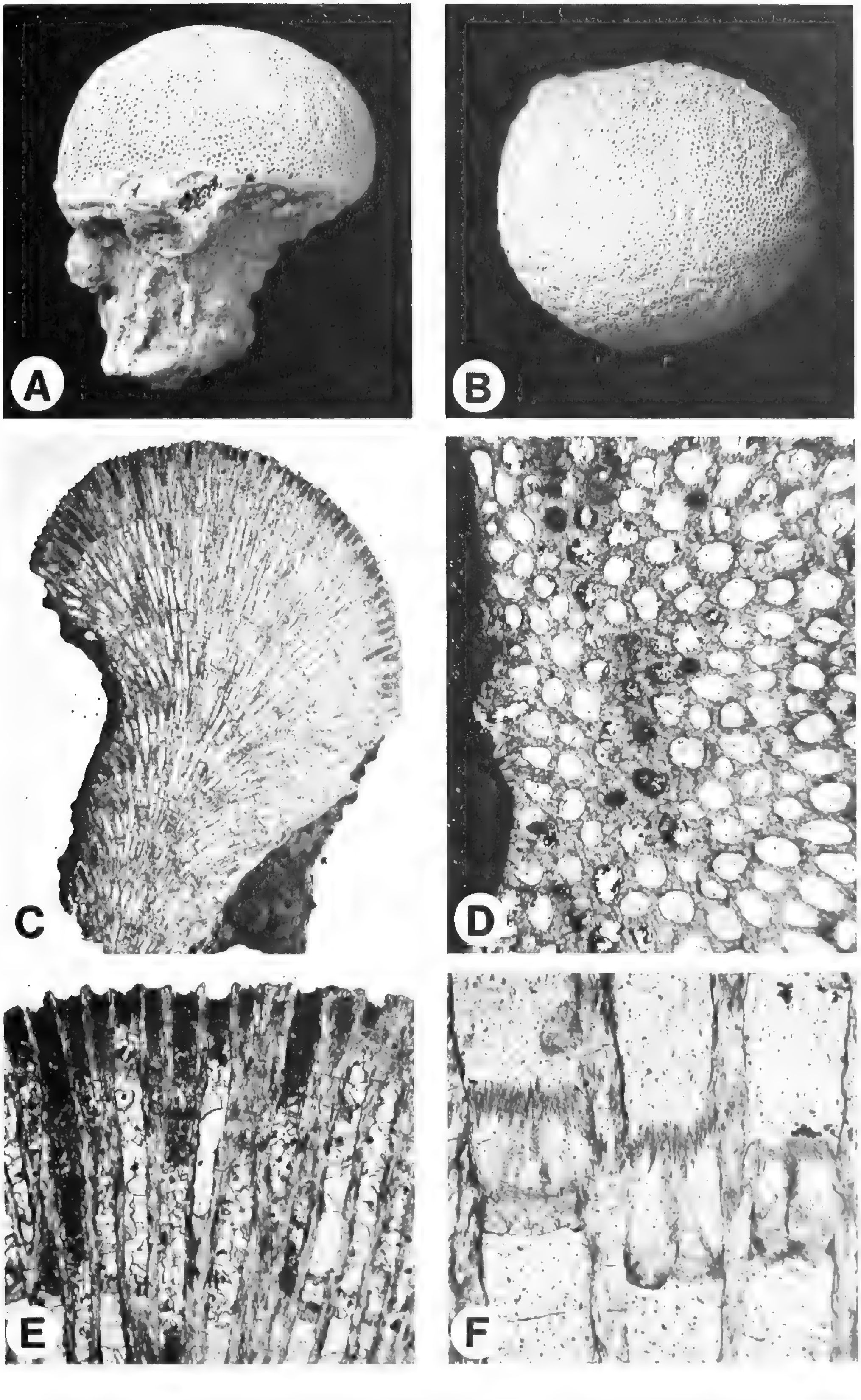

Fig. 8 *Atrochaetetes lagaaiji* (Bizzarini & Braga). Cassian Fm., St Cassian. S10469. A, side view, × 3·3. B, top view showing astrorhizae, × 3·3. C, longitudinal section showing bands of tabulae, × 4·9. D, transverse sections of calicles and epitheca (left), × 21. E, longitudinal section of calicles, × 21. F, tabulae with straight lower edges, × 89.

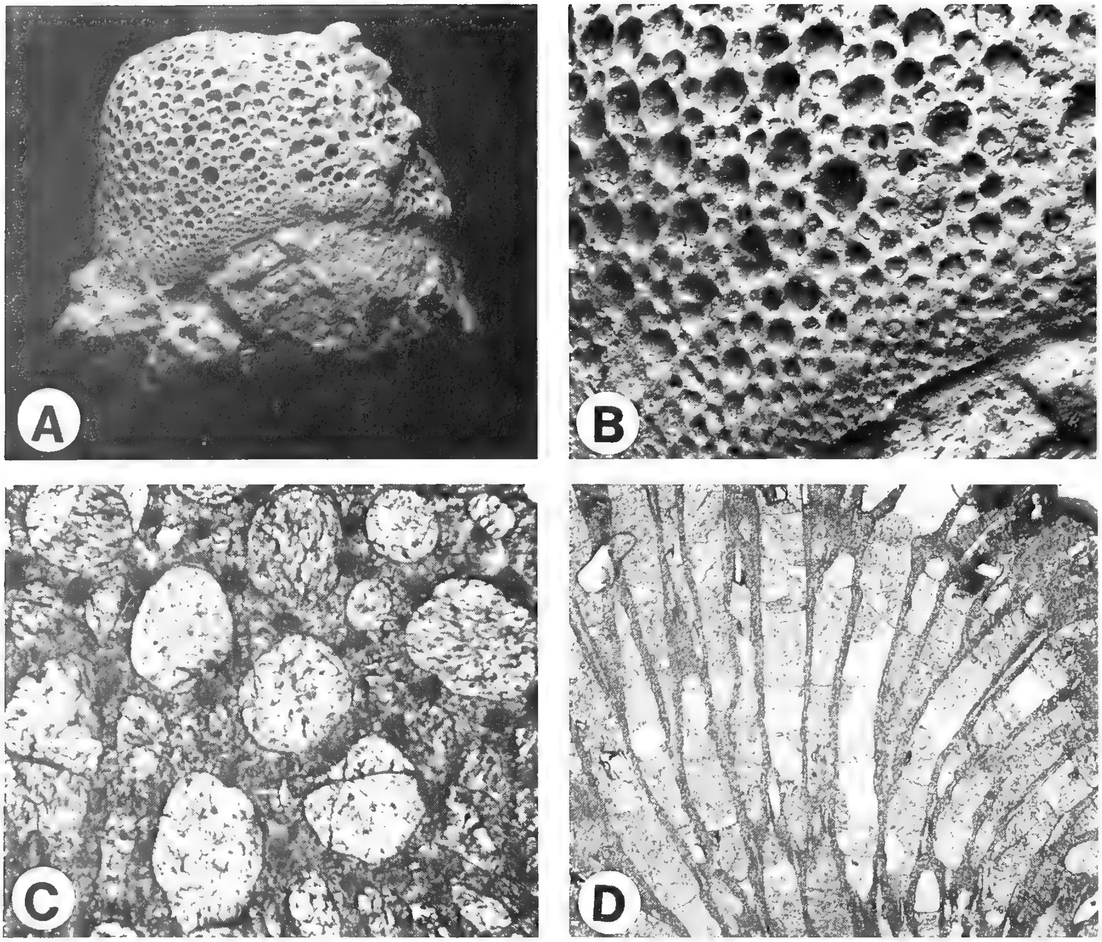

Fig. 9 *Dyscritella zardinii* Schäfer & Fois. Cassian Fm., St Cassian. D54220. A, scanning electron micrograph of colony, × 13. B, micrograph of growing edge, × 41. C, tangential acetate peel showing autozooecia, exilazooecia and styles, × 89. D, oblique longitudinal peel of zooecia, × 31.

LOCALITY AND HORIZON. St Cassian, Italy; Cassian Formation, lowermost Carnian.

DESCRIPTION. A high dome-shaped colony, small (*c.* 4 mm in diameter), with rounded autozooecial apertures, very occasionally petaloid, arranged semi-regularly over the upper surface of the colony and interspersed with and typically surrounded by smaller, variably-sized apertures of exilazooecia. At the edge of the colony close to the basal lamina are immature zooecial buds with very small apertures. Maculae cannot be distinguished.

In section, differentiation between endozone and exozone is poor; zooecial walls are of about the same thickness (0·03 mm) in the endozone as the exozone. Zooecia curve gently towards the colony surface. Exozonal walls in longitudinal section show rounded laminations. Styles with clear cores are abundant, originating in the endozone and continuing into the exozone, and sometimes having a diameter very slightly greater than endozonal zooecial wall width, in which case they indent zooecial chambers. They are of one size only, and about 6–8 styles surround each zooecium in the endozone. Thin-walled basal diaphragms are fairly numerous in the autozooecia, spaced semi-regularly at distances between 0·18 and 0·28 mm, and are flat or slightly concave orally.

MEASUREMENTS (in mm, from the colony surface)	D54220
autozooecial apertural diameter	0·14–0·18, mean 0·16
exilazooecial apertural diameter	0·05–0·11, mean 0·08

REMARKS. The Klipstein Collection specimen differs only in detail from the original description of this Cassian Formation species by Schäfer & Fois (1987).

DISCUSSION

With the exception of one specimen, all of the supposed bryozoans in the Klipstein Collection, including figured type specimens of Klipstein's new species, are sponges and not bryozoans. This confirms the opinion of Boardman (1984: 24) that many Alpine Triassic fossils originally described as bryozoans (see Flügel 1963) belong to other groups. Whereas most of these questionable or non-bryozoans have been previously regarded as cerioporine cyclostomes, there are many records of undisputed Triassic bryozoans assigned to the trepostomes (Bizzarini & Braga 1982; Boardman 1984; Hu 1984; Morozova & Zharnikova 1984; Sakagami 1985; Morozova 1986; Schäfer & Fois-Erickson 1986; Schäfer &

Fois 1987), and some cystoporates, cryptostomes (Schäfer & Fois 1987) and tubuloporine cyclostomes (Bizzarini & Braga 1985 and references therein).

Difficulties in distinguishing between Triassic sponges and bryozoans are a consequence of similarities in overall colony-form, and the size and arrangement of the calicles/zooecia. However, the following morphological criteria can be used when deciding the affinities of problematical Triassic fossils:

1. Skeletal composition. All calcified bryozoans older than late Cretaceous, and all known stenolaemate bryozoans, have calcitic skeletons. Although aragonitic skeletons occur in some species of cheilostomatous gymnolaemates (see Poluzzi & Sartori 1975), cheilostomes usually have box-like zooecia which are quite unlike the long tubular zooecia found in the questionable bryozoans from the Triassic, and make their first appearance in the latest Jurassic. Calcified demosponges can have calcitic or aragonitic skeletons. Therefore, an aragonitic composition strongly suggests a sponge affinity.

2. Skeletal microstructure. Stenolaemate bryozoans generally have walls with a lamellar microstructure, sometimes divided into several distinct units. The laminae usually parallel growth surfaces but can be perpendicular (Boardman *in* Boardman *et al.* 1983). Walls between zooecia (interzooecial walls which constitute the bulk of the skeleton in cerioporine cyclostomes and in trepostomes) are often bilaterally symmetrical and may have a median granular layer (see Tavener-Smith & Williams 1972). In contrast, the walls of calcified demosponges have fibrous microstructures, the fibres arranged either in spherules or in radiating fans (cligonal or water-jet structure), or alternatively, lamellar microstructures. There is no clear median division of the wall. The finding of a fibrous microstructure in a Triassic fossil of questionable affinities permits its identification as a sponge.

3. Spicules. Although cheilostome bryozoans belonging to the Family Thalamoporellidae have calcareous spicules in their zooids (Soule & Soule 1970), spicules are not known to occur in stenolaemates or any pre-Cenozoic bryozoans. Some species of calcified demosponges incorporate originally siliceous spicules into the calcareous walls of the calicles (e.g. Fig. 3F). Therefore, the occurrence of spicules in a Triassic fossil is a reliable indicator of a sponge affinity.

4. Styles. Many Palaeozoic stenolaemate bryozoans contain within their walls skeletal rods termed styles (= acanthopores or acanthostyles). Styles have a cone-in-cone microstructure, often with a non-laminated core, may project as spines at the colony surface and indent the outlines of the zooecial apertures (see Boardman *in* Boardman *et al.* 1983). There are no equivalent structures in calcified demosponges.

5. Budding. Patterns of zooecial budding in stenolaemate bryozoans vary (McKinney 1975, 1977), but new buds always arise by the splitting of a zooecial wall such that there is no confluence between the chambers of the parent and daughter zooecia. Although a similar form of budding may be observed in calcified demosponges, where it is known as intraparietal budding, fissipar budding in which the calicles are confluent may also occur.

6. Wall-chamber boundaries. These boundaries are invariably sharp in stenolaemate bryozoans, whereas they are often ragged and indistinct in calcified demosponges.

7. Diaphragms/tabulae. Stenolaemate zooecia are often partitioned horizontally by diaphragms (see Boardman *in* Boardman *et al.* 1983) secreted by epithelial tissue situated on their oral or aboral sides. They have a lamellar microstructure, are typically thin-walled and of an even thickness, and in cerioporine cyclostomes may be penetrated by pseudopores. Tabulae, the equivalent structures in calcified demosponges, often differ from diaphragms in being thick-walled and varying considerably in thickness across the calicle.

8. Backfilling. Some calcified demosponges partially or completely fill the old parts of their calicles with calcification. Stenolaemate bryozoans are not known to do likewise.

9. Endozone–exozone differentiation. Colonies of stenolaemate bryozoans, notably trepostomes and cerioporine cyclostomes with arborescent branching growth-forms, are frequently divisible into an axial endozone surrounded by an exozone. The endozone contains the proximal parts of the zooecia which tend to be thin-walled and orientated parallel to the growth direction of the branch. Budding of new zooecia may be concentrated in or confined to the endozone. Passing from the endozone into the exozone, the zooecia bend abruptly until their long axes are typically subperpendicular to branch growth direction. The walls of the zooecia in the exozone are usually relatively thick, and various morphological characters (e.g. diaphragms, styles) may be present in only one zone or may change in frequency between zones. Such endozone–exozone differentiation, although not developed in all stenolaemates, has no equivalent among calcified demosponges.

10. Monilae. Some trepostomes and cerioporine cyclostomes have annularly thickened zooecial walls which are described as moniliform (see Boardman 1984). These thickenings can be very regular, and are unlike any structures described in calcified demosponges.

11. Pores. Cerioporine cyclostomes are characterized by the presence of small pores in the zooecial walls; trepostomes always lack such pores. Pores are often distributed in the thin-walled parts of the walls between moniliform thickenings and many thin sections fail to intersect them. Small regular pores are generally absent in calcified demosponges which may, however, possess large, irregular gaps in the walls of the calicles.

12. Zooecium/calicle diameter. One of the reasons for the persistent confusion between calcified demosponges and bryozoans is undoubtedly the similarity in diameter of the tubes in the two groups. However, the largest calicles in calcified demosponges exceed the range of variation known for stenolaemate bryozoans. Zooecial diameter in most trepostomes is between 0·1 and 0·3 mm, with a maximum value of 0·46 mm (Anstey & Perry 1972). Calicle diameter in living and fossil calcified demosponges ranges from about 0·12 to *c.* 1·2 mm, although the maximum size in living species is about 0·6 mm (Scrutton 1987). Therefore, any problematical fossil with a tube diameter in excess of 0·5 mm must be suspected to be a calcified demosponge.

13. Early growth stages. The first-formed zooid–the ancestrula–in a stenolaemate bryozoan colony is distinctive in possessing a hemispherical proximal part, termed the protoecium, out of which there emerges a distal ancestrular tube (e.g. Podell & Anstey 1979). Although the ancestrula is normally overgrown by later zooecia, sections cut at the base of the colony may reveal the presence of an ancestrula and permit inference of bryozoan affinity.

14. Astrorhizae. Some calcified demosponges have on their surface a system of shallow, radiating grooves–astrorhizae which reflect the distribution of exhalant canals in the living sponge. The only bryozoan structures likely to be confused with astrorhizae are the stellate maculae found in the

cystoporate family Constellariidae (see Utgaard *in* Boardman *et al.* 1983). However, the radial structure in stellate maculae is formed by rays composed of zooecia and inter-rays of vesicles. Furthermore, constellariids range no higher than the Lower Silurian.

15. Brood chambers. Spacious skeletal chambers are present in cerioporine cyclostomes for the brooding of larvae. Brood chambers have pseudoporous roofs which are typically supported by occasional zooecia and septa that penetrate the chamber; they are normally easy to recognize in thin section (e.g. Nye 1976: pl. 32, figs 1e–f). Both trepostome bryozoans and calcified demosponges are lacking structures of this morphology.

For both calcified demosponges and bryozoans, the Triassic represents a critical time in their evolutionary history. The phylogenetic relationships between Palaeozoic and post-Palaeozoic representatives in each group are poorly understood. Clarification of these problems must include a re-evaluation of supposed fossil sponges and bryozoans from the Triassic to ascertain their true taxonomic affinities.

Study of a small number of specimens in the Klipstein Collection from St Cassian has revealed the existence of eight different calcified demosponge species. There is a clear need for further studies to obtain a more accurate estimate of the full diversity of the rich St Cassian sponge fauna, and to provide more complete descriptions of the sponge species and their variability.

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Larval shells of four Jurassic bivalve molluscs

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Synopsis. Well-preserved bivalve larval shells of Jurassic age are described for the first time, from four species of Pteriomorpha from the south of England, *Liostrea plastica, L. irregularis, Oxytoma* sp. and *Meleagrinella* sp. They are compared with modern counterparts and inferences concerning larval development are tentatively drawn.

INTRODUCTION

Between 1982 and 1984 four attempts were made, by staff of the British Museum (Natural History) Department of Palaeontology, to recover the remains of a plesiosaur from the Upper Kimmeridge Clay Formation, at NGR SY 706722, the foot of Grove Cliff on the east side of the Isle of Portland, Dorset, U.K. (Fig. 1). This successful enterprise resulted in the unification of material, previously collected and in the Dorset County Museum, with that collected by BM(NH) staff. A report on the plesiosaur was made by Brown (1984), and on the associated fauna and stratigraphical position by Palmer (1988). This account deals with juvenile shells which have larval shells, 'prodissoconchs', still preserved in place at the umbones of the valves.

Stratigraphical position of material

The oldest horizon present on the Isle of Portland is a 25·4 cm bituminous indurated shale, the Blackstone in the Upper Kimmeridge Clay, which crops out on the shore north of Castletown at the extreme north end of the island. With a southerly dip and little or no major faulting, it follows that all the Kimmeridge Clay down to Mean High Water is above the Blackstone and equivalent to shales with *Pectinatites, Pavlovia* and *Virgatopavlovia* of the main outcrops at Chapman's Pool.

The fauna contained two species of ammonite, *Pavlovia rotunda* and *P. concinna*, which, together with the associated fauna, allowed an exact correlation to be made with bed 2 'hard bituminous shales' of Cope (1978) in the Rotunda Zone in Chapman's Pool. This shelly horizon has a wide distribution in southern England, from Hartwell in Buckinghamshire to the Bristol Channel (Palmer 1988).

Method of treatment

It was evident at the excavation site, even with a c 10 hand lens, that some bedding planes were covered with juvenile oysters up to 2 mm long, while some had prodissoconchs well preserved on the umbones. Slabs of shale were broken up and repeatedly boiled in a strong solution of Sainsbury's Liquid Cleaner, which proved effective and yielded a rich microfauna. Foraminiferans, ostracods, juvenile molluscs, together with arm hooks of a coleoid cephalopod, brachiopods, echinoderms, cirripedes and numerous skeletal fragments and teeth of fish were present, and were hand-picked from insoluble mineral residue under low-power stereo magnification. Spat of *Liostrea, Oxytoma* and *Meleagrinella* were isolated and mounted on 100-cell microslides, and were measured using a light microscope fitted with a graticule eyepiece. Figs 6–8 summarize these measurements and show that ultimate size of the prodissoconchs was rather variable. The measurements are probably accurate within the limits f 0·003 mm.

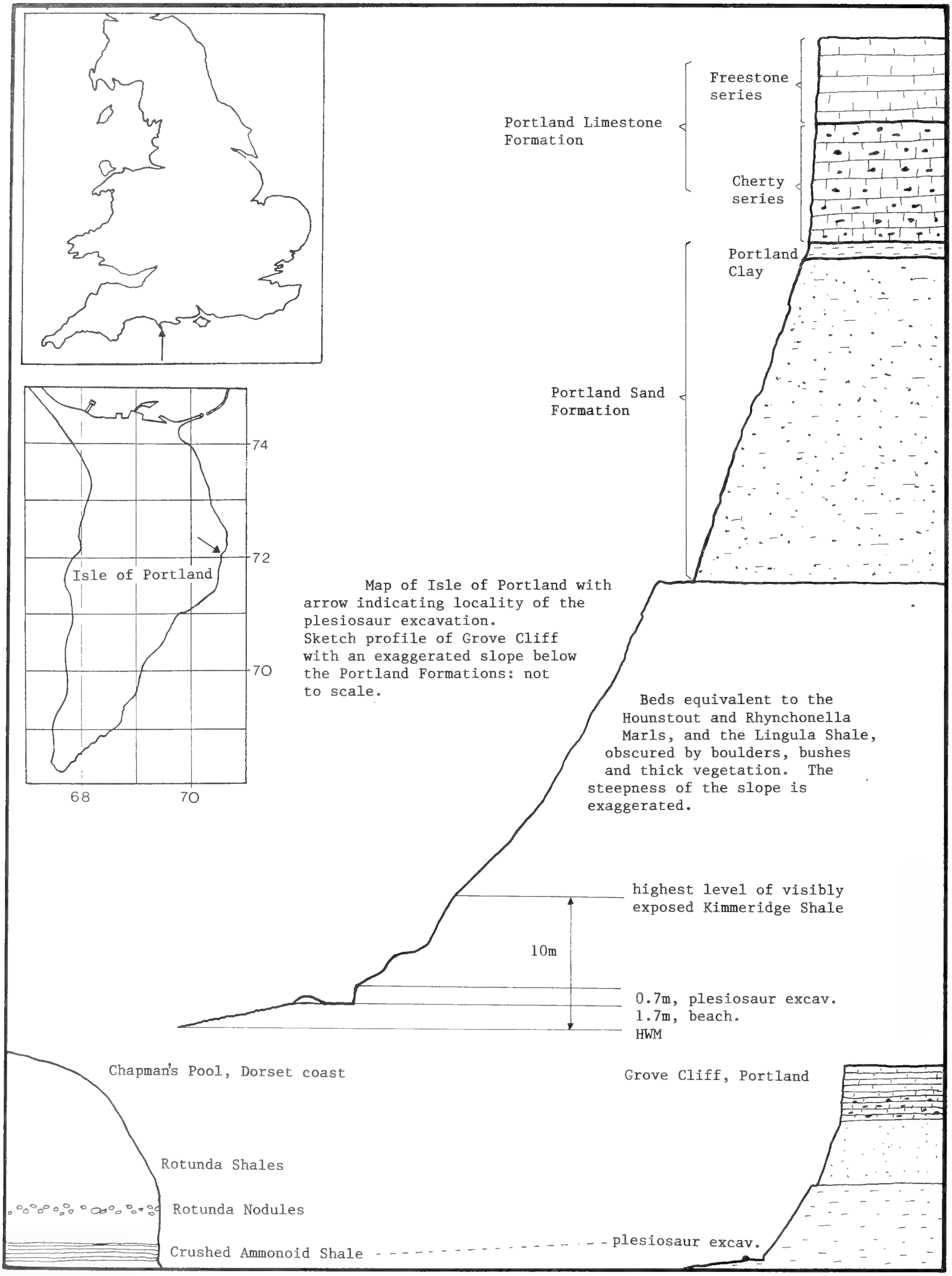
Some of the better-preserved spat were selected for photography under the scanning electron microscope (SEM) of the BM(NH) EM Unit, using low magnification of uncoated specimens as recommended by Taylor (1986). The SEM micrographs form the basis of Plates 1–5 of this report, except Plate 2, figs 9–11. The latter were made with normal light photography since the shell of *Plagiostoma gigantea* was too large to fit into the 'environmental chamber' of the SEM, while the prodissoconchs were not sufficiently well preserved to allow accurate measurements to be made.

All the material is deposited in the BM(NH) Dept. of Palaeontology.

DEFINITION OF TERMS

The following terms are used in describing bivalve larval development, and are listed in order of development.

1. Non-incubatory: release of gametes into sea where fertilization and larval development takes place.
2. Incubatory: retention of fertilized eggs within the mantle cavity by female and released at veliger stage.
3. Trochophore: non-feeding invertebrate larval stage with biconical outline, and with a ciliated equatorial band and an apical tuft.
4. Planktotrophic: feeding in the plankton.
5. Lecithotrophic: obtaining nourishment for development from the yolk of an egg.
6. Veliger: feeding molluscan larval type following on from trochophore stage. Veligers develop a shell, have a through gut and a ciliated swimming velum in an anteroventral position.
7. Velum: bi- to multi-lobed ciliated tissue developed from either side of the head in gastropods, or anterior to the foot in bivalves.
8. Prodissoconch: complete larval shell of bivalve mollusc up to metamorphosis.
9. Prod. I: initial area of prodissoconch laid down as a single sheet of shell by the shell gland, but lacking co-marginal growth.
10. Prod. II: region of prodissoconch with co-marginal growth increments.



Map of Isle of Portland with arrow indicating locality of the plesiosaur excavation.
Sketch profile of Grove Cliff with an exaggerated slope below the Portland Formations: not to scale.

Beds equivalent to the Hounstout and Rhynchonella Marls, and the Lingula Shale, obscured by boulders, bushes and thick vegetation. The steepness of the slope is exaggerated.

Fig. 1 Diagram of section and maps showing occurrences of material described.

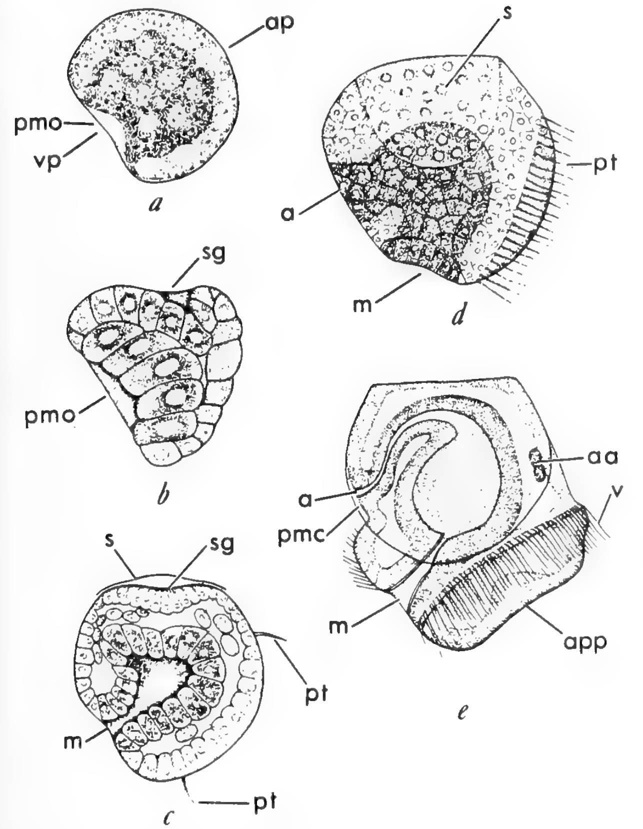


Fig. 2 Early development of *Ostrea edulis*, redrawn from Horst (1882), with presumptive dorsal region (shell gland and later the hinge) at top and anterior to right: *a*, gastrula; *b*, early trochophore; *c*, middle trochophore; *d*, late trochophore; *e*, early veliger. (a = anus, aa = anterior adductor, ap = animal pole, app = apical pit, m = mouth, pmc = presumptive mantle cavity, pmo = presumptive mouth opening, pt = prototroch, s = shell, sg = shell gland, v = velum, vp = vegetal pole.) (Fig. 1 of Waller, 1981.)

11. Pediveliger: terminal phase of Prod. II when larva briefly develops a foot for crawling and searching for a suitable substrate for cementation.
12. Metamorphosis: loss of velum, foot and change of shell growth direction, accompanying settlement of veliger, cementation and beginning of benthic mode of life.
13. Dissoconch: co-marginal shell growth after metamorphosis, together with internal shell thickening.

DESCRIPTION OF MATERIAL

Liostrea plastica (Trautschold 1860) Fig. 4; Plates 1, 2

See Kelly (1984) for synonymy, which includes *Liostrea bononia* (Sauvage & Rigaux, 1871).

MATERIAL. 56 juveniles with prodissoconchs well preserved, 51 RV and 5 LV; together with 60 pediveliger prodissoconchs, with no dissoconch growth, which are all more or less crushed and distorted. Figured specimens LL41326–32, BM(NH).

DESCRIPTION. More or less equivalve, strongly opisthogyrous, longer than high, demarcation between Prod. I and Prod. II not sharply defined, Prod. II with around 30 concentric ridges covering about 0·8 of the height; junction between prodissoconch and dissoconch at metamorphosis very sharply defined with a tendency for final four or five concentric ridges to become crowded. The colour of the prodissoconch in daylight is a pale bluish grey; that of the dissoconch a dark brownish grey.

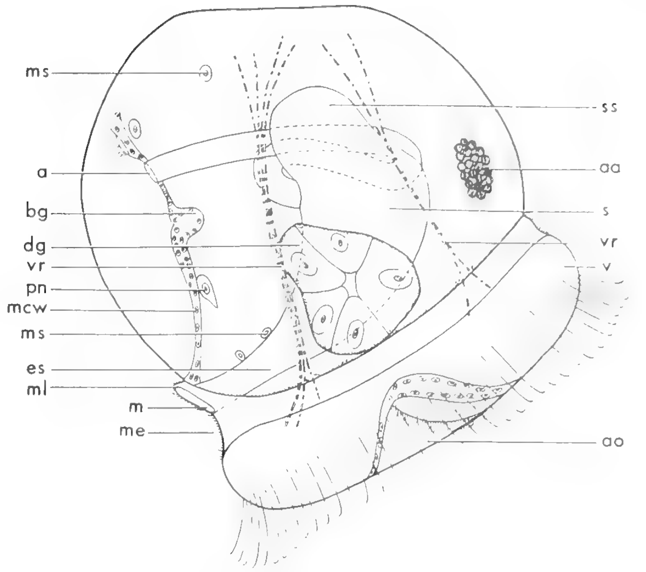


Fig. 3 Anatomy of a young, newly released, six-day-old veliger larva of *Ostrea edulis*, redrawn from Erdmann (1935). (a = anus, aa = anterior adductor, ao = apical organ, bg = primordial byssal gland, dg = digestive gland, es = esophagus, m = mouth, mcw = mantle cavity wall, me = mouth embayment, ml = mouth lobe, ms = free mesenchymal cell, pn = protonephridium, s = stomach, ss = style sac, v = velum, vr = velar retractor.) (Fig. 2 of Waller, 1981.)

DIMENSIONS. 50 prodissoconchs on the umbones of juveniles were measured for height (h) and length (l); then h/l was calculated as a percentage, together with mean, maximum, minimum and standard deviation for height, length and h/l(%). This is summarized in Table 1, with standard deviation, SD, based on n–1.

Table 1 Dimensions of prodissoconchs of *Liostrea plastica* (Trautschold).

	Mean	Max.	Min.	SD
height µm	368·8	480	310	33·73
length µm	435·6	520	360	38·9
h/l %	85·2	110·5	75·0	7·59

A histogram showing the frequency distribution of height and length is given in Fig. 6.

DISCUSSION. Comparison of larval shell of *Liostrea* and *Ostrea* (Waller 1981: figs 33, 66, 67, 137, 141, 142; and Plates 1 and 2 herein) show that, though both are undoubtedly oysters, the larval shells are very different. The shell of *Liostrea* has the overall appearance of a heterodont bivalve while the ribs remind one of *Astarte* or a venerid bivalve; *Ostrea edulis*, by contrast, has a smooth and rounded subspherical outline with

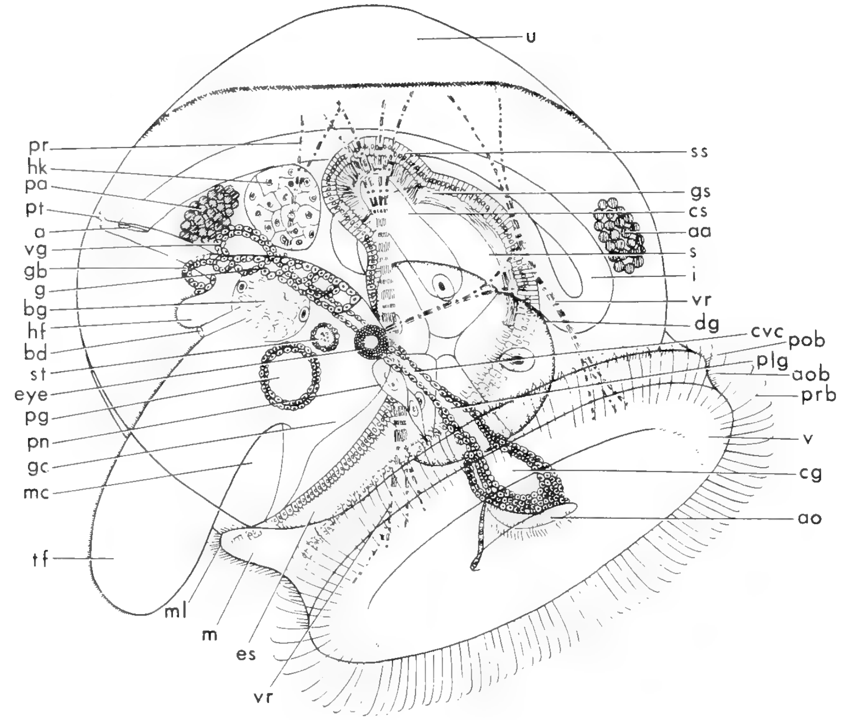


Fig. 4 Anatomy of a pediveliger larva of *Ostrea edulis*, redrawn from Erdmann (1935). (a = anus, aa = anterior adductor, ao = apical organ, acb = adoral ciliary band, bd = byssal gland duct, bg = byssal gland, cg = cerebral ganglion, cs = crystalline style, cvc = cerebropleural–visceral connective, dg = digestive gland, es = esophagus, eye = eye, g = gill primordium, gb = gill bridge, gc = gill cavity, gs = gastric shield, hf = heel of foot, hk = primordium of heart and kidney, i = intestine, m = mouth, mc = mantle cavity, ml = mouth lobe, pa = posterior adductor, pg = pedal ganglion, plg = pleural ganglion, pn = protonephridium, pob = postoral ciliary band, pr = pedal retractor, prb = preoral ciliary band, pt = postanal ciliary tuft, s = stomach, ss = style sac, st = statocyst, tf = toe of foot, u = umbo, v = velum, vg = visceral ganglion, vr = velar retractor.) (Fig. 3 of Waller, 1981.)

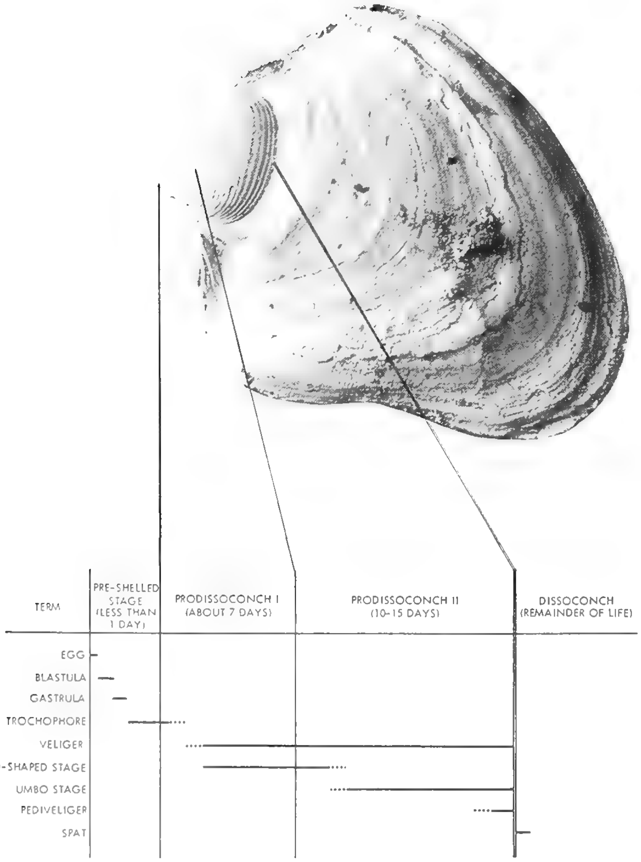


Fig. 5 Correlation of development stages of *Ostrea edulis* with *Liostrea plastica*. (Modified after fig. 4 of Waller, 1981.)

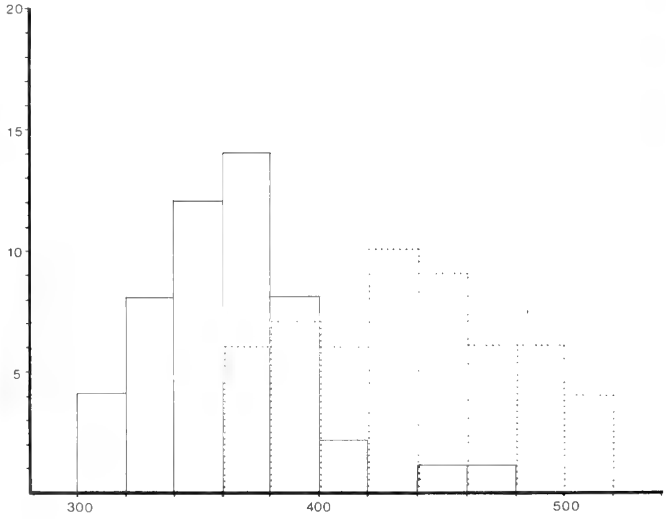
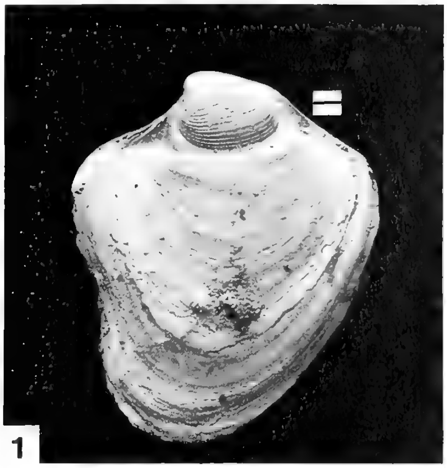


Fig. 6 Frequency distribution of height and length of pediveliger of *Liostrea plastica* at metamorphosis. The *x* axis represents dimensions in microns μ; *y* axis represents frequency; solid lines = height; dotted lines = length.

a relatively large Prod. I development (Waller 1981: figs 90–96) compared with Prod. II.

Ostrea edulis does not release gametes into the sea where external fertilization can take place, but employs a more advanced reproductive strategy. Instead, nearby males release sperm into the sea which is drawn into the female mantle cavity by feeding currents, where it fertilizes eggs contained in a 'brood pouch'. Zygotes then undergo development through blastula, gastrula and trochophore stages within the egg (Fig. 2), at which stage they are released as free swimming veliger larvae (Fig. 3).

Fig. 5 is an adaptation of Waller's (1981: 11, fig. 4) diagram correlating the development stages of the living *Ostrea edulis*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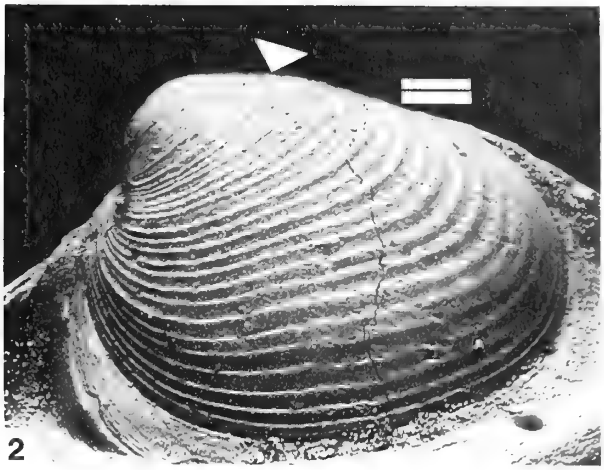
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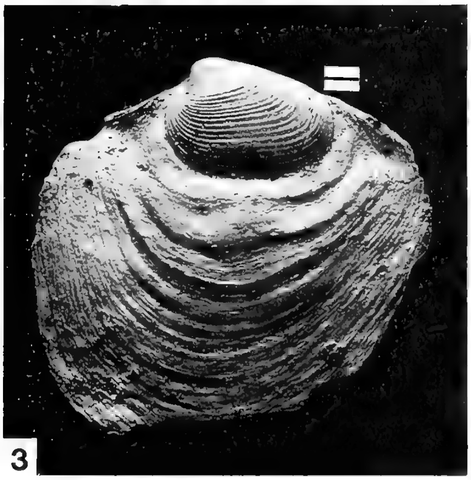
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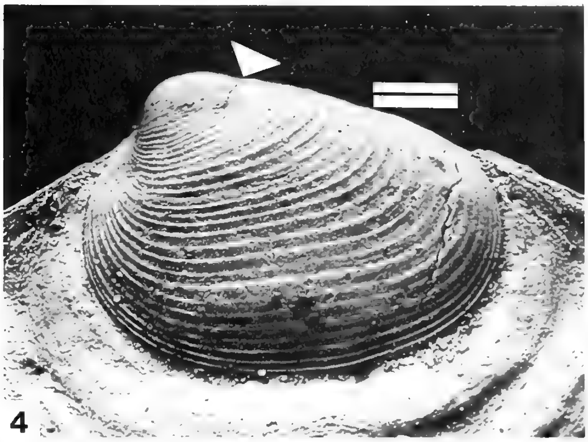
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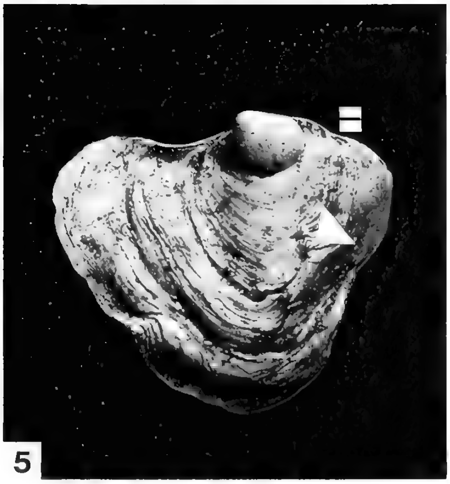
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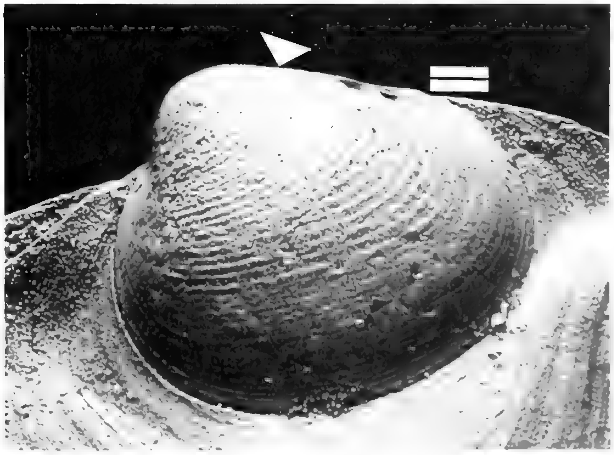


PLATE 1 *Liostrea plastica*.

Fig. 1 Complete right valve of juvenile with prodissoconch, LL41326; scale bar = 100 μ.

Fig. 2 Enlarged view of prodissoconch in fig. 1; arrow indicates inferred Prod. I/Prod. II boundary; scale bar = 50 μ.

Fig. 3 Right valve, broken ventrally, with prodissoconch, LL41327; scale bar = 100 μ.

Fig. 4 Enlarged view of prodissoconch in fig. 3; arrow indicates inferred Prod. I/Prod. II boundary; scale bar = 50 μ.

Fig. 5 Right valve of juvenile with prodissoconch, showing shell repair in dissoconch (arrow) and pronounced development of posterior margin, LL41328; see also Pl. 2, fig. 3 for enlarged view of repair; scale bar = 100 μ.

Fig. 6 Enlarged view of prodissoconch in fig. 5; arrow indicates inferred Prod. I/Prod. II boundary; scale bar = 50 μ.

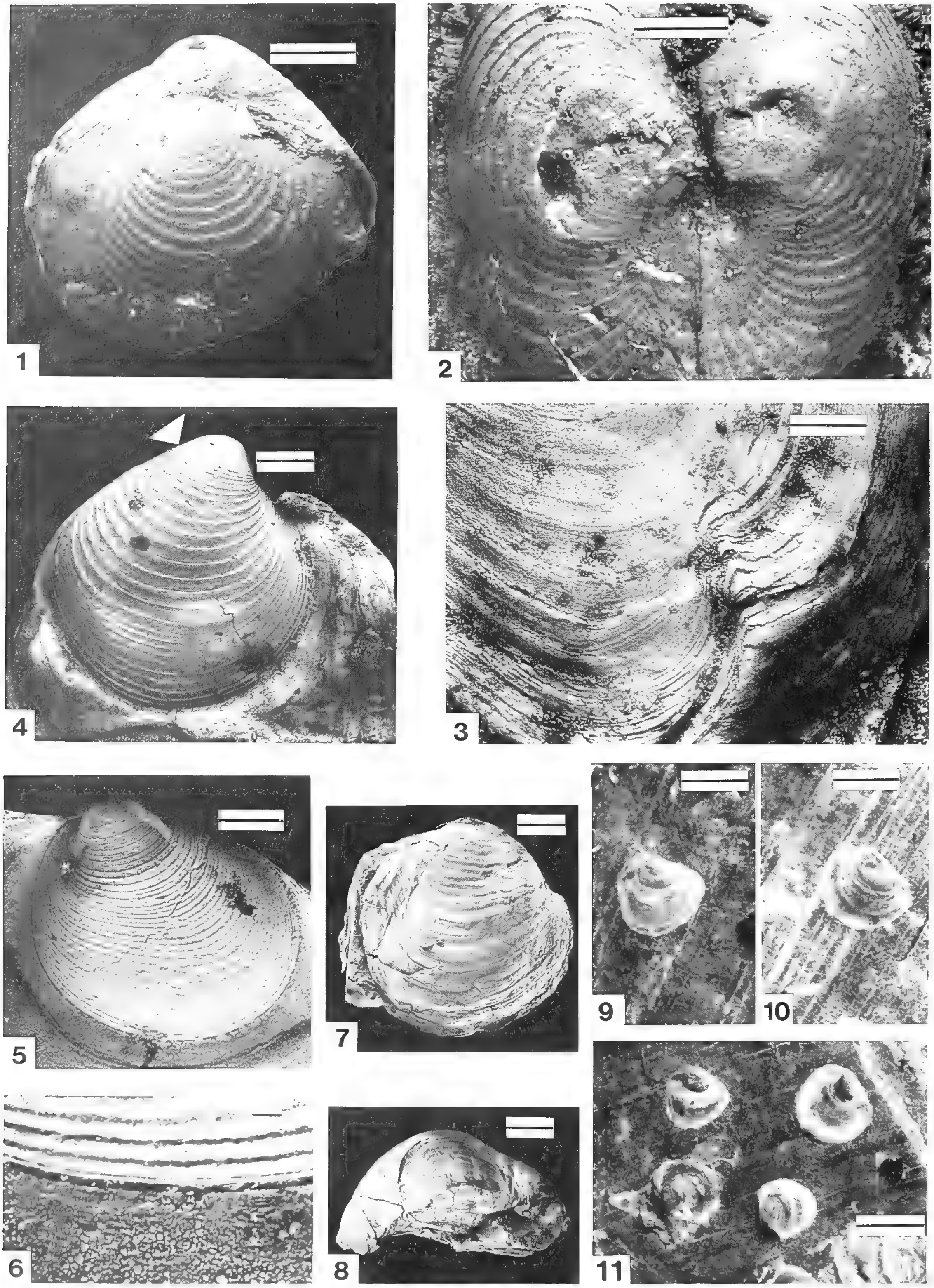


PLATE 2 *Liostrea plastica*, figs 1–8; *Liostrea irregularis*, figs 9–11.

Fig. 1 Uncrushed complete pediveliger viewed from right valve, LL41329; arrow indicates inferred Prod. I/Prod. II boundary; scale bar = 100 μ.

Fig. 2 Enlarged posterodorsal view of fig. 1, right valve on the right; no evidence of posterodorsal notch; scale bar = 50 μ.

Fig. 3 Enlarged view of the shell repair shown in Pl. 1, fig. 5, LL41328; scale bar = 100 μ.

Fig. 4 Left valve of juvenile with prodissoconch showing very high h/l % ratio and clear Prod. I/Prod. II boundary (arrow), LL41330; scale bar = 100 μ.

Fig. 5 Prodissoconch with well-defined boundary with dissoconch at metamorphosis, LL41331; scale bar = 100 μ.

Fig. 6 Enlarged view of prodissoconch/dissoconch boundary shown in fig. 5; scale bar = 10 μ.

Fig. 7 Complete right valve of adult *Liostrea plastica* showing xenomorphic 'ornament' on posterior surface, LL41332; scale bar = 10 mm.

Fig. 8 Dorsal view of fig. 7; scale bar = 10 mm.

Figs 9–11 Right valves of juvenile *Liostrea irregularis* attached to *Plagiostoma gigantea*, from the Lower Jurassic, Hettangian, Angulata Zone of Southam, Warwick, LL41333; scale bars = 1 mm.

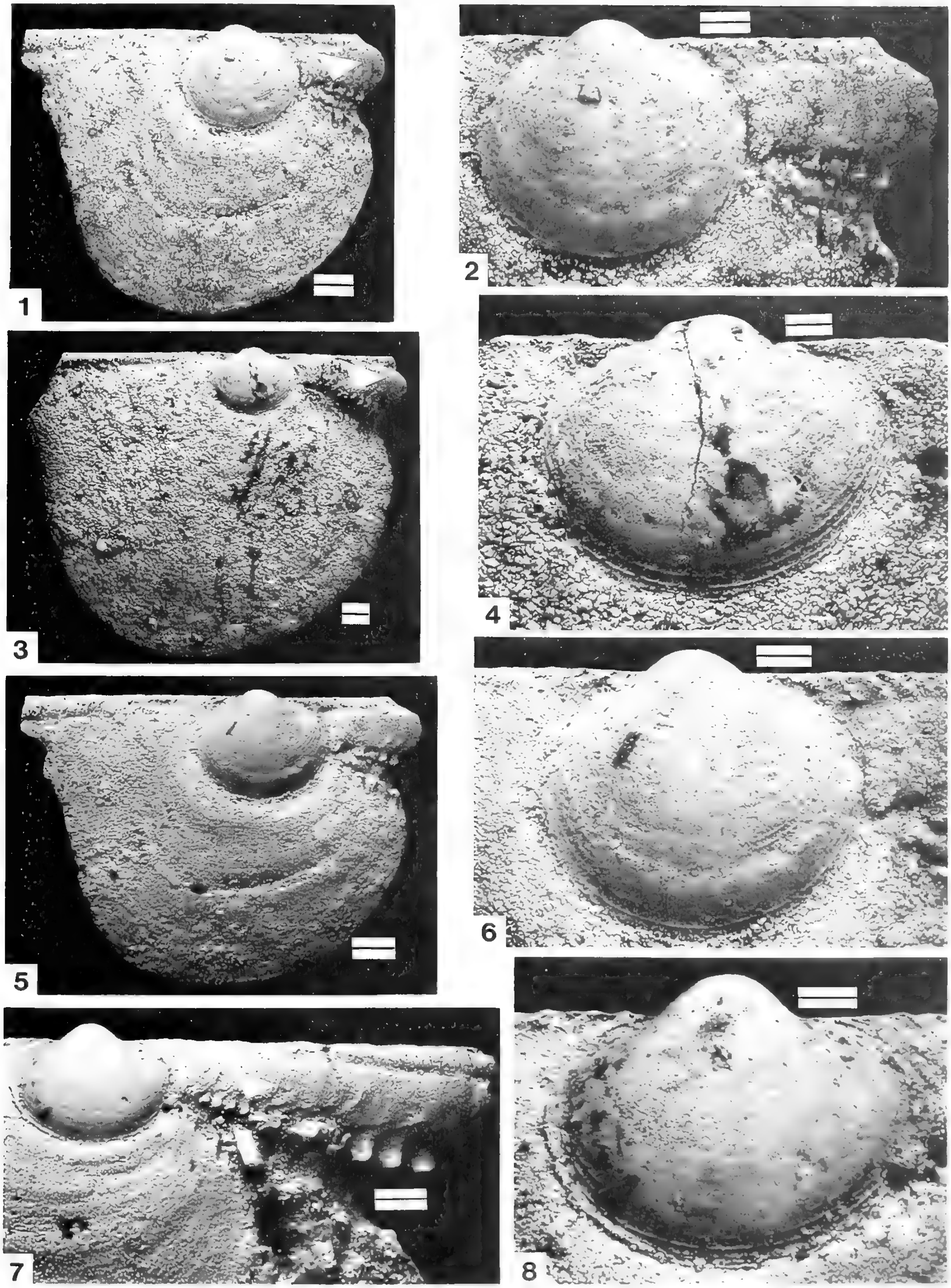


PLATE 3 *Oxytoma* sp., right valves only.

Fig. 1 Complete juvenile with prodissoconch and early development of ctenolium (arrow), LL41334; scale bar = 100 μ.
Fig. 2 Enlarged view of prodissoconch shown in fig. 1; scale bar = 50 μ.
Fig. 3 Juvenile with prodissoconch and well-developed ctenolium (arrow), LL41335; scale bar = 100 μ.
Fig. 4 Enlarged view of prodissoconch shown in fig. 3; scale bar = 50 μ.
Fig. 5 Complete juvenile with prodissoconch, LL41336; scale bar = 100 μ.
Fig. 6 Enlarged view of prodissoconch shown in fig. 5; scale bar = 50 μ.
Fig. 7 Enlarged section of anterodorsal region of juvenile showing ctenolium (arrow) and prodissoconch, LL41337; scale bar = 100 μ.
Fig. 8 Enlarged view of prodissoconch shown in fig. 7; scale bar = 50 μ.

with *Liostrea* from the Kimmeridge Clay. The duration of stages given at the head of the column are for *Ostrea edulis* only. Stages from egg to trochophore are short, less than a day: the change from trochophore to veliger larva marks the initiation of primary shell, laid down in one sheet by the shell gland and lasting about seven days – Prod. I. Co-marginal growth produces the concentric ridges and the development of an umbo during 10–15 days – Prod. II. Though the number of concentric ridges formed by *Liostrea* during Prod. II is variable, the mean of seven specimens was 29 ridges, almost twice the maximum number of days, 15, taken by *Ostrea edulis* to pass through Prod. II phase. On the assumption, therefore, that each concentric ridge represents 1 day's growth, this implies that the larval planktotrophic Prod. II phase of *Liostrea* would be roughly twice as long as in *O. edulis*. Since *O. edulis* incubates its eggs it can be expected to have a short planktotrophic veliger phase, which is normal for incubatory molluscs. If *Liostrea* did not incubate its eggs then a longer larval stage might be expected, so the implied discrepancy between the Prod. II phases of *O. edulis* and *Liostrea* may not be inconsistent with known larval durations.

At the end of Prod. II the veliger sinks to the sea floor to begin its benthic existence, and develops a foot (pediveliger phase), with which it crawls about searching for a suitable substrate upon which to cement itself by the left valve. During this phase the velum atrophies, while the shell retains the form of the prodissoconch. Upon cementation the foot also begins to atrophy, and the shell changes colour and growth direction, forming the familiar oyster-shape of the dissoconch. The junction between prodissoconch and dissoconch shell growth is sharply demarcated on all spat examined.

Clearly, the brief pediveliger phase is critical in the life of an oyster. If no suitable substrate is found then the oyster cannot cement itself and will almost certainly die. Similarly, high mortality at this phase is evident in the large number of crushed and distorted prodissoconchs of *Liostrea*, easily identified by their pale bluey-grey colour, with no dissoconch growth.

Liostrea irregularis (Münster, 1833) Pl. 2, figs 9–11

See Stenzel 1971 for synonymy.

MATERIAL. A *Plagiostoma gigantea* J. Sowerby 1814, 115 mm in length, with numerous adherent juvenile oysters most of which are under 1·3 mm in length with prodissoconchs in place. Associated with these is an adult *Liostrea irregularis* 49 mm in height, on the evidence of which the juvenile oysters are assigned to Münster's species. LL41333, BM(NH).

DESCRIPTIONS AND DIMENSIONS. Shells apparently smooth with strongly opisthogyrous umbones coinciding with the posterior edge, resembling in outline the nuculoid *Nuculoma*. The demarcation between Prod. I and Prod. II is far from clear in most specimens, but Plate 2, fig. 9 shows a prodissoconch RV with a shining hemispherical dome which is one eighth of the length of the prodissoconch. Rough measurements, made on a scaled photograph, indicate the length of prodissoconch at *c*. 0·5 mm; the Prod. I stage is thus of the order of *c*. 60 µm across. These measurements are the best the author could achieve.

Oxytoma sp. Plates 3, 4

MATERIAL. 52 juvenile shells with prodissoconchs well preserved, 16 RV and 36 LV. Figured specimens LL41334–41, BM(NH).

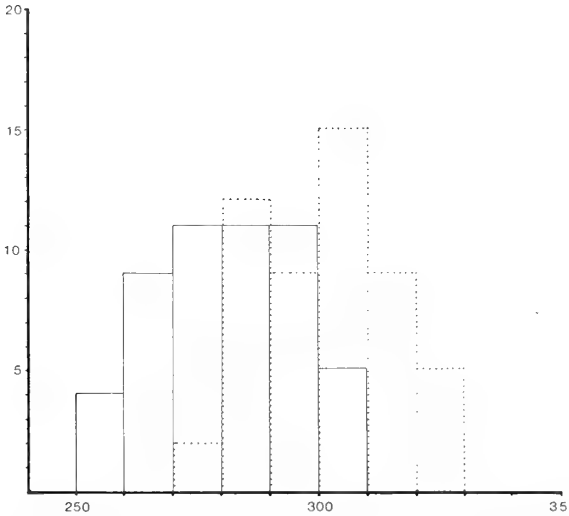


Fig. 7 Frequency distribution of height and length of prodissoconch of *Oxytoma* sp. at metamorphosis. The *x* axis represents dimensions in microns µ; *y* axis represents frequency; solid lines = height; dotted lines = length.

DESCRIPTION. Equivalve, almost ovate in outline with a prominent and centrally placed, rounded umbo interrupting the dorsal outline; slightly longer than tall, shell almost smooth but with fewer than 14 faint concentric ridges at the anterior and posterior surfaces, and fewer than 3 along the ventral margin. The junction between Prod. I and Prod. II is obscure and the faint concentric ridges give no clear indication where it is. No pediveliger two-valved specimens, lacking dissoconch growth, were seen in the picked sample, though there would have been no difficulty in recognizing them if present. Colour of prodissoconch in daylight not distinguishable from the dark brownish grey of the dissoconch.

DIMENSIONS. Though left and right valves were measured separately, no significant difference was observed so that, for purposes of calculation, left and right valves were taken together in Table 2; n = 52.

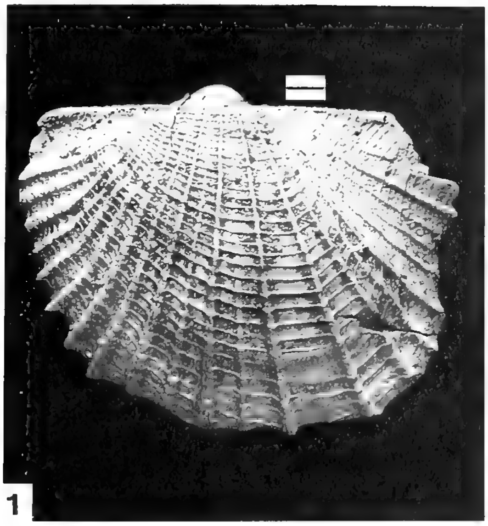
Table 2 Dimensions of prodissoconchs of *Oxytoma* sp.

	Mean	Max.	Min.	SD
height µm	276·5	300	250	14·8
length µm	295·9	320	270	13·7
h/l %	93·68	103·57	84·97	3·76

A histogram showing the frequency distribution of height and length is given in Fig. 7.

DISCUSSION. An unresolved difficulty lies in assigning these juvenile *Oxytoma* to an adult named form. L. R. Cox held the view that *O. inequivalvis* ranged almost throughout the Jurassic: W. J. Arkell held that it was confined to the Lower Jurassic. Until the stratigraphical taxonomics of this group are worked out the species name of these prodissoconchs is best left open.

Waller (1984) reminds us of three forms of ctenolium structures to be distinguished. A true ctenolium is formed by the mantle along the margin of the disc beneath the auricular notch. It is composed of lathic calcite, part of the internal structure of the shell. He compares this with the callus, or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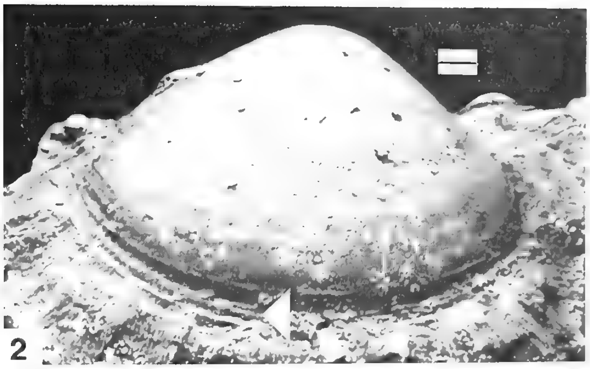
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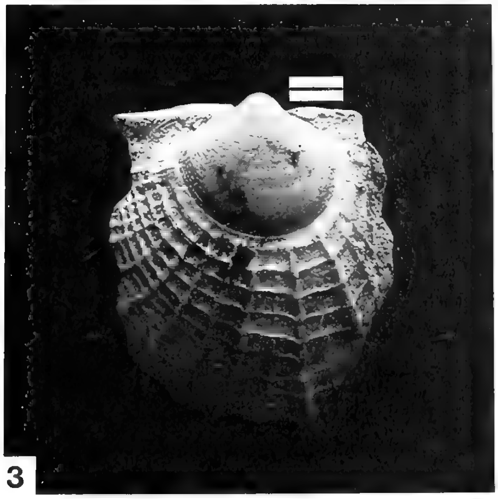
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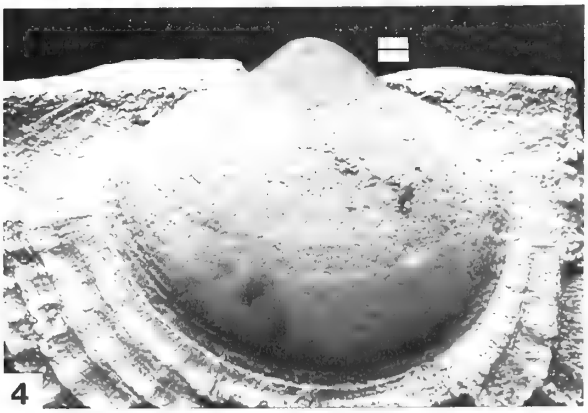
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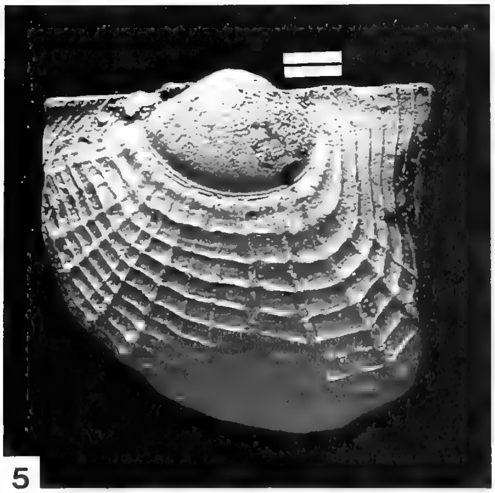
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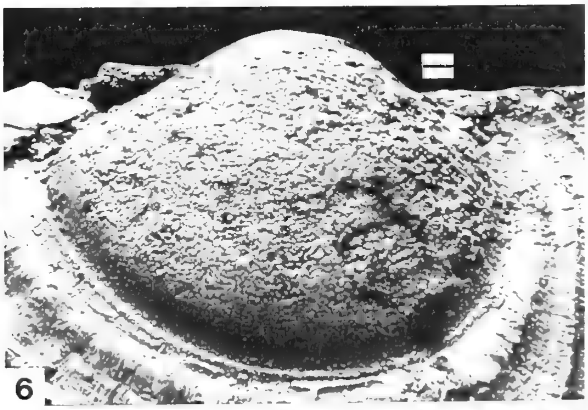
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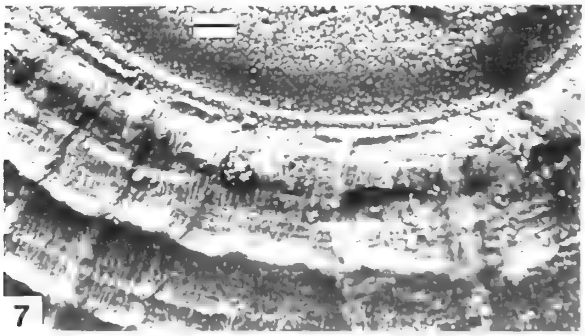
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PLATE 4 *Oxytoma* sp., left valves only.

Fig. 1 Advanced juvenile with prodissoconch showing scalariform 'ornament', LL41338; scale bar = 200 µ.

Fig. 2 Enlarged view of prodissoconch of another specimen, LL41339, showing four strong growth halts at prodissoconch/dissoconch boundary (arrow); scale bar = 20 µ.

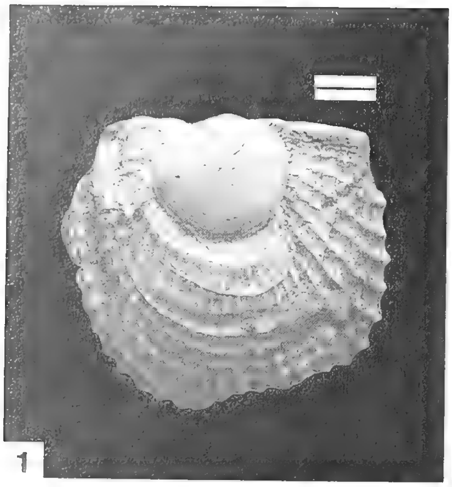
Fig. 3 Broken juvenile with prodissoconch, LL41340; scale bar = 100 µ.

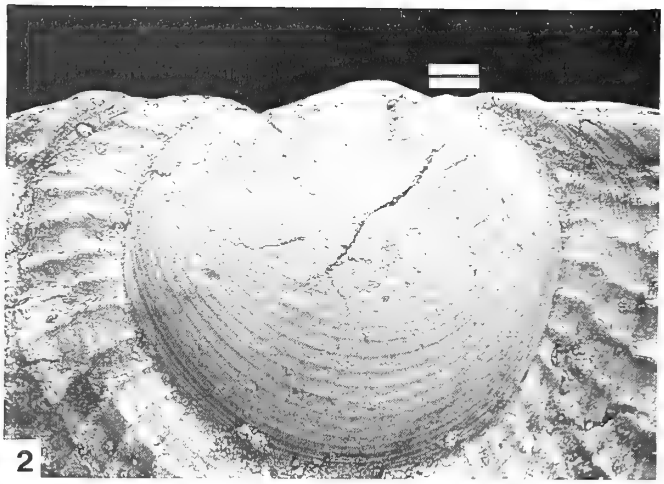
Fig. 4 Enlarged view of prodissoconch in fig. 3, showing growth halts at prodissoconch/dissoconch boundary and immediate fine divaricate 'ornament' ventral to the boundary; scale bar = 20 µ.

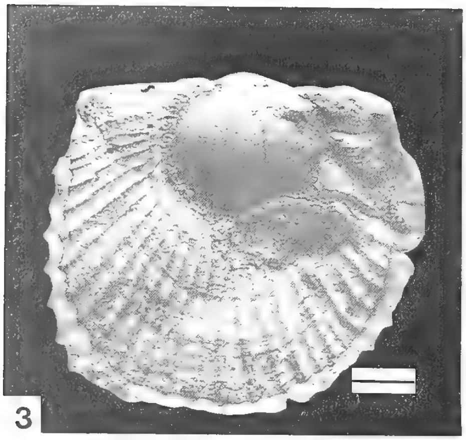
Fig. 5 Juvenile with prodissoconch, LL41341; scale bar = 100 µ.

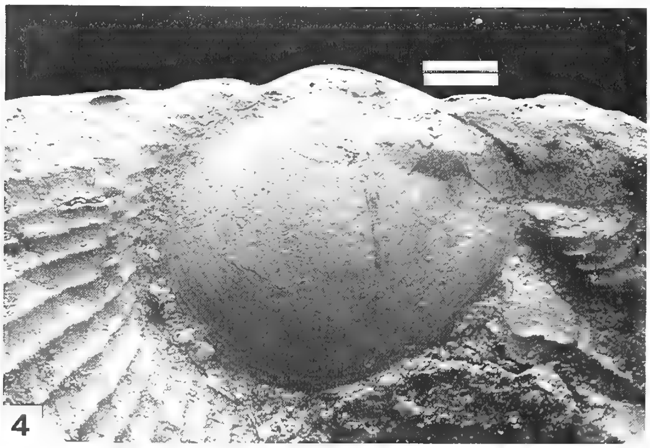
Fig. 6 Enlarged view of prodissoconch of fig. 5, showing two pronounced growth halts at prodissoconch/dissoconch boundary; scale bar = 20 µ.

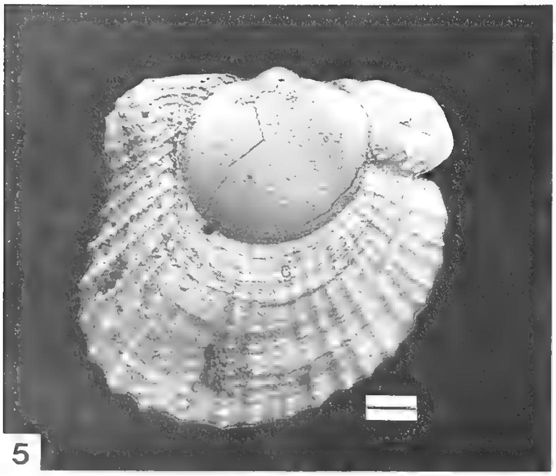
Fig. 7 Enlarged view of fig. 5 showing immediate formation of radial ribs and divaricate 'ornament' ventral to prodissoconch/dissoconch boundary; scale bar = 20 µ.











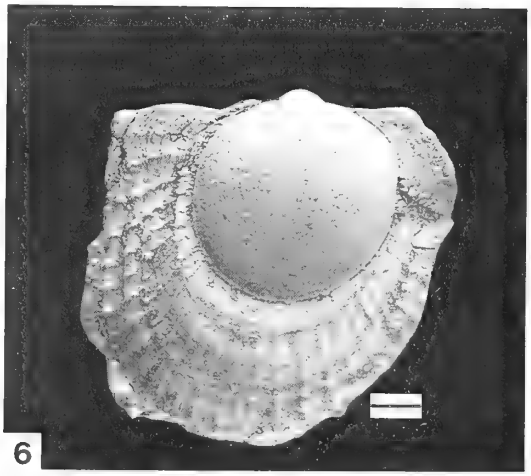


PLATE 5 *Meleagrinella* sp.

Fig. 1 Complete left valve with prodissoconch, LL41342; scale bar = 200 μ.

Fig. 2 Enlarged view of prodissoconch of fig. 1, showing approximation of growth halts before prodissoconch/dissoconch boundary, and immediate formation of radial ribs after boundary; scale bar = 50 μ.

Fig. 3 Complete two-valved juvenile viewed from right valve, LL41343; scale bar = 200 μ.

Fig. 4 Enlarged view of prodissoconch in fig. 3, slightly crushed anteriorly, showing ctenolium formed immediately after metamorphosis; scale bar = 50 μ.

Fig. 5 Complete right valve with prodissoconch and well-developed anterior auricle, showing three teeth of ctenolium (arrow), LL41344; scale bar = 100 μ.

Fig. 6 Complete right valve with larger than average prodissoconch and obscurely developed anterior auricle (arrow), LL41345; scale bar = 100 μ.

inductura, of gastropods. A pseudoctenolium is a similar line of denticles in the same position, but composed of the primary shell layer, prismatic calcite. A third category is a line of denticles on the ventral side of the right anterior auricle (Pl. 3, fig. 7). The juveniles illustrated in Plate 3 show clearly that auricular spines and a pseudoctenolium are present, since the latter is composed of prismatic calcite which is continuous with the disc (Pl. 3, fig. 2). This simply confirms Waller's earlier observation and is illustrated in his (1984) figure 3c.

Waller succinctly summarizes the function of the ctenolium as follows. 'The function of the ctenolium is to separate the threads of the byssus by hooking the threads and preventing their accumulation in the apex of the byssal notch. The flat band of byssal threads passing over the disk flank when the foot is retracted is more resistant to rotational forces on the shell than would be a cord-like narrow strand of threads. The byssal attachment is thereby strengthened' (1984: 217).

Pl. 3, figs 1–6 and Pl. 4. fig. 7 confirm that prismatic calcite is confined to the right valve only in *Oxytoma*.

Meleagrinella sp. Plate 5

MATERIAL. 57 juvenile shells with prodissoconchs well preserved, 42 RV and 15 LV. Figures specimens LL41342–5, BM(NH).

DESCRIPTION. Almost equivalve, outline subcircular, with small, centrally placed umbones interrupting the dorsal outline; shell surface with faint concentric growth ridges apparently terminating at the base of rounded hemispherical umbones. The junction between Prod. I and Prod. II is assumed to be at the position where faint concentric ridges terminate at the base of the umbones. No pediveligers were seen, though, again, they would have been clearly apparent if present, these prodissoconchs being noticeably larger and rounder than those of either *Liostrea* or *Oxytoma*. About 26–30 concentric ridges were counted from the base of the umbones to the prodissoconch/dissoconch boundary. The anterior edge shows a faint inflection at the point where the anterior auricular notch will be developed in the dissoconch (Pl. 5, fig. 6). The colour of the prodissoconch and dissoconch is not noticeably different.

DIMENSIONS. Since left and right valves were not significantly different in height and length dimensions, they were calculated together; but note that 57 lengths were measured, but only 54 heights and 54 h/l% calculations.

Table 3 Dimensions of prodissoconchs of *Meleagrinella* sp.

	Mean	Max.	Min.	SD
height µm	398·2	440	360	21·44
length µm	403·9	440	340	20·94
h/l %	98·95	105·88	90	3·76

A histogram showing the frequency distribution of height and length is given in Fig. 8.

DISCUSSION. Since no adult specimens of *Meleagrinella* were seen in the macrofauna it is not possible to assign these prodissoconchs and juveniles to a species. The relatively large size of these compared with *Oxytoma*, together with the count of approximately 24–30 concentric ridges, suggests, if each ridge represents a day's growth, that these veligers had a long larval life. In view of their absence in the macrofauna it is evident that the benthic conditions were not suitable for their development. This reminds us of Thorson's (1950: 17) observation that veligers, and other invertebrate larvae, can prolong their larval life until a suitable substrate is found.

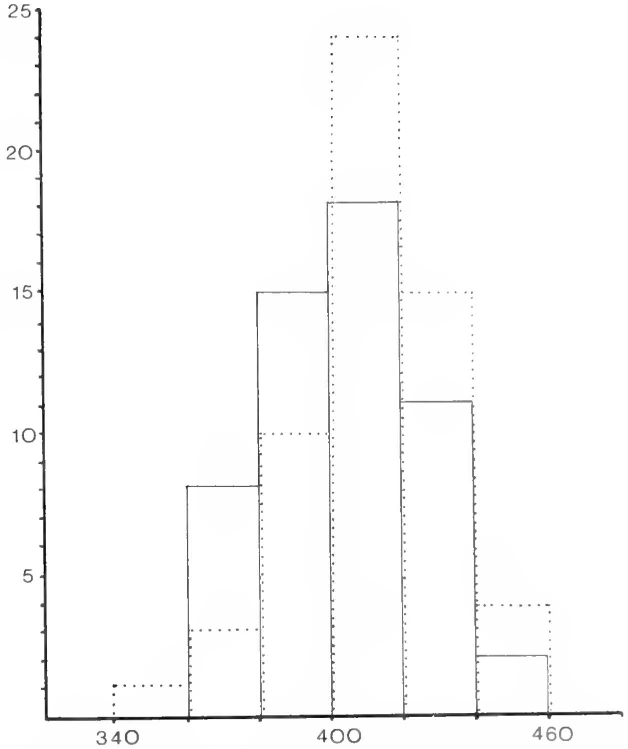


Fig. 8 Frequency distribution of height and length of prodissoconch of *Meleagrinella* sp. at metamorphosis. The *x* axis represents dimensions in microns µ; *y* axis represents frequency; solid lines = height; dotted lines = length.

The auricular notch indicates a functioning byssus, but no trace of a ctenolium or pseudoctenolium was seen. The ventral edge of the right anterior auricle does, however, display a series of rounded knobs each of which coincides with a growth line (Pl. 5, fig. 5). These, though functioning as a ctenolium, are analogous with Waller's (1984) 'auricular spines', seen also in *Oxytoma*.

DISCUSSION

Literature on the larval development of Jurassic bivalves is almost non-existent; though Jablonski & Lutz (1983) have assembled a vast literature dealing with the subject of larval ecology, the greater part is, not surprisingly, concentrated on living animals.

A great deal of work has been carried out on the larval development, from fertilized egg to metamorphosis, of the European oyster *Ostrea edulis* Linné 1758. Virtually all this work was brought together and amplified in a superbly illustrated synthesis by T. Waller (1981), which was used (pp. 59–64) as a basis for interpreting *Liostrea plastica*. Figs 2–5 here are modified reproductions of Waller's originals, and they alone tell the outline story of the larval development with the minimum of words, while Waller's figs 9–150 provide an abundance of detail concerning the development of the veliger larva through Prod. II to metamorphosis.

In the absence of descriptions of larval development of Pectinacea the larval shells of *Oxytoma* and *Meleagrinella* can only be described. Cope (1968) discussed the well-known oyster infestation of Upper Kimmeridgian ammonites; and figured (1968: pl. 2, fig. 2) a *Pectinatites* plastered with *Liostrea multiformis* (Koch & Dunker). He concluded that their presence as adults was 'dependent entirely on the presence of vacated ammonite shells on the sea floor'.

Palmer (1988) has argued an alternative hypothesis, since some ammonites are 'infested' on both sides, that the idea of delicate hydrostatic adjustments in ammonites implies the presence of shell-cleaning behaviour in all ammonites as being close to a biological necessity. Therefore some of the ammonites were 'infested' after the animal was dead but while the shell was still floating. The evidence seems to indicate that examples to fit both hypotheses could be present.

Thorson (1950) stressed the significance of limiting ecological factors controlling the distribution of marine invertebrates; and he isolated three which act upon the weakest link in the chain of development, the larval stage. First, it was found that the temperatures required to induce spawning are considerably higher than the normal temperature requirements of adults; second, that gamete production takes place at the top end of the salinity range tolerated by adult animals; third, the food requirements of larval marine invertebrates is between 5 and 10 times higher than for adults. In order to achieve a coincidence of these critical and very definite factors, some marine animals migrate from places that the adults can tolerate, to a place where the larvae can survive (Thorson 1950).

If the weakest link lies in the larval life where mortality is highest, then another stage of high mortality for *Liostrea* lies in the dissoconch stage, from metamorphosis to around 2 mm length. The number of pediveligers and juvenile dissoconchs up to 2 mm far exceeds the number of adult oysters collected.

No pediveligers of *Oxytoma* or *Meleagrinella* were seen, though adults of the former do occur, but not the latter; while juvenile dissoconchs, up to 2 mm, of both genera were about equally common. This again indicates a critical stage.

Clearly, then, the limiting factor is the substrate: the shales of the Kimmeridge Clay were once a soft muddy bottom which was suitable for neither cementing oysters not byssally attached pectinaceans. The lucky ones found an empty ammonite shell to grow on (Cope 1968) or a floating one (Palmer 1988). The rest did not survive growth beyond 2 mm. Several authors, including Thorson (1946, 1950), have suggested that early post settlement is the time of greatest mortality. Quantitative tests, though difficult with living animals, are virtually impossible with fossil bivalves.

If the Prod. I/Prod. II boundaries in the three genera described here have been correctly identified, then it is evident that Prod. I is an order of size smaller than Prod. II. This would rule out incubation of eggs: it therefore appears that all three genera had wholly planktotrophic development from relatively small eggs. At the same time the relatively large Prod. II phase of *Meleagrinella* may indicate a prolonged larva phase necessitated by the lack of suitable substrate for byssal attachment. It is known that larvae of molluscs can delay settlement and metamorphosis until a sutiable substrate is encountered (Thorson 1946).

PALAEOECOLOGICAL REMARKS

Palmer (1988) has argued that the plesiosaur excavation at Portland is stratigraphically equivalent to Cope's (1978) bed 2, hard bituminous shale, at Chapman's Pool on the coast of Dorset. This correlation is founded on ammonites, *Pavlovia* spp., and supported by the presence of shell beds with the same benthic and pelagic faunal elements at both localities.

Casey (1967) showed that the Upper Lydite Bed at Hartwell, Bucks, is equivalent to beds, at Chapman's Pool, from the Rotunda Nodule Bed up to the base of the Portland Sands. The Hartwell Clay below the Upper Lydite Bed is therefore equivalent to shales below the Rotunda Nodule Bed at Chapman's Pool; that is, bed 2. The correlation is supported by the arcticid bivalve *Venericyprina argillacea* Casey, present in the Hartwell Clay and also at Chapman's Pool, and in the plesiosaur excavation at Portland.

Lloyd *et al.* (1973) reported pavloviid ammonites in Kimmeridge Clay, 10 km north of Combe Martin in the Bristol Channel. The ammonites correlate with either bed 1 or 2 at Chapman's Pool; but the author has argued, on the evidence of cirripeds at both localities and at Portland, a correlation with bed 2 at Chapman's Pool and the plesiosaur excavation at Portland.

If these correlations are correct then it is evident that benthic shelly beds occur, at the same stratigraphical level, at Portland, Chapman's Pool and Hartwell in one direction and in the Bristol Channel in another direction. These rich benthic horizons are unlikely to be purely local events and fortuitously at the same stratigraphical level, but part of a widespread ecological event resulting in rich living for benthic communities. An abundant microfauna of ostracods and foraminiferans, together with numerous filter-feeding bivalves, fish and plesiosaurs, are all elements of an elaborate food chain founded on a widespread plankton field which was stable for several thousand years.

CONCLUSIONS

Liostrea, Oxytoma and *Meleagrinella* all had planktotrophic larvae with a prolonged veliger Prod. II stage which may have been related to a lack of suitable habitats for cementing oysters and bysally attached pectinaceans. A period of 30 days veliger Prod. II phase is suggested on the evidence of rib counts on larval shells of *Liostrea*. A high mortality characterized the phase from pediveliger to dissoconch development up to 2 mm.

Those oysters that attached themselves to empty ammonite shells, either on the sea floor or while still floating, were able to grow to maturity; but the greater majority settled on a muddy sea floor and died at 2 mm of dissoconch growth. All this took place in the context of a postulated widespread plankton field, extending, at least, from Portland to the Bristol Channel and Buckinghamshire.

Acknowledgements. I am grateful to Susan Barnes of the Electron Microscope Unit for teaching me to use a scanning electron microscope; to the Photographic Unit for producing the prints making up Plates 1–5; to Paul Taylor for helpful advice on using this unfamiliar technique; to my colleague Noel Morris for helpful discussions concerning larval development; and to Tom Waller for permission to reproduce his text-figures.

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The holotype of the Carboniferous marattialean fern *Lobatopteris miltoni* (Artis)

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SYNOPSIS. Previously reported as lost, the holotype of *Lobatopteris miltoni* (Artis) Wagner is stored in the British Museum (Natural History). The illustration published with the protologue misrepresents the proportion of pinnatifid pinnules in the frond, which has had important consequences for establishing its taxonomic position. Provisionally retained in *Lobatopteris*, it may eventually have to be transferred to another form-genus for larger, more divided fronds producing trilete spores.

INTRODUCTION

Lobatopteris miltoni (Artis) Wagner (syn. *Pecopteris miltoni* auctt.) is one of the most widely reported ferns from the Middle and Upper Carboniferous palaeo-equatorial floras, with over 200 pre-1961 references to it listed in *Fossilium Catalogus*. The traditional approach was to assign to it almost any piece of fern frond with predominantly elongate, pinnatifid pinnules. Dalinval (1960) has provided a much tighter circumscription, however, and has shown that many of the previous records were misidentifications. His is the best available analysis of the species, but one important aspect remains to be fully documented – the holotype. The only published illustration of it is the engraving accompanying the protologue (Artis 1825: pl. 14) and this does not clarify many of the details necessary to confirm Dalinval's interpretation. It has been stated that the specimen is lost (e.g. Wagner 1971), but it is in fact in the collections of the Department of Palaeontology, British Museum (Natural History). Since there are a number of discrepancies in Artis' illustration, we are providing here a photographic record of the specimen (Pl.1), together with a brief description and discussion.

Provenance and current location of specimen

The specimen was collected from 'that part of El-se-car new colliery, situated near Milton Furnace' (Artis 1825). The present-day Elsecar Colliery (NGR SE 392003) lies 1 km east of Milton, and is approximately midway between Sheffield and Barnsley. Artis gave no stratigraphical details, but the specimen was probably found near the Barnsley Seam (middle Westphalian B).

The specimen is now stored in the Department of Palaeontology, British Museum (Natural History), register no. V.4290. The wash drawing made in 1824 by J. Curtis, on which Artis based his illustration, is bound in with the museum's copy of the 1838 reprint of Artis' work.

DESCRIPTION

The specimen shows a part of a tri-/quadripinnate structure 15 cm long by 17·5 cm wide. 13 cm of primary rachis is preserved, which is 2·2–2·7 cm wide, with fine longitudinal striations.

Two secondary racheis, 0·4–0·5 cm wide, are attached 6 cm apart on the right side of the primary rachis (no secondary racheis are preserved on the left side). They are attached to the primary rachis at 50°–60°, arch sharply near their point of attachment and then lie at *c.* 80° to the primary rachis for most of their length. The secondary pinnae are parallel-sided as far as they are preserved. The longest pinna fragment is 15 cm, but is evidently very incomplete.

Tertiary racheis are attached at 80°–90° to the secondary racheis at intervals of 1·4–2·1 cm. They are *c.* 0·1 cm wide. The tertiary pinnae are parallel-sided for most of their length, and have a blunt terminal.

Most lateral pinnules are broadly attached, linguaeform to subtriangular, and lie at 60°–90° to the rachis. They are 0·6–1·0 cm long and 0·2–0·3 cm wide. The midvein is *c.* 0·05 cm wide, often decurrent at the base, and extends for at least three-quarters of the pinnule length. The pinnules are fertile, which masks details of the lateral veins. In most cases, all that remains of the sorus is the pedicle. Occasionally, however, isolated oval sporangia, *c.* 0·1 cm long, are still preserved. No structural details of the sporangia could be observed.

In the basiscopic part of the tertiary pinnae, the pinnules are more elongate, up to 1·2 cm long and 0·4 cm wide, and become pinnatifid. The pinnule lobes are rounded and *c.* 0·15 cm wide.

The apical pinnules are subrhomboidal, with a round apex, and are fused to the adjacent lateral pinnules.

DISCUSSION

Artis (1825) gave only the briefest description of the specimen:

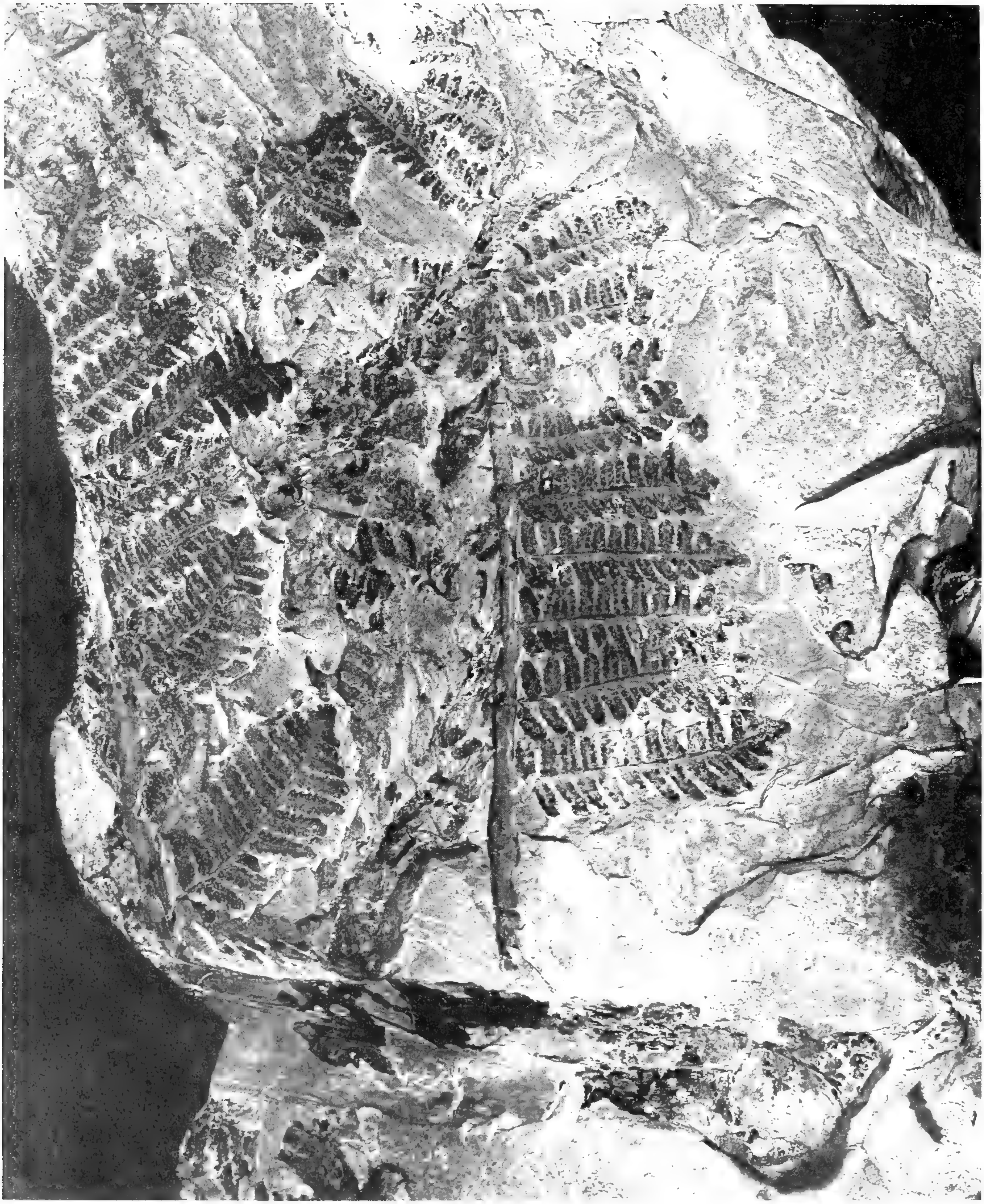

Plate 1 *Lobatopteris miltoni* (Artis) Wagner. Holotype (V.4290) photographed under cross-polarized light. Natural size.

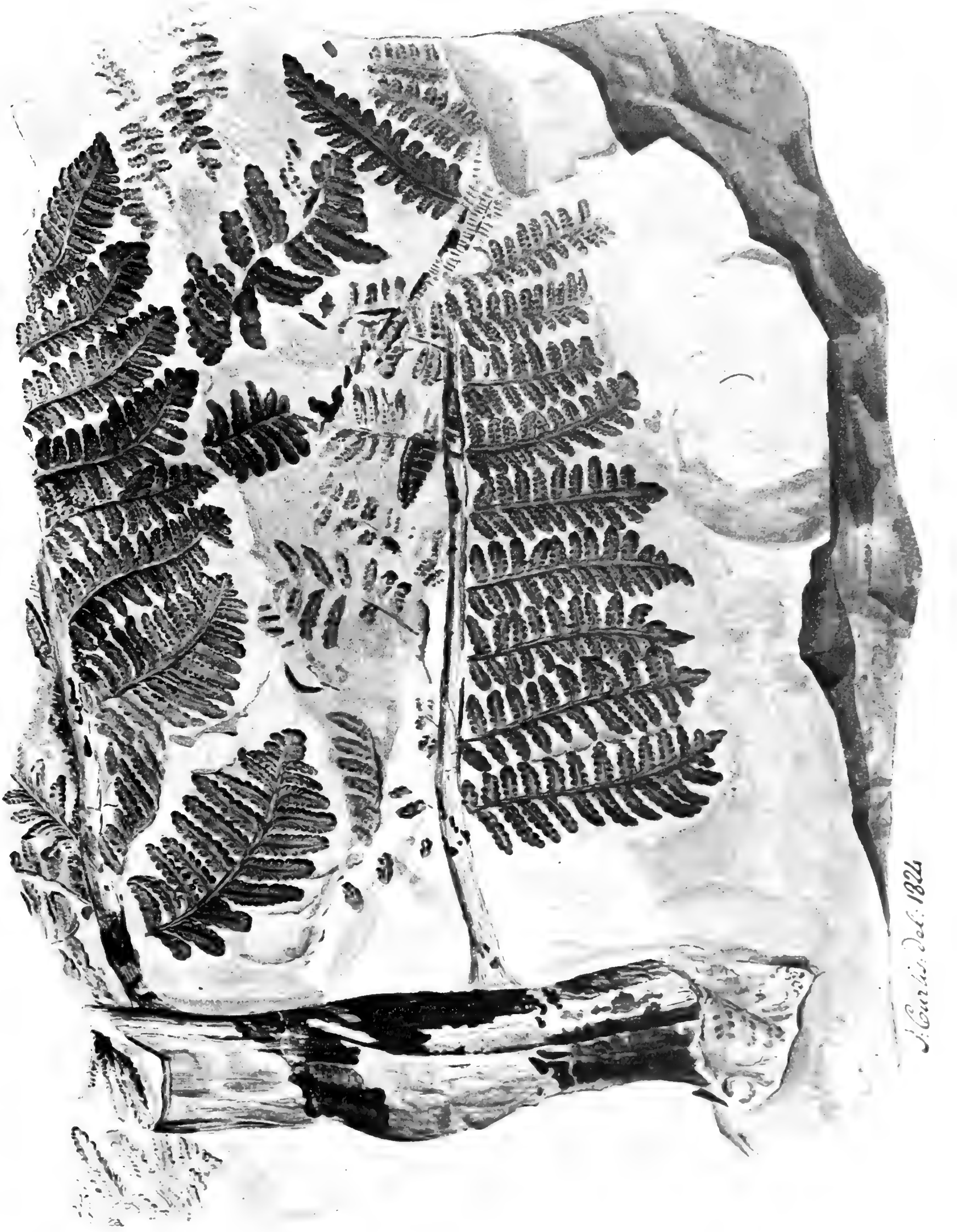

Plate 2 *Lobatopteris miltoni* (Artis) Wagner. Wash drawing of the holotype, made by J. Curtis, used as the basis for Artis' (1825: pl. 14) engraving. Natural size.

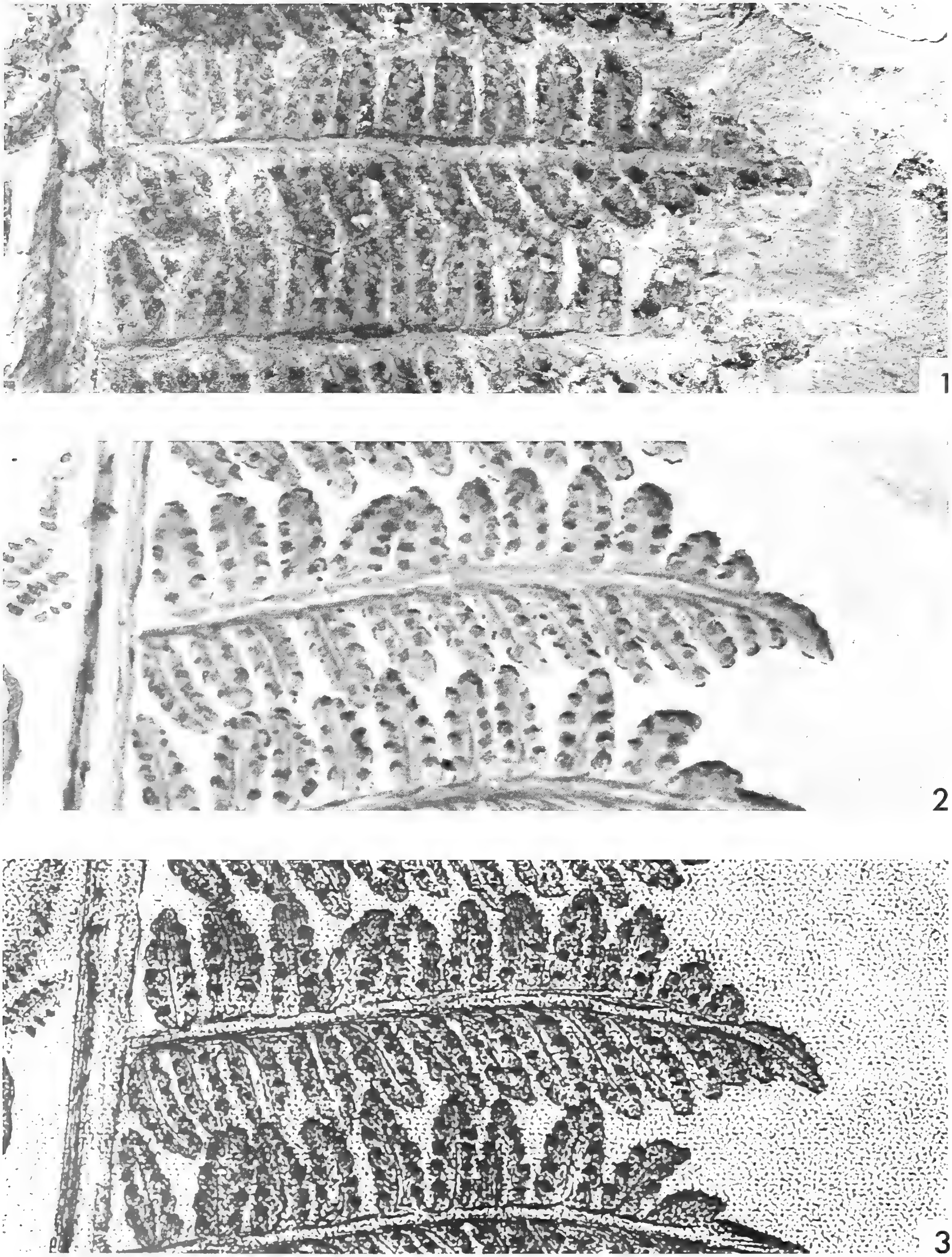

Plate 3 *Lobatopteris miltoni* (Artis) Wagner. Close-ups of part of holotype, all × 3. Fig. 1, photograph. Fig. 2, Curtis' wash. Fig. 3, Artis' engraving.

> *Frond tripinnate; stipes large, strong. Leaflets linear, tip rounded. Fructifications surrounding the leaflets near, but not entirely on, the margin.*

He also admitted that the illustration was not entirely accurate. This inaccuracy probably arose during the engraving of the printing plate, since Curtis' original wash gives a somewhat better impression of the specimen (Pl. 2). In particular, the engraving grossly exaggerates the proportion of the pinnules that are pinnatifid; in fact only one ultimate pinna, near the base of the more distal secondary pinna, has well-developed pinnatifid pinnules. To illustrate this point, we have provided close-ups of part of the specimen as actually seen, as shown in Curtis' wash, and as represented in Artis' engraving (Pl. 3, figs 1–3). The error seems to have been because the specimen was fertile. Although few sporangia are preserved, there is a remnant disc of carbon where each sorus was originally attached to the pinnule, and this has imparted a superficially undulate appearance to the pinnule margin. The inaccuracy of the protologue illustration has had important implications in the interpretation of the species, which was widely believed (until Dalinval's 1960 revision) to be characterized by predominantly pinnatifid pinnules (e.g. Kidston 1924).

The holotype compares well with Dalinval's material in having blunt tertiary pinna terminals, and linguaeform to subtriangular lateral pinnules with a prominent, decurrent midvein. In particular, it is very similar to the large specimen in Dalinval's pl. 32, fig. 1. The primary rachis of the holotype is about twice as wide as in Dalinval's specimen and probably comes from a more proximal position in the frond. This may explain the smaller pinnules and more slender secondary racheis in Dalinval's specimen.

Because the holotype is fertile, it has not been possible to determine details of the lateral veins or whether there are epidermal hairs, which Dalinval regarded as important for distinguishing *L. miltoni* (Artis) from *Pecopteris bourozii* Dalinval and *P. lobulata* Dalinval. However, the holotype of *L. miltoni* (Artis) has much blunter pinna terminals and a more decurrent midvein than the other two species.

As already stated, although the holotype is fertile, only a very few, isolated sporangia are preserved. It is not possible, therefore, to determine the organization of the sori from this specimen. Wagner (1971) argued that Artis' engraving showed small fructifications near the margin of the pinnules, but these structures are in fact only the pedicles of the sori together with small, remnant discs of pinnule lamina which underlay the fructifications. However, a rather better preserved specimen of *L. miltoni* (Artis) figured by Dalinval (1960: pl. 40, fig. 2) shows closely spaced sori, comprised of four sporangia *c.* 0·05 cm in diameter. They correspond with the fructifications identified as *Cyathocarpus* Weiss (= *Asterotheca* auctt., *non* Presl) by Mosbrugger (1983), who established the combination *Cyathocarpus miltoni* (Artis).

Wagner (1959) has proposed that species with such fructifications could be further subdivided on characters of the sterile foliage. Using this principle, he established the form-genus *Lobatopteris*, for species with a high proportion of pinnatifid pinnules and a distinctive veining pattern (see also Cleal 1984: fig. 11). This pattern was described by Wagner (1959) as follows.

> ... *the nervation ... in its most simple form consists of only once bifurcate nervules, of which the upper branch dichotomizes mostly as well, so as to provide a characteristically threefold nervation. Afterwards, the middle branch of each nervuary group dichotomizes, which example is then followed by the lower and upper branches ...*

Wagner's diagnosis only mentions characters of the sterile foliage. However, he states in a preamble to the diagnosis that it belongs to the subfamily Miltonoidaea (family Caulopteridaceae), which Corsin (1955) defined on a number of characters, including the presence of *Asterotheca* auctt., *non* Presl sporangial clusters and the attachment of the fronds to *Caulopteris*-type stems. Consequently, *Lobatopteris* is not merely a generalized form-genus for a particular type of sterile foliage, but has a circumscription limited also by features of the fructifications and stem. Species such as *Pecopteris volkmannii* Sauveur, with lobatopteroid-like sterile foliage but different fructifications (in this case, of the *Senftenbergia*-type – Dalinval 1960), should be excluded from *Lobatopteris*.

Such a classification based on sterile characters might be regarded as suspect, and was not adopted by Mosbrugger. However, the species included in *Lobatopteris* by Wagner (such as *L. vestita* (Lesquereux), *L. micromiltoni* (Corsin) and *L. lamuriana* (Heer)) do appear to be significantly distinct from cyathocarpids with fewer pinnatifid pinnules and a simpler nervation (including *Cyathocarpus arborescens* (Brongniart), *C. cyatheus* (Brongniart) and *C. hemitelioides* (Brongniart)), and the generic distinction is probably justified.

Lobatopteris typically occurs in upper Westphalian D to Stephanian floras, but Wagner (1959) also included *L. miltoni* (Artis), which ranges from the Westphalian A to lower Westphalian D (Dalinval 1960). The branching of the lateral veins necessary to confirm this assignment cannot be seen in the holotype, but the sterile specimen figured by Dalinval (1960: pl. 32, fig. 1b) appears to show the diagnostic nervation pattern.

Unlike the more typical lobatopterids, *L. miltoni* (Artis) fronds have a much lower proportion of pinnatifid pinnules. This may simply be because these fronds are larger and more divided, the tertiary pinnae being equivalent to the pinnatifid pinnules of the more typical lobatopterids. There may be an analogy here with the medullosan pteridosperms, whose fronds were smaller and less divided in the Stephanian than in the Westphalian, probably in response to changing climatic conditions (Laveine 1967). Another possible difficulty is that Laveine (1970) has reported that *L. miltoni* (Artis) produced trilete spores (our attempt to prepare spores from the holotype was unsuccessful), in apparent contrast to the monolete spores produced by the more typical lobatopterids, such as *L. lamuriana* (Heer) and *L. micromiltoni* (Corsin). Here, again, the distinction may not be significant, however, since it is well documented that marattialean ferns can produce both trilete and monolete spores, sometimes even in the same plant (Hill & Camus 1986).

The generic position of *L. miltoni* (Artis) cannot be finally ascertained without more work on its morphological variation and fructifications. We have provisionally followed Wagner (1959) and retained it within *Lobatopteris*, but recognize that it (perhaps together with *Pecopteris lobulata* Dalinval and certain other Westphalian pecopteroid species) may eventually be transferred to another, possibly new, form-genus for larger, more divided fronds producing trilete spores

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Classification and review of the brachiopod superfamily Plectambonitacea

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CONTENTS

SYNOPSIS. All nominal plectambonitacean genera are reviewed, and 79 are accepted whilst 26 are placed in synonymy or rejected. New criteria for familial and subfamilial classification are established, in order of importance (i) the nature of the cardinal process (simple, trifid or trifid and undercut), (ii) the presence of a bema, and (iii) the presence of side septa. These result in 10 families of which 6 have between two and five subfamilies: the Family Grorudiidae and the Subfamilies Pelonomiinae, Spanodontinae, Palaeostrophomeninae and Craspedeliinae are new. Three new genera are erected, *Rurambonites, Jonesea* and *Cooperea*. Lectotypes are here selected of *Strophomena nubigena* and *S. aranea*, both of Salter, *in* Salter & Blanford 1865, and now ascribed to *Toquimia*.

INTRODUCTION AND HISTORY OF RESEARCH

The Plectambonitacea were a widespread and diverse superfamily during the Ordovician and Silurian, lingering on with a few representatives into the Devonian. They were the first brachiopods to develop the pseudopunctae so characteristic of the Order Strophomenida and were the stem group of that order, so that the Strophomenacea, Chonetacea and all the Suborder Productidina were their descendants. Over a hundred plectambonitacean genera have been named, as compared with the 61 genera in the *Treatise on Invertebrate Paleontology* (Williams 1965), and since so many genera, both old and new, have been erected without adequate comparison with their closest relatives, the time now seems ripe for a complete review of the entire superfamily. We have also reviewed all the families and subfamilies and tried to compile a classification built on consistent principles, with the varied form of the cardinal process taking first precedence over other features such as the possession or absence of bema or side septa, which are themselves considered more important than the possession of a platform or the valve shape and outline, which we consider of generic rather than familial importance. Ornament is so variable within the family that it seems of specific importance rather than being the basis of genera, and there is also surprising variability in other features such as the presence or absence of a pedicle valve median septum and the shape and form of the muscle fields and their bounding ridges. However, our newly defined criteria for classification appear to recognize a real evolutionary strategy, and we have completed the task with a much clearer picture of the superfamily as a whole. We have diagnosed each family, subfamily and genus, concentrating in each case only on those features which distinguish it from its close relatives and trying not to include details which are common to the group as a whole or of only specific importance within the genus.

Because so much earlier literature is obscure or neglected, and because the library facilities and collections at the British Museum (Natural History) are so good, we have also tried to list all the described species of the superfamily, over 600 in number, and to assign them to an appropriate genus, but this task is made more difficult because of the lack of adequate illustrations in so many of the original descriptions. In our opinion there is no point in erecting any further new species of Plectambonitacea unless the brachial valve interior is properly figured; when only the mould of a valve is available in the rock, then a latex cast should be made and figured as well.

Although individual genera and species of Plectambonitacea were erected and discussed during the nineteenth and early twentieth centuries, it was not until the monograph by Jones (1928) that a survey of the group as a whole was made. Jones worked mainly on Caradoc, Ashgill and Llandovery forms and erected the Subfamily Plectambonitinae and the key genus *Sowerbyella*, as well as *Leptelloidea* and *Chonetoidea*. His study laid the foundations for subsequent discussion of the Plectambonitacea as separate from the Strophomenacea and Chonetacea. This work was followed soon by a penetrating series of papers by Öpik (1930, 1932, 1933) whose excellent illustrations and descriptions of species, particularly those from the Lower Ordovician of Estonia, were amongst the best works on brachiopods of any age or groups for their time. North American early and middle Ordovician forms, including many new genera, were published by G. A. Cooper (particularly in Ulrich & Cooper 1938 and in Cooper 1956), and all the genera erected before about 1964 were extensively reviewed in the *Treatise on Invertebrate Paleontology* (Williams 1965). Williams also assessed and revised the familial and subfamilial classification, and his compilation has formed the basis for all subsequent work. Havlíček too made valuable contributions in the substantial revision, including many new taxa, of the important Bohemian area (e.g. 1967) and indeed of the whole Mediterranean region (e.g. 1971 on

Fig. 1 Brachial valve of *Leangella scissa* (Davidson) illustrating the difference between a bema (which originates close to the anterior end of the socket plates) and a platform (which originates laterally to the structures surrounding the cardinal process)

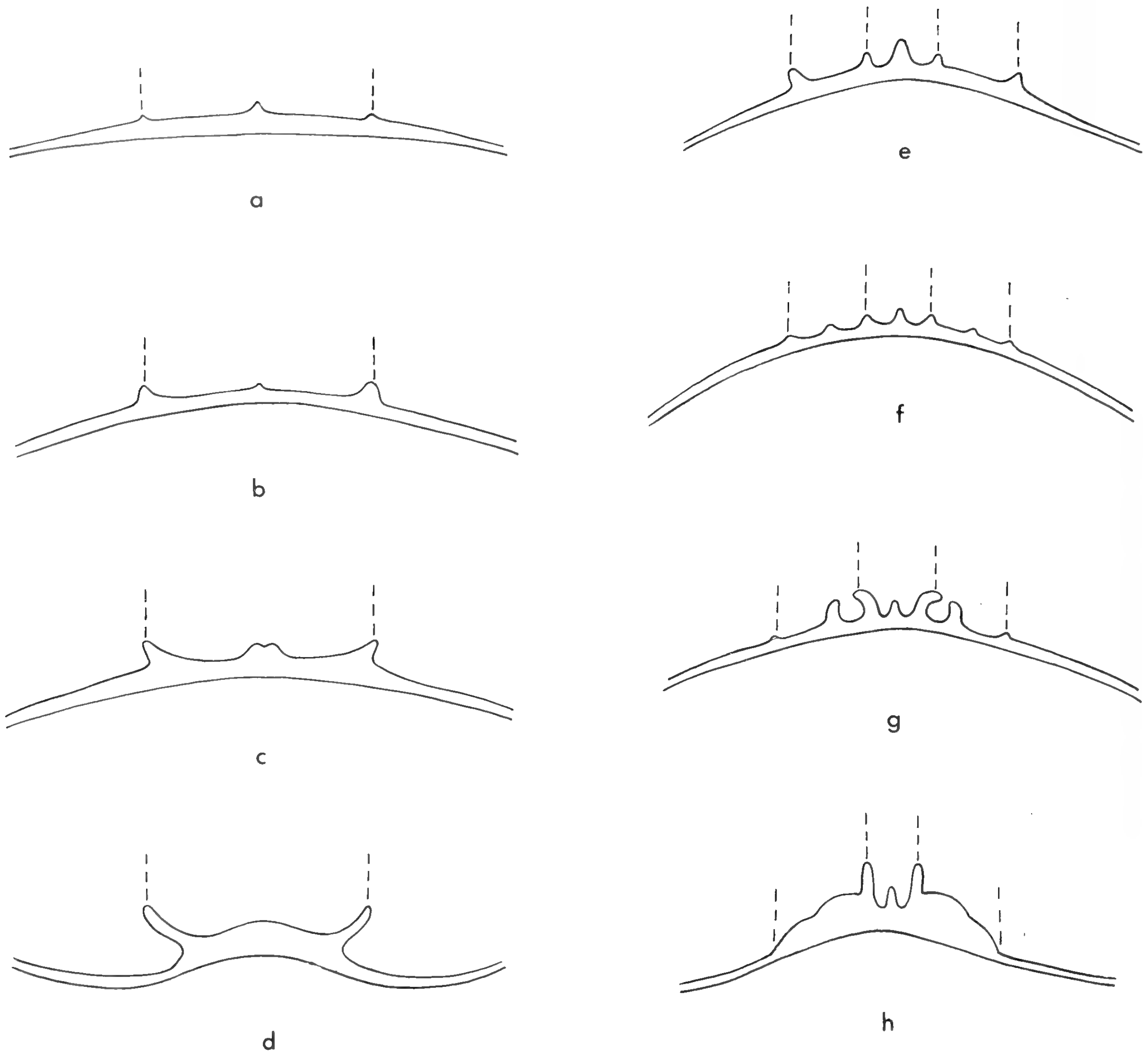


Fig. 2 Cross-section through various brachial valves to illustrate the different types of bema. The dotted lines indicate the limits of the bema, a–d are entire and e–h are divided; c and d are elevated; g and h illustrate the more extreme modifications. a, *Aegiria*; b, *Rurambonites*; c, *Leangella*; d, *Xenambonites*; e, *Bilobia*; f, *Anisopleurella*; g, *Eoplectodonta*; h, *Bimuria*.

Morocco), and Cocks (1970) revised the Silurian species of the superfamily. Many plectambonitacean species and genera have been erected or revised in other papers and monographs (see the references at the end of this work), but no revision of the group as a whole has been published since Williams (1965).

MORPHOLOGICAL TERMINOLOGY

In general we follow the nomenclature used by Williams (*in* Williams *et al.* 1965), but the following terms need further elucidation.

Bema: An elevated pad of secondary shell material in the brachial valve originating from or close to the anterior end of the socket ridges or plates (Fig. 1). It may be divided into several types:

a) entire (e.g. Figs 2a–d), divided (e.g. Figs 2e–h), or bilobed (e.g. Fig. 1)
b) elevated (e.g. Figs 2c, d) or not elevated (e.g. Fig. 2a)

Cardinal process: The brachial valve attachment area for the diductor muscles. In the Plectambonitacea it is usually trifid (when viewed from the posterior), but may be a simple central ridge. The type of cardinal process may be divided into two main groups:

a) simple, or not undercut, in which the central lobe is connected anteriorly to the median part of the valve floor (the notothyrial platform), often with a myophragm (e.g. Fig. 3g)
b) undercut, in which there is no anterior support for the central lobe (e.g. Fig. 4a)

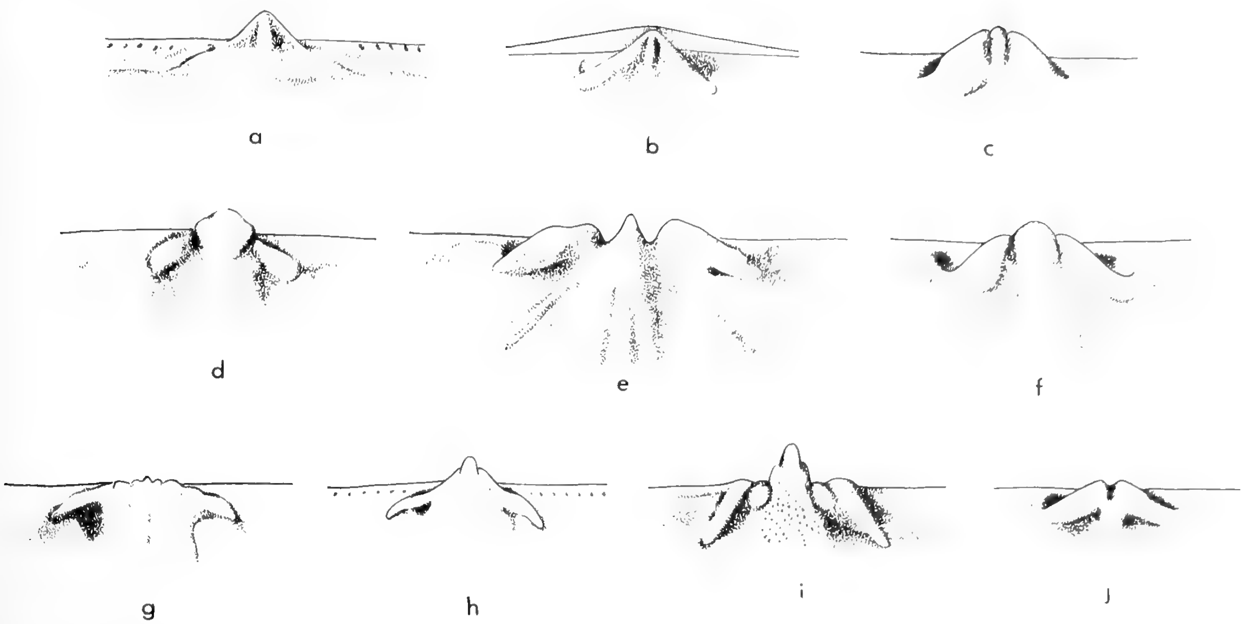


Fig. 3 Different types of cardinal process within the Plectambonitacea. a, simple, not undercut, projecting posteriorly from hinge line, *Ingria nefedyevi* (Eichwald), × 10 (after Öpik 1932: pl. 6, fig. 32); b, simple, not undercut, not projecting posteriorly from hinge line, *Ahtiella baltica* Öpik, × 6 (after Öpik 1933: pl. 4, fig. 6); c, simple, not undercut, *Spanodonta hoskingiae* Prendergast, × 6 (from BC 10605); d, trifid, not undercut, *Toquimia kirki* Ulrich & Cooper, × 6 (after Cooper 1956: pl. 164, fig. 13); e, simple, not undercut, *Bimuria superba* Cooper, × 6 (from BC 7270); f, simple, not undercut and merging anteriorly with the posterior end of the double septa, *Isophragma ricevillense* Cooper, × 12 (from BC 7211); g, simple, not undercut, *Leptellina tennesseensis* Ulrich & Cooper, × 6 (from BB 1228); h, trifid, not undercut, *Rurambonites ruralis* (Reed), × 6 (from BC 7204); i, trifid, not undercut, *Leptelloidea leptelloides* (Bekker), × 6 (from B 5169); j, simple, not undercut, *Leptella* (*Petroria*) *rugosa* (Wilson), × 6 (from Cooper 1956: pl. 221, fig. 33).

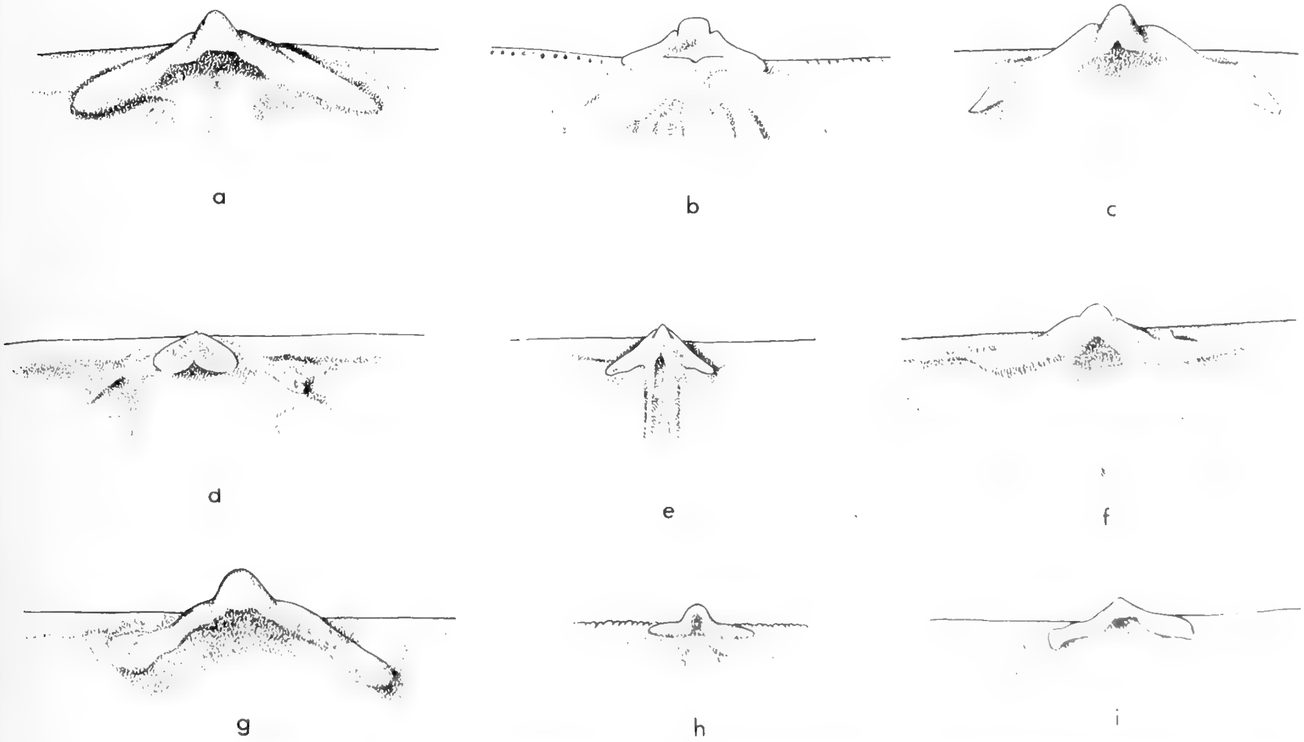


Fig. 4 Different types of cardinal process within the Plectambonitacea; all are trifid and undercut. a, *Sowerbyella eximia* Cooper, × 10 (after Cooper 1956: pl. 204, fig. 32); b, *Eoplectodonta duvalii* (Davidson), × 6 (from BB 31837); c, *Sowerbyella liliifera* Öpik, × 12 (from BB 5149), d, *Ptychoglyptus virginiensis* Cooper, × 6 (from BC 10316); e, *Gunningblandella resupinata* Percival, × 5 (after Percival 1979: fig. 9.7); f, *Anisopleurella tricostellata* Cooper, × 25 (from BB 32855); g, *Aegiria* (*Aegiria*) *aquila* (Barrande), × 25 (from BB 33341); h, *Dalejodiscus comitans* (Barrande), × 7 (after Havlíček 1967: pl. 7, fig. 9); i, *Kassinella* sp., × 12 (from NIGP 101835).

Clavicular plates: Term used for structures in the brachial valve homologous to socket plates, but when there are no corresponding teeth in the pedicle valve (e.g. *Eoplectodonta*).

Dental plates: Plates in the pedicle valve going from the hinge line to the valve floor and supporting the teeth.

Denticles: Small elongate teeth distributed along the hinge line.

Median septum: Longitudinal septum in the centre of either valve. A few plectambonitaceans have a 'double' median septum consisting of a central raised area in the brachial valve with a less conspicuous median trough (e.g. Fig. 23, p. 91).

Muscle bounding ridges: Curved elevated structures in either valve bounding the muscle field laterally and/or anteriorly. In the brachial valve the muscle bounding ridges may form the edge of the bema (e.g. Fig. 94, p. 124).

Myophragm: Median raised area in either valve between muscle scars, but not extending beyond them (e.g. Fig. 37b, p. 96).

Notothyrial platform: Median thickening of brachial valve floor immediately anterior of the cardinal process.

Papillae: Distinctive small elevations on the interior of either valve, usually sub-circular: although they may coincide with the prolongation of a pseudopuncta, this is not always so, and they are usually larger than a pseudopuncta.

Peripheral rim: Raised rim near the anterolateral margin of either valve. It may be continuous as a small ridge (e.g. Fig. 75, p. 115) or discontinous and indicated only by prominent papillae or septules (e.g. Fig. 116, p. 129).

Platform: Brachial valve structure originating near the alae (as opposed to a bema which originates at or near the socket plates). The platform (Fig. 1) may or may not be elevated from the valve floor, and may or may not be continuous.

Septules: Small elongated structures in either valve, sometimes merely elongated papillae, sometimes nearly approaching side septa in size (e.g. Fig. 95, p. 125).

Side septa: Paired brachial valve septa which may or may not be confined to the bema (some other workers have used the term 'anderidia').

Socket plates or ridges: Paired brachial valve structures attached to the hinge line and arising from near the notothyrial platform (their function varied: sometimes they were used to mesh with the teeth, sometimes they may have provided support for the posterior part of the brachiophore; see also 'clavicular plates').

Tubercles: We restrict the term within the Plectambonitacea to paired posterolateral protruberances within the pedicle valve of some genera (e.g. Fig. 114, p. 129).

FUNCTIONAL MORPHOLOGY AND EVOLUTION

It is probable that the earliest plectambonitaceans, like their orthide ancestors, had a functional pedicle and were simply attached to a variety of substrates. Their feeding mechanisms and gape would have been typical of other brachiopods, with a relatively simple lophophore. Brunton (1972) has elegantly reconstructed the lophophore and possible water current system for a generalized chonetacean with small side septa (sometimes termed anderidia) which shows a lobed trocholophe with a single series of filaments rather than the more complex double filaments seen in most living brachiopods today. Such chonetaceans have a very similar general valve morphology to many early plectambonitaceans, such as *Taffia*, and we therefore think it likely that most primitive plectambonitaceans would have had a comparable lophophore. As with many brachiopods today, the dorsal valve simply opened very widely and stayed open without movement for feeding and respiratory purposes.

However, the interpretation of the functional morphology of the many plectambonitaceans with a variety of more substantial brachial valve structures, such as bema, side septa and platforms, is far less easy. No living articulate brachiopod has such a relatively small space between the valves, and when a very incurved plectambonitacean such as *Eoplectodonta* had its valves shut, there was very little room between them (Cocks 1970: fig. 4). In addition, the muscle scars of most plectambonitaceans appear to have been much larger than other brachiopods of comparable size. These facts led Cocks (1970) to postulate that in some advanced plectambonitaceans such as *Eoplectodonta* the flow of water over the lophophore must have been very strong whenever the valves opened or closed, and that such valve movement could have played a major part in respiration and feeding, perhaps leading to their replacing the ciliary beat as the prime method of water circulation within the shells. Such a change in function may even have led the lophophore to degenerate in size. Since then, the subject of 'flapping valves' in brachiopods has received more attention, with, for example, Cowen (1975) demonstrating that for some coral-shaped richthofeniids, it was probably the method employed (as opposed to contrary, but to our minds less compelling, views expressed by some other workers). Hurst (1975: 63) has also discussed the feeding and lophophore arrangement in *Eoplectodonta*, and concluded that the flapping mechanism for feeding was unlikely because (a) filtered and unfiltered water would have been mixed in the same channel, (b) no modern brachiopod does it, and (c) it runs against the general trend of brachiopods for the lophophore to have been reduced in size. From further experience, we would now agree with Hurst's third point, and consider it improbable that the lophophore would have degenerated in size; however, none of his other arguments against the use of valve flapping for water circulation seem strong when compared with the arguments originally presented by Cocks (1970: 149–150). Hurst agreed that the strong muscles were probably developed initially to return to a living position valves which had been overturned, but, once having developed such strength, it seems difficult to believe that it was not also used to enhance the water flow between the two valves in incurved genera of the superfamily. It is also difficult to account for the function of platforms, since, as the cross-section through *Leangella* shows (Cocks 1970: fig. 4a), there would have been no room for a lophophore anterior of the platform once the valves were shut. The lophophore was probably attached to the posterior edge of the platform anteriorly, so that when the valves were closed the lophophore was accommodated between the platform and the bema edge. Living *Argyrotheca* has comparable restricted brachial cavities, with septa crossing the cavity when the two shells are closed.

The life positions of various genera also varied greatly. Many genera, particularly the earlier and more primitive ones, had functional pedicles, and these presumably lived umbones downwards and with their shells either vertical or slightly inclined. However, many of the more advanced genera, in particular the later Sowerbyellidae such as *Eoplectodonta*, did not have functional pedicles in adult life, and thus can only have lived freely on the sea floor, obviously with their concave sides upwards to keep the valve gape clear of the substrate.

Ultrastructural studies (Brunton 1972) have shown that the plectambonitacean primary layer is similar to both chonetaceans and strophomenaceans. However, the secondary shell layer differs within the Plectambonitacea: the sowerbyellids have standard fibrous secondary shell structure, but *Aegiromena*, *Jonesea* and *Sericoidea* display a modified shell structure termed 'transitional fibrous' by Brunton (1972: 18). The earliest chonetaceans also show an ultrastructure comparable (but not identical) with the Aegiromeninae. However, given the conservative nature of the cardinal process throughout the phylum as a whole, it seems to us more probable that the chances that the development of the strophomenacean bifid cardinal process was a monophyletic evolutionary event seem higher than that of the pattern of shell structure repeating itself. Therefore, we consider it most probable that the strophomenaceans developed in the early Ordovician (Llanvirn) from the Plectambonitacea by a change from a simple to a bifid cardinal process, and that the chonetaceans developed in the late Ordovician (Ashgill) from the strophomenaceans (either rafinesquinids or pholidostrophiids) by the simple acquisition of hinge line spines and with no change in the character of the cardinal process. Thus we do not consider the Plectambonitacea as the immediate ancestors of the Chonetacea.

The pattern of evolution of the superfamily is set out in Fig. 5. It assumes that the most important character is the development of the cardinal process from simple to trifid and from trifid to undercut. Each of these three major cardinal process stages also developed bemas and side septa to give the pattern of families which we have identified. The oldest plectambonitaceans are of Tremadoc age and are essentially indistingishable from their orthide (probably billingsellacean) ancestors except by their pseudopunctate shell. The only definite plectambonitacean of late Tremadoc age is *Plectella* (Plectambonitidae); *Leptella*? *exigua* is also of certain late Tremadoc age although there are no interiors known of it. There is also uncertainty about the affinities of the undoubtedly late Tremadoc genus *Akelina* (see below p. 88). True *Leptella* (Taffiidae) are known from the Lower Arenig, and we have indicated the Taffiidae as the ancestral plectambonitaceans in our evolutionary diagram because we regard the absence of side septa (as in the Taffiidae) as representing a more primitive state than their presence (as in the Plectambonitidae). The great period of plectambonitacean diversification occurred in Llanvirn times, which is also the age of the oldest known strophomenacean, the presumed descendant of one of the plectambonitacean stocks; perhaps one related to some leptellinid like *Apatomorpha* or *Toquimia*. In fact eight out of the ten plectambonitacean families had evolved by the end of the Llanvirn. From that time until their extinction in the early middle Devonian, the morphological changes appear to have been far less radical in character.

CRITERIA FOR CLASSIFICATION

After studying specimens and/or photographs of all the type species of all the plectambonitacean genera, we conclude that the brachial valve characters are those upon which the most suitable family and subfamily classification can be built. In particular, the nature of the cardinal process enables us to identify a more primitive group which shares with its parent orthides a simple cardinal process which is supported directly anteriorly by a swollen notothyrial platform. This simple cardinal process was subsequently joined by a pair of lateral processes to form the normal trifid cardinal process typical of most plectambonitids. A more advanced group of genera consists of those in which all the support comes from the lateral structures joined to the bases of the socket plates or ridges, leaving a space immediately anterior to the cardinal process; this type we term as having an undercut cardinal process. Some authors in the past have used a morphological term for this space in front of the cardinal process, for example 'Schlössgrube' (Öpik 1933) or 'alveolus' (Muir-Wood 1962); however, we feel it misleading to use positive terms for negative features, and prefer to think of this space as a gap between structures, rather than as a structure in its own right, and so a special name is not used in this paper.

However, despite the generally conservative nature of the cardinal process, on some occasions it does not appear to have developed at all, for example in *Taffia* it is generally absent, although appearing occasionally within a population (Neuman 1977), and also in *Leptella*, where it is not known at all. Nevertheless, the general morphology of *Leptella* is extremely close to some other taffiids and thus the genus has been placed in the Taffiidae with some confidence. Another difficult decision is to determine whether or not the trifid cardinal process evolved once or twice. In particular, on Fig. 5 the Syndielasmatidae are shown as arising from the Plectambonitidae because the morphologies of the two families are so close. However, although we have chosen this as the most likely alternative, it may have been that the trifid cardinal process only evolved once and the Syndielasmatidae (with their side septa and no bema) may have been derived through a cryptic route unrepresented by known fossils. Apart from the possible exception of the Syndielasmatidae the evolution of the cardinal process appears to have taken place in unique and irreversible steps.

The second prime criterion for familial classification is the presence or absence of a bema. This structure has often in the past been confused with or taken as a homologue of a platform, but they differ fundamentally in that the bema originates at or very near the anterolateral ends of the socket plates or ridges, whilst the platform originates laterally from these sites, along the hinge line and often well into the alae. *Leangella*, for example, possesses both bema and platform, and Fig. 1 shows both of them extending well into the alae. The definition and consistent recognition of the bema has caused confusion and lack of consistency among previous authors. For example, Cooper sometimes used 'visceral disk' when he was describing a platform (e.g. in *Leptellina bella*; 1956: 749) and sometimes when he was describing a bema (e.g. in *Bilobia virginiensis*; 1956: 762); Williams used the term 'lophophore platform' for a platform (e.g. in *Leptellina rhacta*; 1963: 164) and sometimes for a bema (e.g. in *Leangella* cf. *hamari*; 1963: 172), and Havlíček, although for the most

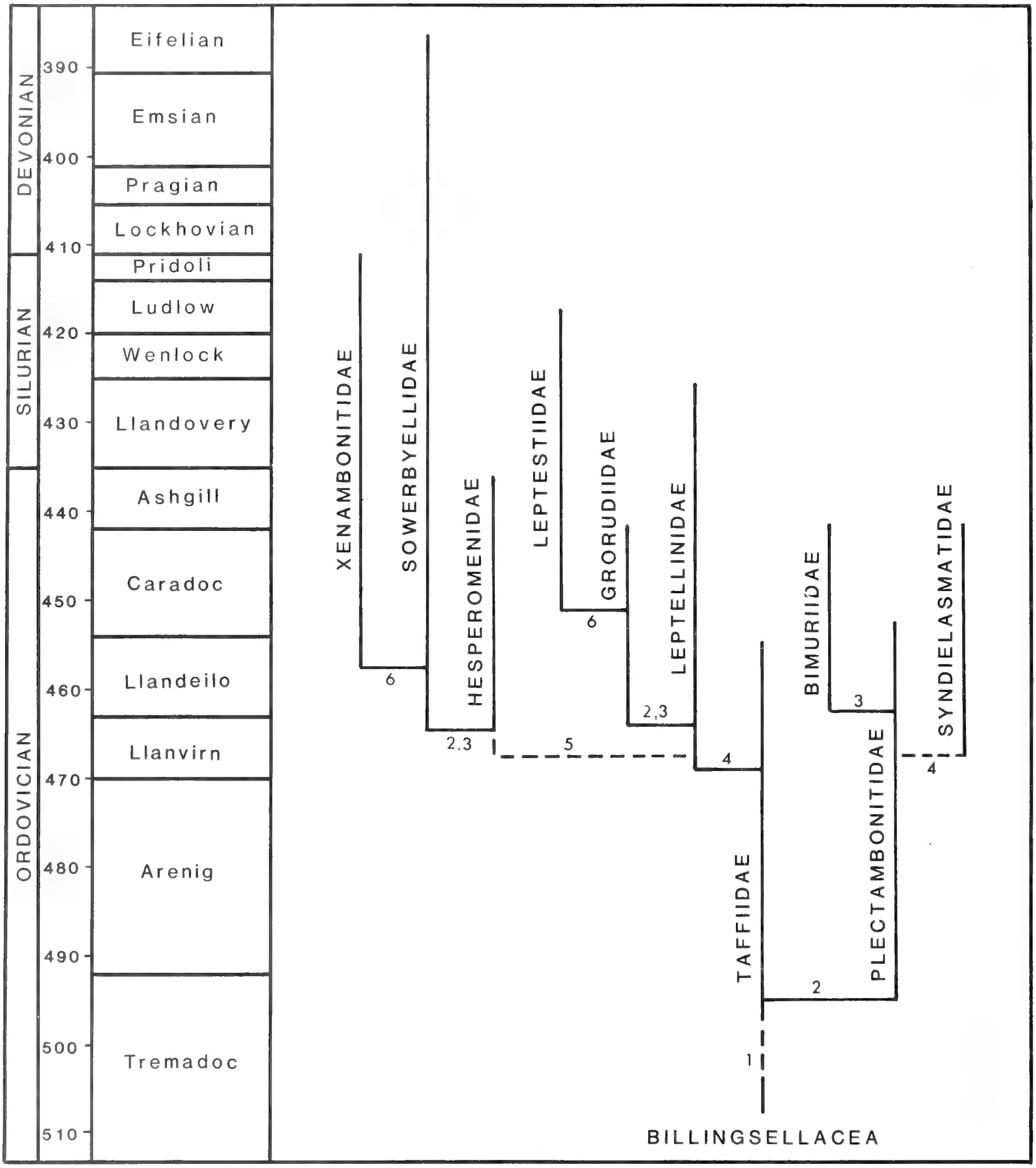


Fig. 5 Range chart and phylogeny of the families of the Plectambonitacea. The numbers indicate the acquisition or loss of critical characters as follows: 1. acquisition of pseudopunctae; 2. acquisition of side septa; 3. acquisition of bema; 4. acquisition of trifid cardinal process; 5. acquisition of undercut cardinal process; 6. loss of side septa.

part he consistently termed the bema a 'visceral field' (e.g. in *Anisopleurella ovalifera*; 1967: 65), he sometimes called it a 'visceral platform' (e.g. in *Leptestiina prantli*; 1967: 30), and often called the platform the 'diaphragma' (e.g. in *Tufoleptina tufogena*; 1967: 34). However, in a few cases, Havlíček confused 'diaphragma' with 'visceral platform'. For example, there is a platform in *Anoptambonites moneta* (Havlíček 1967: 36), which was called by him a 'visceral platform'. We have found the presence or absence of a platform to be a less fundamentally important character in classification, and useful only in identifying and grouping subfamilies and sometimes only in the separation of two otherwise closely-related genera (for example *Titanambonites* and *Ishimia*). The third character which we have used on our familial separations has been the presence or absence of side septa in the brachial valve, which has been useful in some cases, but appears to have been less fundamental in strategic evolutionary importance and also to have occurred on several different occasions (Fig. 5).

Therefore, using the three stages of development of the cardinal process and the presence or absence of a bema and side septa, there are twelve possible permutations and combinations, and we have identified plectambonitaceans belonging to ten of them, as follows:

1. Cardinal process simple, no bema, with side septa, e.g. *Plectambonites* (Fig. 12, p. 87).
2. Cardinal process simple, no bema, no side septa, e.g. *Borua* (Fig. 32, p. 95).
3. Cardinal process simple, with bema, with side septa, e.g. *Bimuria* (Fig. 46, p. 101).
4. Cardinal process trifid, no bema, with side septa, e.g. *Syndielasma*.
5. Cardinal process trifid, no bema, no side septa, e.g. *Leptellina* (Fig. 49, p. 105).
6. Cardinal process trifid, with bema, no side septa, e.g. *Leptestia* (Fig. 78, p. 118).
7. Cardinal process trifid, with bema, with side septa, e.g. *Tetraodontella* (Fig. 68, p. 113).
8. Cardinal process undercut, with bema, no side septa, e.g. *Aegiria* (Fig. 94, p. 124).
9. Cardinal process undercut, no bema, no side septa, e.g. *Anoptambonites* (Fig. 107, p. 127).
10. Cardinal process undercut, with bema, with side septa, e.g. *Eoplectodonta* (Fig. 137, p. 136).

This forms the basis for the ten families recognized in this paper. There are more than enough familial-rank names already erected by previous workers to suffice for this classification, but application of our new concepts for family classification has meant that the definition and scope of the family grouping has had to be changed in all cases, as becomes clear in the systematic section below; and in addition it has been necessary to erect one new familial and four new subfamilial names.

We have found that the pedicle valves in the Plectambonitacea are of much simpler construction than the brachial valves, and thus display a great deal of homoeomorphy, and so are not useful for familial or subfamilial classification, although in a few cases the pedicle valve morphologies have been useful in separating closely related genera.

One of the biggest problems in identifying and classifying plectambonitacean genera and species is the very large amount of variation seen in some populations and between populations. An example is the development of a short median septum in the pedicle valve of *Bilobia hemisphaerica* Cooper, which is present in most specimens of the type population (Cooper 1956: pl. 193, figs 29, 30), scarcely visible in some specimens (Cooper 1956: pl. 193, fig. 28) and absent in others (Cooper 1956: pl. 193, fig. 27). There are comparable occurrences in *Bilobia etheridgei* (Davidson), in which the median septum usually occurs (Mitchell 1977: pl. 14, figs 17, 20), but is sometimes absent (Mitchell 1977: pl. 14, fig. 24) and also in *Jonesea grayi* (Davidson), in which the septum also sometimes occurs (Cocks 1970: pl. 17, fig. 13) and is sometimes absent (Cocks 1970: pl. 17, fig. 11). These examples bring into question the true generic differentiation between, for example, *Leangella*, which has no pedicle valve median septum, and *Diambonia*, which has virtually identical morphology to *Leangella* except for the development of a pedicle valve median septum, and thus we follow Mitchell (1977: 78) in placing *Diambonia* within the synonymy of *Leangella*. In the same way, we have found the morphology and proportion of the muscle scars within the pedicle valve to be extremely variable, and of value at most in only specific differentiation, and thus genera such as *Benignites*, which is only differentiated from *Leptellina* in 'having a slender adductor scar narrowing to the front of the ventral muscle field (but never surrounded by diductors)' (Havlíček 1976: 368), are not recognized as valid in this paper. The only exception we have found is the development of distinctive tubercles in the posterolateral parts of the pedicle valve, which appear to differentiate consistently the genera *Kassinella*, *Trimurellina* and *Jonesea* from their relatives within the families Hesperomenidae and Xenambonitidae.

The basic shell form, including the development of resupination, geniculation or rugation, can be of importance at the generic level, but these shapes have all arisen several times polyphyletically, and thus do not appear to be useful in distinguishing familial groupings or subfamilial groupings by themselves. For example, resupination occurs in the very unrelated genera *Ahtiella* and *Gunningblandella*, and geniculation in *Craspedelia* and *Xenambonites*. Two different types of rugation can be developed, one which is continuous (like the strophomenid *Leptaena*) and which is developed in many plectambonitacean genera near the alae, and over the whole shell surface in *Reinversella*, and a second type which is discontinuous (like the stropheodontid *Cymostrophia*) which is seen in the Plectambonitacea in the unrelated *Ptychoglyptus* and *Rugosowerbyella*.

Thus the most important characteristics for the families we recognize may be tabulated as follows:

	Cardinal Process	Bema	Side Septa
Plectambonitidae	simple	No	Yes
Taffiidae	simple	No	No
Bimuriidae	simple	Yes	Yes
Syndielasmatidae	trifid	No	Yes
Leptellinidae	trifid	No	No
Groruriidae	trifid	Yes	Yes
Leptestiidae	trifid	Yes	No
Xenambonitidae	undercut	Yes	No
Hesperomenidae	undercut	No	No
Sowerbyellidae	undercut	Yes*	Yes

* A few Sowerbyellidae lack a bema (see below under individual genera), but we consider that their relationships with other members of the family are so close that the bema appears to have been secondarily lost in those cases.

SYSTEMATIC PALAEONTOLOGY

In this section we review each plectambonitacean genus in turn and include a simple diagnosis which merely picks out the salient points for distinguishing the taxon from its close relatives. These genera are distributed among the various families and subfamilies following the criteria outlined in the section above. In addition we also append to each genus a list of species with their authors, original references and the geological horizon and brief locality of the holotype, together with a note of the major and most recent taxonomic revision if this has occurred. The species list is divided into 'species assigned', 'species questionably assigned' and 'species rejected' for each genus and is based partly on the inspection of original material in the British Museum (Natural History) and elsewhere and partly on inspection of the original published illustrations. Sadly, there is often a substantial difficulty in allocating species to genera, since this can only be done with any confidence when the brachial valve interior is adequately illustrated – it appears to us to be a waste of time and effort both in the past and future to try to describe formally and name any brachiopod without both interior and exterior illustration of both valves.

Superfamily **PLECTAMBONITACEA** Jones, 1928

1928 Plectambonitinae Jones: 394
1929 Plectambonitidae Kozlowski: 108
1952 Plectambonitacea Cooper & Williams: 332
1953 Plectambonacea Williams: 6
1965 Plectambonitacea Williams: H370
1967 Plectambonitacea Havlíček: 26
1970 Plectambonitacea Cocks: 154

DIAGNOSIS. Brachiopods with pseudopunctate shell: cardinal process simple or undercut, with a single process or trifid (although there are a few genera with no cardinal process), never bifid. Shell shape variable, but hinge line always straight.

DISCUSSION. The formal diagnosis of the Plectambonitacea is simplified. As far as is known, the acquisition of pseudopunctae only occurred once in the history of the Brachiopoda and thus the Plectambonitacea are a monophyletic group. However, they are also the stem group for the rest of the Strophomenida, and differ from other groups in that order only in the lack of bifid cardinal process. A few plectambonitaceans lack any cardinal process, but are clearly related in all other characters to other members of their assigned families, and the loss of the cardinal process in this superfamily can therefore be considered a secondary character.

RANGE. Lower Ordovician (U. Tremadoc) to Middle Devonian (Eifelian).

Family **PLECTAMBONITIDAE** Jones, 1928

1928 Plectambonitinae Jones: 394 *pars*
1930 Plectambonitidae Öpik: 55 *pars*
1930 Plectellinae Öpik: 55 *pars*
1930 Plectambonitinae Öpik: 58 *pars*
1933 Plectambonitidae Öpik: 9
1938 Plectellinae Ulrich & Cooper: 185
1953 Plectambonitidae Williams: 6 *pars*
1956 Leptestiidae Cooper: 700 *pars*
1956 Taphrodontidae Cooper: 742
1965 Plectambonitidae Williams: H370
1965 Leptestiidae Williams: H372 *pars*

DIAGNOSIS. Simple cardinal process, not undercut. No bema. Side-septa usually present.

REMARKS. The presence of a platform in all of the genera except *Isophragma* does not contribute to our diagnosis of this family or its constituent subfamilies; however we do divide the family into two subfamilies, partly on the basis of the denticles to be found only in the Plectambonitinae and partly on the double septum to be found in the Taphrodontinae.

SUBFAMILIES ASSIGNED. Plectambonitinae Jones, 1928; Taphrodontinae Cooper, 1956.

RANGE. Upper Tremadoc to Lower Caradoc.

Subfamily **PLECTAMBONITINAE** Jones, 1928

1928 Plectambonitinae Jones: 394 *pars*
1930 Plectellinae Öpik: 55 *pars*
1930 Plectambonitinae Öpik: 58 *pars*
1938 Plectellinae Ulrich & Cooper: 185
1965 Plectambonitinae Williams: H370

DIAGNOSIS. Like Taphrodontinae, but with hinge-line denticles and without double median septum.

REMARKS. The presence of a platform in all the genera included in this subfamily does not, however, contribute to our diagnosis of the subfamily, neither do the presence of the pseudodeltidium and chilidium. Our family corresponds to the Plectambonitinae of the *Treatise* (Williams 1965) apart from the possible addition of *Akelina*. All three genera also have side septa within the pedicle valve.

GENERA ASSIGNED. *Ingria* Öpik, 1930 (including *Palinorthis* Ulrich & Cooper, 1936); *Plectambonites* Pander, 1830; *Plectella* Lamansky, 1905; ?*Akelina* Severgina, 1967.

RANGE. U. Tremadoc (*Plectella uncinata*) to L. Caradoc (*Plectambonites radiatus*).

INGRIA Öpik, 1930
Figs 6–11

1930 *Ingria* Öpik: 57
1932 *Ingria* Öpik: 13
1936 *Palinorthis* Ulrich & Cooper: 625
1965 *Ingria* Williams: H370

TYPE SPECIES. By original designation, *Orthisina nefedyevi* Eichwald, 1855. Type species of *Palinorthis* is *P. cloudi* Ulrich & Cooper, 1936.

DIAGNOSIS. Flat to gently resupinate. Complex side septa similar to *Plectambonites*. Small pseudodeltidium, leaving delthyrium mainly open.

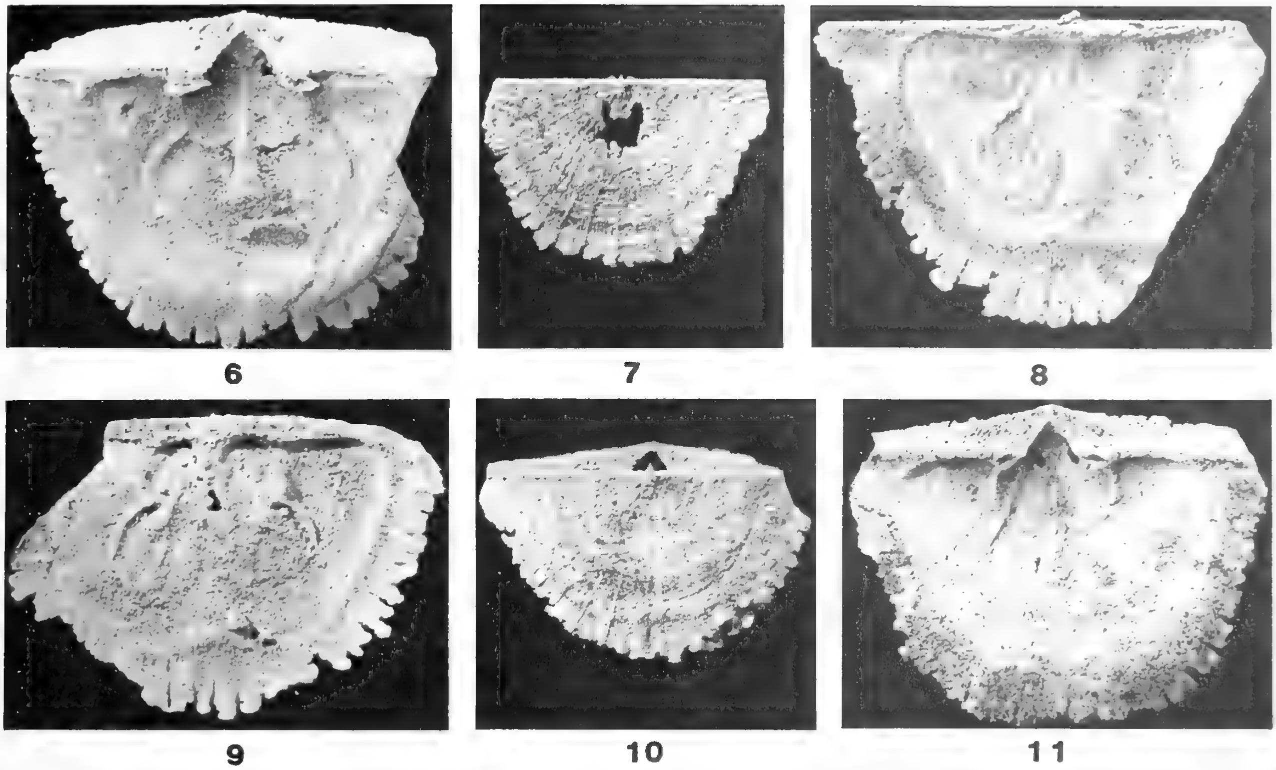
REMARKS. *Ingria* is a very variable genus, for example side septa are usually well developed, but the type species *Ingria nefedyevi* (Eichwald) almost lacks them (Öpik 1932: pl. 6, fig. 32). Because of this variability, we accept Cooper's (1938: 185) synonymy of *Ingria* with *Palinorthis* from Nevada.

SPECIES ASSIGNED.

Ingria aka Öpik, 1932: 32, pl. 9, figs 39, 40 from Arenig–Llanvirn beds, Obuchowa, near Wolchow, USSR.

Palinorthis cloudi Ulrich & Cooper, 1936: 626 from the Upper Pogonip Fm. (Llanvirn) of Nevada, USA (revised Ulrich & Cooper 1938: 185; pl. 38, figs 4–8; pl. 57, figs 17–24).

Ingria expressa Öpik, 1932: 29; pl. 2, figs 10, 11 from the *Asaphus eichwaldi* beds (Llanvirn), Suhkrumägi, Tallinn, Estonia, USSR.



Figs 6–11 *Ingria cloudi* (Ulrich & Cooper, 1936), topotypes, all silicified specimens from the *Orthidiella* Zone (L. Llanvirn), first ridge east of Frenchman's Flat, Nevada, USA. Fig. 6, pedicle valve interior BC 10312; Fig. 7, brachial valve exterior BC 10309; Fig. 8, brachial valve interior BC 10306; Fig. 9, brachial valve interior BC 10307; Fig. 10, exterior view of two conjoined valves BC 10313; Fig. 11, pedicle valve interior BC 10310. All × 3.

Ingria flabellum Öpik, 1932: 22; pl. 10, fig. 42 from Lower Llanvirn beds, Wassilkowo, USSR.

Ingria holtedahli Öpik, 1939: 128; pl. 4, figs 3, 5–9 from Expansus Shale (L. Llanvirn), Krekling, Norway.

Ingria malinovensis Andreeva, 1985: 40; pl. 4, figs 20–23 from Tarlikskaya Formation (Middle Ordovician), River Uyuk, Tuva, USSR.

Orthisina nefedyevi Eichwald, 1855: pl. 36, fig. 13 from Expansus Beds, now Kunda Formation (L. Llanvirn), Iswos am Wolchow, Estonia, USSR (revised Öpik 1932: 17; pl. 6, fig. 32; pl. 7, fig. 34; pl. 10, figs 41, 43, 44).

Ingria occidentalis Öpik, 1939: 129; pl. 3, fig. 12; pl. 5 figs 3–4 from Expansus Shale (L. Llanvirn), Hedenstad, Norway.

Ingria pakriana Öpik, 1932: 23; pl. 1, figs 1–4; pl. 2 figs 7–9; pl. 6, fig. 33 from the Rogo Sandstones (L. Llanvirn), Paldiski, Estonia, USSR.

Ingria sp. of Neuman 1977: 29; pl. 6, figs 19–23, 26–28, ?figs 24, 25, 29 from Arenig–Llanvirn of New World Island, Newfoundland, Canada.

Ingria sp. A of Öpik 1932: 21; pl. 1, fig. 5 from Rogo Sandstone (L. Llanvirn), Halbinsel Paldiski, Estonia, USSR.

Ingria sp. B of Öpik 1932: 29; pl. 1, fig. 6 from Rogo Sandstone (L. Llanvirn), Little Rogo Island, Estonia, USSR.

Ingria sp. C of Öpik 1932: 31; pl. 2, fig. 13 from Megalaspid Limestone (U. Arenig), Little Rogo Island, Estonia, USSR.

SPECIES QUESTIONABLY ASSIGNED

Ingria sp. Öpik, 1939: 129 (*Ingria* ? sp. in pl. 4, fig. 4) from Expansus shale (L. Llanvirn), Krekling, Norway (only a single brachial valve external illustrated).

PLECTAMBONITES Pander, 1830
Fig. 12

1830	*Plectambonites* Pander: 90 *pars*
1892	*Plectambonites* Hall & Clarke: 295 *pars*
1933	*Plectambonites* Öpik: 11
1965	*Plectambonites* Williams: H370

TYPE SPECIES. *Plectambonites planissimus* Pander, 1830 [nom. correct. from *Plectambonites planissima* Pander] (subsequent designation Hall & Clarke 1892: 296).

DIAGNOSIS. Normal concavo-convex convexity. Similar to *Plectella* but more convex (sometimes geniculate) and with the side septa in the brachial valve more pronounced, more numerous and more complex. Chilidium and pseudodeltidium both pronounced.

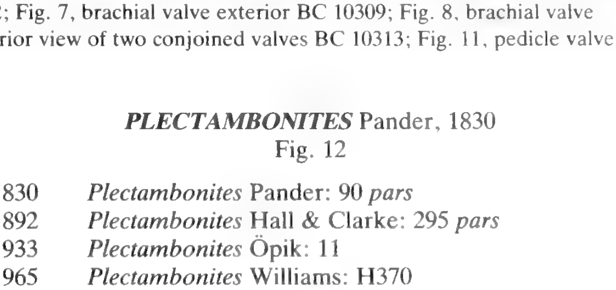


Fig. 12 *Plectambonites planissimus* Pander, 1830, from C_1 Beds (Llanvirn–Llandeilo), Baltic, USSR (after Williams 1965 fig. 237.2c), × 4

REMARKS. Pander (1930: 90), in erecting the genus *Plectambonites*, listed and briefly described twelve species, each of which, plus a further species *Plectambonites inversa*, were illustrated with two or three views on his pl. 19, all showing only the conjoined valve externals. In addition, on pl. 3, he depicted two views showing the interiors of a brachial and pedicle valve which he attributed to the genus *Plectambonites*, but without referring them to any particular species. All came from the St Petersberg (Leningrad) area, but without detailed locality data apart from a footnote (Pander 1830: 52) indicating that most of the shells came from the Iumalasaari, Peselowa and Podolowa areas, which all lie SSE of Leningrad in Upper Arenig, Llanvirn, and Llandeilo limestones. Hall & Clarke (1892) resuscitated the generic name and distinguished it from *Leptaena*, and attributed to it most of what we now know as the Plectambonitacea, although they also erected and separated off the *Leptella* group under that generic name, and furthermore erected *Christiania* (now a strophomenacean) to which they attributed one of Pander's species, *Plectambonites oblonga*.

SPECIES ASSIGNED

Plectambonites aranea Öpik, 1933: 14; pl. 1, figs 1–3 from C_i Beds (Llanvirn–Llandeilo), Leningrad, USSR.

Plectambonites planissimus Pander, 1830: 90; pl. 19, fig. 1; neotype designated Öpik, 1933: 12; pl. 1, figs 4–6; pl. 3, fig. 2 from C_1 Beds (Llanvirn–Llandeilo), Pavlovsk, Leningrad, USSR.

Strophomena radiata Schmidt, 1858: 215; lectotype selected Öpik, 1930: 122; pl. 7, figs 82–83 from C_1–C_2 boundary beds (Llandeilo–Caradoc), Ärra, Estonia, USSR.

DOUBTFUL SPECIES (all from U. Arenig–Llandeilo, S of Leningrad, USSR):

Plectambonites convexa Pander, 1830: 91; pl. 91, fig. 5.
Plectambonites crassa Pander, 1830: 91; pl. 19, fig. 4.
Plectambonites inversa Pander, 1830: pl. 19, fig. 13.
Plectambonites lata Pander, 1830: 91; pl. 19, fig. 3.
Plectambonites ovata Pander, 1830: 92; pl. 19, fig. 9.
Plectambonites semiglobosa Pander, 1830: 91; pl. 19, fig. 8.
Plectambonites testudinata Pander, 1830: 91; pl. 19, fig. 6.
Plectambonites transversa Pander, 1830: 90; pl. 19, fig. 2.
Plectambonites triangularis Pander, 1830: 91; pl. 19, fig. 11.

SPECIES QUESTIONABLY ASSIGNED

Plectambonites? jacuticus Rozman, 1964: 146; pl. 14, figs 7–11 from U. Taryniuriakh Formation (M. Ordovician), Kalychan, Selenniakh Mountains, NE USSR (no interiors known).

SPECIES REJECTED

Plectambonites imbrex Pander, 1830: 91; pl. 19, fig. 12 (to Strophomenidae).

Plectambonites oblonga Pander, 1830: 92; pl. 19, fig. 10 (to *Christiania*).

Plectambonites uncinata Pander, 1830: 91; pl. 19, fig. 7 (to *Leptella*).

Plectambonites arca Shaler, 1865: 64; from Jupiter Formation (U. Llandovery), Anticosti Island, Quebec, Canada (transferred to *Brachyprion* by Twenhofel 1928: 189).

Plectambonites concentriliratus Grubbs, 1939: 556; pl. 62, figs 12, 15–17 from middle Silurian (probably Wenlock) nodules in dolomite, west Chicago, Illinois, USA (no interiors figured, but ornament, shape and outline all look like a pholidostrophid strophomenacean).

Plectambonites producta Hall & Clarke, 1894: 360; pl. 84, figs 23–25 from 'Niagara dolomites', Yellow Springs, Ohio, USA (shape and form appear to be like *Christiania*, but the locality information suggests a Silurian age: the species requires reinvestigation).

Plectambonites yenlacensis Mansuy, 1916: 49; pl. 7, fig. 3 from Kim-lu shales (?Ludlow), Kim-lu, Tonkin, Vietnam (no interiors known, but exteriors look similar to associated chonetaceans).

In addition, numerous subsequent authors, particularly before 1928, erected species originally ascribed to *Plectambonites*, but these are listed under their revised genera in this paper as well as being listed under *Plectambonites* in the index.

PLECTELLA Lamansky, 1905

1905	*Plectella* Lamansky: 156
1932	*Plectella* Öpik: 10
1933	*Plectella* Öpik: 16
1965	*Plectella* Williams: H372

TYPE SPECIES. *Plectambonites uncinata* Pander, 1830.

DIAGNOSIS. Normal convexity. Similar to *Plectambonites* but gentler convexity and with less pronounced side septa.

REMARKS. This is one of the earliest plectambonitaceans, but unfortunately the interior of the brachial valve is known only from the two rather poorly preserved specimens figured by Öpik (1933: pl. 4, figs 4, 5). The two specimens are from the same locality (not the type locality) but differ in strength of their side septa, the amount of secondary calcite around the cardinalia, and in the development of the platform. Further specimens, including brachial valve interiors, from the type locality and proper taxonomic revision are urgently needed.

SPECIES ASSIGNED

Plectambonites uncinata Pander 1830: 91 from B_{i_β} 1 beds with *Cyrtometopus primigenus* (U. Tremadoc), Maekula, 9 km west of Tallinn, Estonia, USSR (Öpik, 1933: 17; pl. 4, figs 2–5). Lamansky (1905: 159–60) also erected *Plectella gracilis*, *Plectella semiovata*, *Plectella media*, *Plectella eminens*, *Plectella extensa* and *Plectella obtusa* all as new species, but all from the same locality of Popowka. Lamansky (1905: pl. 2) only figured exteriors of these species, and it is not known whether or not they all came from the same horizon, and their validity is doubtful.

?***AKELINA*** Severgina, 1967

Figs 13–17

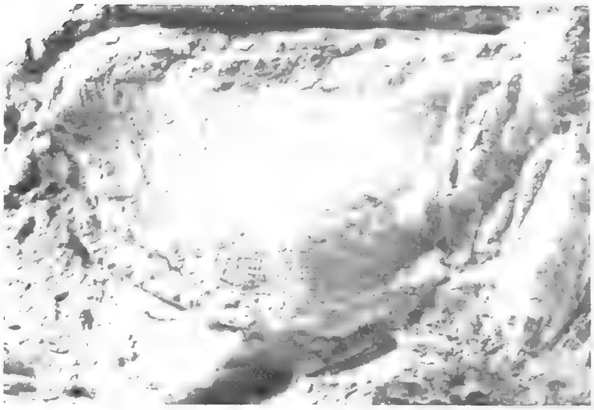
1967	*Akelina* Severgina: 133
1984*b*	*Akelina* Severgina: 49

TYPE SPECIES. *Akelina akelina* Severgina, 1967.

DISCUSSION. There are various doubts still remaining about this genus, but because we consider that, on balance, it is probably a plectambonitacean and, if so, probably a member of the Plectambonitidae, we include it here, albeit with a query.

We are privileged in being able to examine and reillustrate the type specimens of the genus. They are preserved in a variety of lithologies, a partly exfoliated pedicle valve (Fig. 13) and a brachial valve exterior (Fig.14) in limestone; two


13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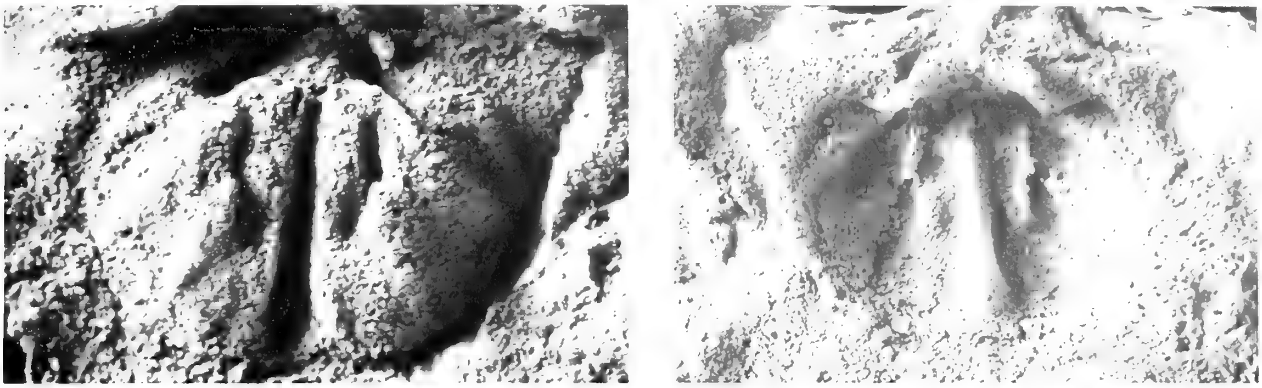
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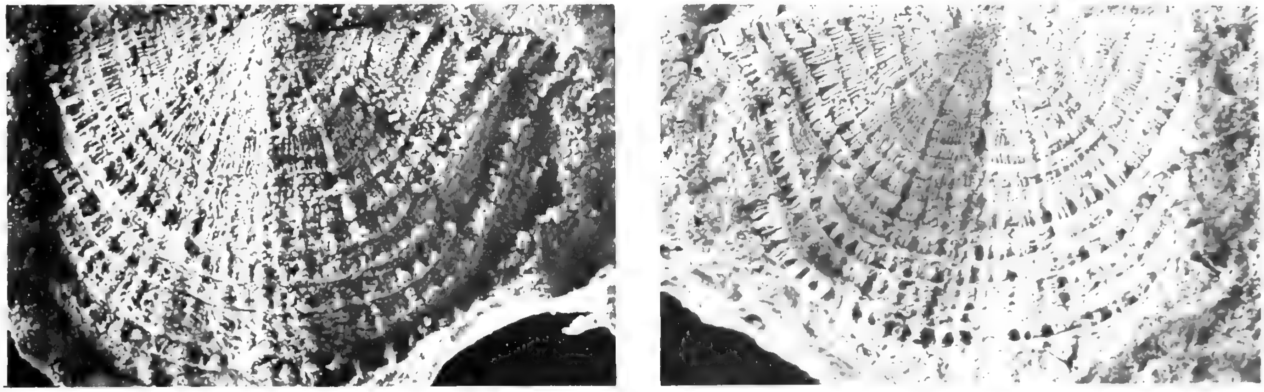
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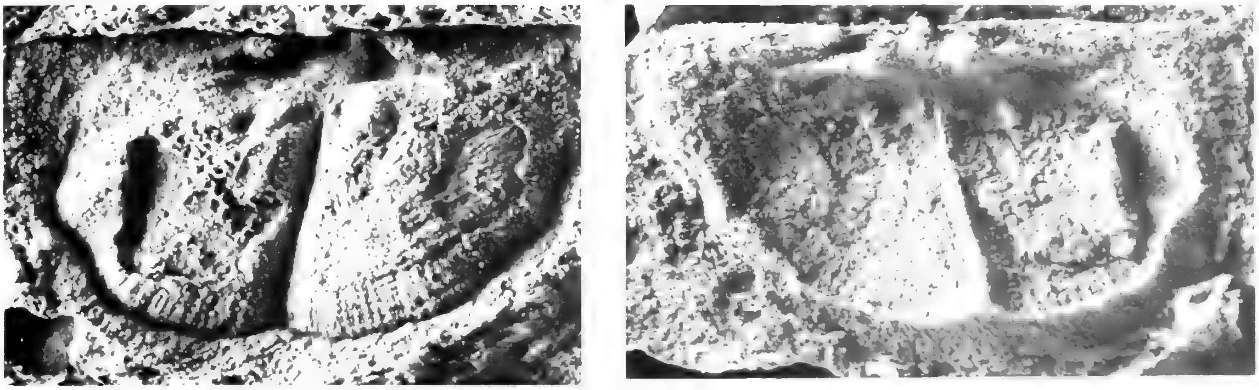
16b


17a

17b

Figs 13–17 *Akelina akelina* Severgina, 1967, all from type locality in the Algan Formation (U. Tremadoc), River Akel, Kusnetz Alatai, Altai Mountains, USSR. Fig. 13, partly exfoliated interior of pedicle valve, the original of Severgina 1967: pl. 5, fig. 8, VSEGEI 424/1323, × 8; Fig 14, partly exfoliated exterior of brachial valve, the original of Severgina 1967: pl. 5, fig. 10, VSEGEI 425/1323, × 6; Fig. 15, internal mould and latex cast of brachial valve, holotype, the original of Severgina 1967: pl. 5, fig. 9, VSEGEI 427/1323, × 6; Fig. 16, latex cast and natural mould of pedicle valve exterior, the original of Severgina 1984: pl. 5, fig. 14, VSEGEI 1030/1323, × 6; Fig. 17, natural mould and latex cast of brachial valve interior, VSEGEI 1027/1323, × 6.

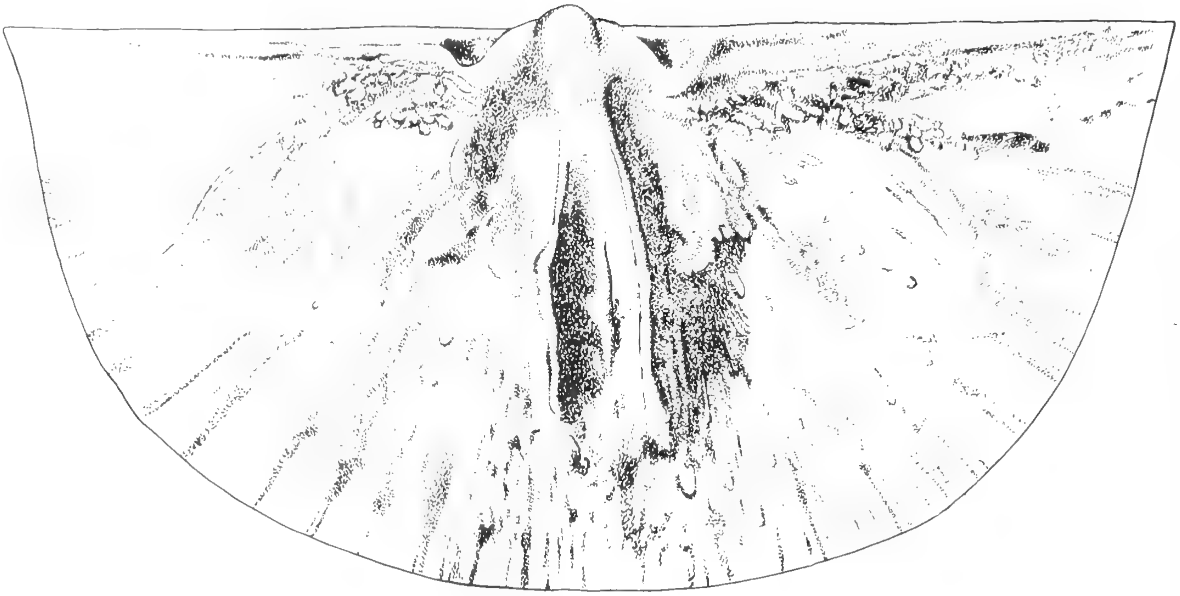


Fig. 18 *Isophragma ricevillense* Cooper, 1956, from base of Athens Formation (L. Caradoc), 4 km SSE of Riceville, Tennessee, USA, interior of brachial valve, based on BC 7211, × 12.

brachial valves, including the holotype (Fig. 15), on a single block of grey decalcified sandstone; and one brachial valve (Fig. 17) in decalcified siltstone. This last specimen (Fig. 17) is the only one to have suffered tectonic distortion. Thus, because of the varied preservation, there is uncertainty as to whether a single stratigraphic unit and single species of brachiopod are really involved, but we have had to proceed on the assumption that all the specimens are truly conspecific. The partly exfoliated pedicle valve (Fig. 13) shows slight pimples, particularly near the umbo, which may be pseudopunctae, and it is on this basis that we provisionally accept *Akelina* as a plectambonitacean. The cardinal process and other details are not clear on the holotype, chiefly on account of the relatively coarse preservation, but the cardinal process appears to consist of a simple knob. On either side of the relatively strong myophragm of the holotype there is a pair of subparallel structures running anterolaterally; we interpret these as possible side septa, which is why the genus is assigned to the Plectambonitidae rather than to the Taffiidae, although on the other better preserved, but tectonically distorted, brachial valve (Fig. 17) these side septa are present only as faint traces.

The Tremadoc age of the material does not appear to be in doubt from the accompanying trilobites (Severgina 1984*b*), and, if *Akelina* is truly a plectambonitid, would be about the same age as the oldest member of the family, which is *Plectella* from the Baltic region.

In any case, a major reinvestigation of the genus from homogeneous large samples would be of great interest in clarifying the earliest history not only of the Plectambonitacea but the whole order Strophomenida.

SPECIES ASSIGNED

Akelina akelina Severgina, 1967: 133; pl. 5, figs 8–10 from Algan Horizon (U. Tremadoc), River Akel, Kuznetz Alatau, Altai-Sayan, USSR.

Subfamily **TAPHRODONTINAE** Cooper, 1956

1956	Isophragminae Cooper: 733
1956	Taphrodontidae Cooper: 740
1965	Isophragmatinae Williams: H375
1965	Taphrodontinae Williams: H376

DIAGNOSIS. Like Plectambonitinae, but with double median septum and without hinge line denticles.

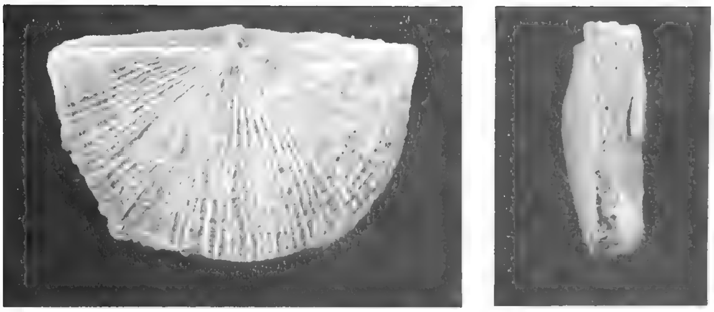
REMARKS. It is difficult to find a precise term for the structure seen in the central part of the brachial valve in some taphrodontids. We term it a double septum, but the space between the two septa does not reach the valve floor, and thus the two side septa become united to form what might be termed a single median septum with a central hollow. However, this structure is unlike a normal median septum, and we analyse the double septum as analagous with side septa in other plectambonitaceans.

Even though Cooper (1956) erected separate familial or subfamilial rank for each of the two genera attributed to this subfamily, he did not directly compare the two, and we can find no subfamilial differences. The resupination which is often seen in *Isophragma* is regarded here as only of generic importance. We use the name Taphrodontinae rather than Isophragminae because, at the time of first erection of both, Cooper (1956) gave the taxon based on *Taphrodonta* familial rank rather than the subfamilial rank of the Isophragminae.

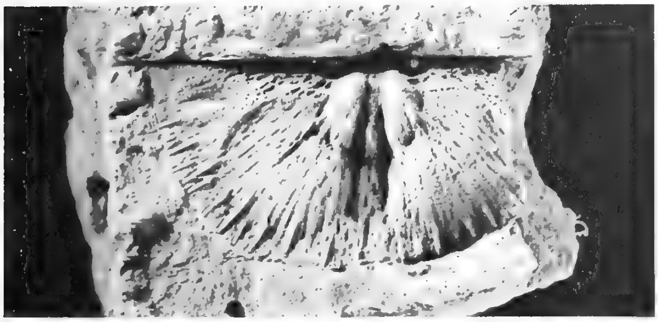
GENERA ASSIGNED. *Isophragma* Cooper, 1956; *Taphrodonta* (*Taphrodonta*) Cooper, 1956; *Taphrodonta* (*Nanambonites*) Liu, 1976.

RANGE. Llanvirn (*Nanambonites paucus*) to L. Caradoc (*Isophragma* spp.).

19a



20a 20b



19b

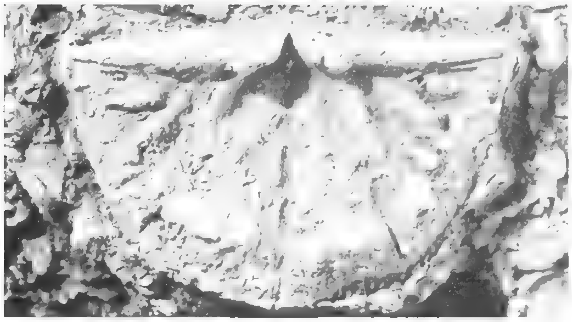


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Fig. 19 *Isophragma ricevillense* Cooper, 1956, topotype, from basal Athens Formation (L. Caradoc), 4 km SSE of Riceville, Tennessee, USA, latex cast and internal mould of brachial valve, BC 7211, × 4.

Figs 20, 21 *Isophragma pseudoretroflexum* (Reed, 1917), topotypes from Balclatchie Conglomerate (L. Caradoc), Balclatchie, Girvan, Strathclyde, Scotland. Fig. 20, exterior of conjoined valves, the original of Reed 1917: pl. 13, figs 18, 18a, b, B73420, × 3; Fig. 21, pedicle valve interior, the original of Reed 1917: pl. 13, fig. 20, B 73427, × 4.

ISOPHRAGMA Cooper, 1956

Figs 18–21

1956 *Isophragma* Cooper: 733
1965 *Isophragma* Williams: H375

TYPE SPECIES. *Isophragma ricevillense* Cooper, 1956.

DIAGNOSIS. Flat to slightly resupinate. No accessory plates between cardinal process and interarea. Side septa variably developed, usually absent.

REMARKS. Sometimes (e.g. Fig. 19) the two central septa in the brachial valve can be traced separately throughout the length of the structure, but at other times the two septa are fused posteriorly to form a single broad structure.

SPECIES ASSIGNED

Isophragma biseptatum Cooper, 1956: 734; pl. 171, figs 20–32 from Benbolt Formation (L. Caradoc), Green Valley, Tennessee, USA.

Isophragma extensum Cooper, 1956: 735 from Arline Formation (L. Caradoc), Friendsville, Tennessee, USA, and subspecies *tricostatum* Williams, 1962: 162; pl. 15, figs 5, 7, 8–13 from Stinchar Limestone (Llandeilo), Girvan, Scotland.

Isophragma imperator Popov, 1980*b*: 147; pl. 2, figs 8–11 from Anderkenski Horizon (U. Llandeilo–L. Caradoc), Katnak Hill, Chu-Ili Mountains, Kazakhstan, USSR.

Isophragma orientale Andreeva, 1985: 40; pl. 4, figs 1–6 from Tarlikskaya Formation (M. Ordovician), River Uiuk, Tuva, USSR.

Isophragma princeps Popov, 1980*a*: 54; pl. 17, figs 1–7 from Erkebidaikski Horizon (M. Ordovician), Chelinograd, N. Kazakhstan, USSR.

Leptella ? pseudoretroflexa Reed, 1917: 874; pl. 13, figs 18–26 from Balclatchie Conglomerate (L. Caradoc), Balclatchie, Girvan, Scotland (revised Williams 1962: 162; pl. 15, figs 14–16, 20).

Isophragma ricevillense Cooper, 1956: 737; pl. 170, figs 1–15 from L. Athens Formation (L. Caradoc), Riceville, Tennessee, USA.

Isophragma subabbreviatum Cooper, 1956: 738; pl. 169, figs 1–9 from M. Arline Formation (L. Caradoc), Friendsville, Tennessee, USA.

SPECIES QUESTIONABLY ASSIGNED

Isophragma ponderosum Cooper, 1956: 737; pl. 210, figs 25–32 from Eureka Group (Llandeilo?), Martin Ranch, Roberts Mountains, Nevada, USA (no interiors figured).

Isophragma sulcatum Cooper, 1956: 739; pl. 170, fig. 16 from U. Llanvirn beds, Pratt Ferry, Alabama, USA (no interiors known).

Isophragma sp. 1 of Cooper 1956: 740; pl. 213, fig. 21 from Pratt Ferry Formation (Llanvirn), Pratt Ferry, Alabama, USA (may be *Syndielasma*).

TAPHRODONTA (TAPHRODONTA) Cooper, 1956

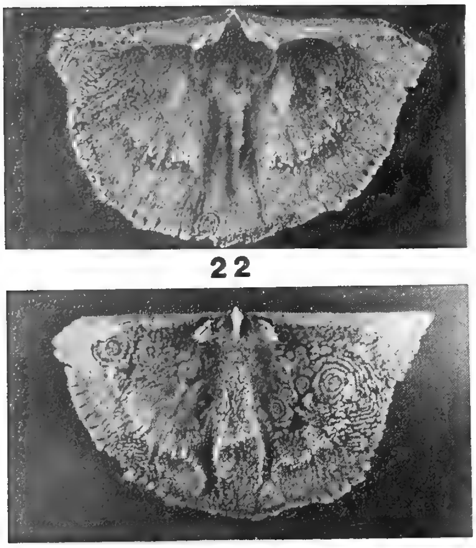
Figs 22, 23

1956 *Taphrodonta* Cooper: 740
1965 *Taphrodonta* Williams: H376

TYPE SPECIES. *Taphrodonta parallela* Cooper, 1956.

DIAGNOSIS. Like *Isophragma* but with no resupination, and shorter pedicle valve muscle field. Two small plates between cardinal process and interarea. No side septa apart from double median septum.

REMARKS. Although *Taphrodonta* has a generally simple cardinal process, in some specimens (e.g. Cooper 1956: pl.



Figs 22, 23 *Taphrodonta parallela* Cooper, 1956, topotypes from Upper Pogonip Group (U. Llanvirn), 1 mile above entrance to Ikes Canyon, Toquima Range, Nevada, USA. Fig. 22, pedicle valve interior, the original of Cooper 1956: pl. 165, figs 7–11, USNM 117562g, × 4; Fig. 23, brachial valve interior, the original of Cooper 1956: pl. 165, figs 20–22, USNM 117562f, × 4.

165, figs 19, 22) there are two very small plates in the chilidial opening between the cardinal process and the interarea; these are not fused to the cardinal process, and thus the cardinal process cannot be described as trifid.

SPECIES ASSIGNED

Taphrodonta parallela Cooper, 1956: 741; pl. 165, figs 1–22 from Antelope Valley Limestone, Upper Pogonip Group (U. Llanvirn), Ikes Canyon, Nevada, USA.

SPECIES QUESTIONABLY ASSIGNED

Taphrodonta bicornigera Nikitin, 1974: 58; pl. 5, figs 6–9 from Sarybidaik Formation (Llandeilo–Caradoc), right bank of Shiderty River, Narulgen, Kazakhstan, USSR (form of cardinal process uncertain from text and photographs).

TAPHRODONTA (NANAMBONITES) Liu, 1976

1976 *Nanambonites* Liu: 145

TYPE SPECIES. *Nanambonites paucus* Liu, 1976.

DIAGNOSIS. Like *Taphrodonta* (*Taphrodonta*) but with chilidium in brachial valve.

REMARKS. *Nanambonites* and *Taphrodonta* are the only two previously defined plectambonitacean genera with the two very small plates in the chilidial opening between the cardinal process and the interarea. The only difference we can find between them is the reported (but not illustrated) presence of a chilidium in *Nanambonites*, and this therefore merits their differentiation into separate subgenera. Liu (1976: 145) also mentioned the shape of the cardinal process and the shape of the double septum as generic differences, but the two taxa seem very similar to us in these respects.

SPECIES ASSIGNED

Nanambonites paucus Liu, 1976: 146; pl. 2, figs 17–19 from lower formation of Jiacun Group (Llanvirn), Mount Jolmo Lungma area, Tibet, China.

Family **TAFFIIDAE** Schuchert & Cooper, 1931

1931	Taffiinae Schubert & Cooper: 243
1936	Taffiidae Ulrich & Cooper: 625
1938	Taffidae Ulrich & Cooper: 180
1953	Taffiidae Williams: 6
1965	Taffiidae Williams: H372 *pars*

DIAGNOSIS. Simple cardinal process. No bema. No side septa.

REMARKS. This family is divided into five subfamilies partly on the basis of shell shape, with the Ahtiellinae separated from the others by its resupination and geniculation, partly on the basis of the chilidium and muscle field, upon which the Spanodontinae differs from the rest, and partly on the platform, whose absence separates the Pelonomiinae from the others. The muscle field of the Spanodontinae is strikingly different in its dalmanelloid appearance as opposed to the more oblique arrangement of most plectambonitaceans, although *Taffia* itself, even though it is not well known, suggests a little similarity to *Spanodonta* in this feature. The Leptellinae is distinguished from the other subfamilies by the lack of a cardinal process; however, the morphology of its only genus, *Leptella*, is close to that of some taffiids, for example *Borua*.

SUBFAMILIES ASSIGNED. Taffiinae Schuchert & Cooper, 1931; Ahtiellinae Öpik, 1933; Leptellinae Williams, 1965; Pelonomiinae subfam. nov.; Spanodontinae subfam. nov.

RANGE. (? Tremadoc) Lower Arenig to Llandeilo.

Subfamily **TAFFIINAE** Schuchert & Cooper, 1931

1931	Taffiinae Schuchert & Cooper: 243
1965	Taffiidae Williams: H372 *pars*
1976	Aporthophylinae Liu: 143

DIAGNOSIS. Concavo-convex. With platform.

REMARKS. Liu (1976) established a new subfamily the Aporthophylinae based on the presence of a cardinal process and placed *Aporthophyla* and *Aporthophylina* with a cardinal process in it, as opposed to the Taffiinae, including *Taffia* alone, with no cardinal process. However, Neuman (1977) established that a cardinal process sometimes occurs within the type species of *Taffia*, and therefore we do not recognize Liu's subfamily.

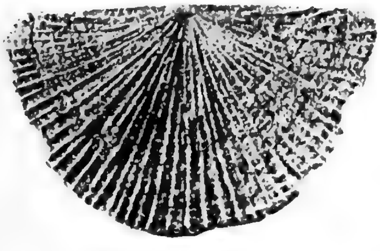
GENERA ASSIGNED. *Aporthophyla* Ulrich & Cooper, 1936, including *Archambona* Cooper, 1988; *Aporthophylina* Liu, 1976; *Taffia* Butts, 1926; *Tourmakeadia* Williams & Curry, 1985.

RANGE. L. Arenig (*Schedophyla striata*) to Llanvirn (several species, e.g. *Aporthophyla kasachstanica*).

APORTHOPHYLA Ulrich & Cooper, 1936

Figs 26–30

1936	*Aporthophyla* Ulrich & Cooper: 625
1938	*Aporthophyla* Ulrich & Cooper: 182
1965	*Aporthophyla* Williams: H372
1970	*Aporthophyla* Ross: 63
1974	*Aporthophyla* Neuman, *in* Neuman & Bruton: 85
1987	*Aporthophyla* Ross & James: 83
1988	*Archambona* Cooper: 186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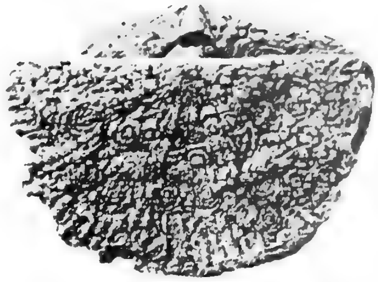
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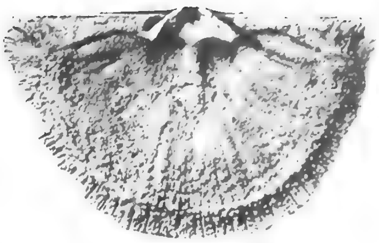
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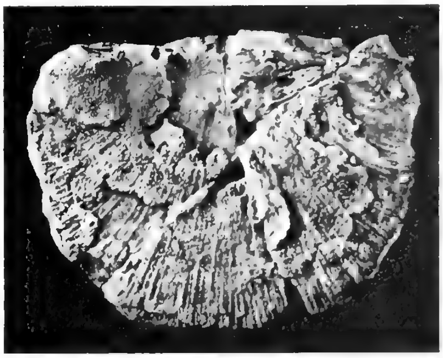
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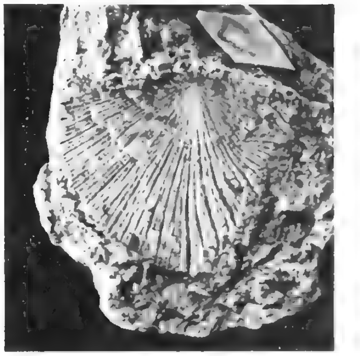
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Figs 24–25 *Taffia planoconvexa* Butts, 1926, from Odenville Formation (L. Arenig). Fig. 24, external and internal views of a brachial valve, the original of Ulrich & Cooper 1938: pl. 37, figs 15, 18 from railway east of Odenville Station, Alabama, USA, USNM 91586, × 3; Fig. 25, conjoined valves, syntype, the original of Butts 1926: pl. 18, fig. 13 and Ulrich & Cooper 1936: pl. 37, fig. 16 from Newhope Church, 7 miles northeast of Pelham, Alabama, USA, USNM 71461b, × 3.

Figs 26–30 *Aporthophyla typa* Ulrich & Cooper, 1936, from lower *Rhysostrophia* Zone, Upper Pogonip Group (Llanvirn), 1 mile above the entrance in Ikes Canyon, Toquima Range, Nevada, USA. Fig. 26, internal mould of pedicle valve, the original of Cooper 1956: pl. 163, fig. 24,USNM 117566, × 2; Fig. 27, mostly exfoliated interior of pedicle valve, syntype, the original of Ulrich & Cooper 1938: pl. 37, fig. 2, USNM 92866a, × 2; Fig. 28, mostly exfoliated interior of brachial valve, syntype, the original of Ulrich & Cooper 1938: pl. 37, figs 7, 8 USNM 92866e, × 3; Fig. 29, conjoined valves USNM 92866c, × 2; Fig. 30, external mould of brachial valve, syntype, the original of Ulrich & Cooper 1938: pl. 37, fig. 3, USNM 92866b, × 2.

TYPE SPECIES. *Aporthophyla typa* Ulrich & Cooper, 1936 (lectotype selected Neuman 1974: 85). Type of *Archambona* is *A. floweri* Cooper, 1988.

DIAGNOSIS. Concavo-convex. Strong dental plates. Chilidium present, pseudodeltidium reduced or absent. Cardinal process always present.

REMARKS. *Aporthophyla* is very close to *Taffia*, particularly since a cardinal process is now known rarely from *Taffia* (Neuman 1977: 34), and also because Ross (1970: 63) discovered a platform in specimens of *Aporthophyla*. In fact the two genera are only separated rigorously here on the size of the pseudodeltidium; however, in practice, specimens without a cardinal process are more likely to be *Taffia*. The types of *Aporthophyla* (Ulrich & Cooper 1938: pl. 37) include relatively small brachial valves (about 20 mm wide), none of which show a platform; however, a larger pedicle valve (Fig. 26, USNM 117566) shows slight traces of a platform, and many of the species listed below have platforms in much smaller specimens. All the features of *Archambona* agree with those of *Aporthophyla* and we cannot separate these two genera.

SPECIES ASSIGNED

Strophomena aurora Billings, 1865: 218 from Table Head Formation (Llanvirn), Port Rich, Newfoundland, Canada (figured Cooper, 1956: pl. 164, figs 1–3 and Ross & James 1987: pl. 2, figs 11–14).

Archambona floweri Cooper, 1988: 186, figs 1.1–22 from Setul Formation (L. Ordovician), Pulau Langgun, Langkawi Islands, Malaysia.

Aporthophyla kasachstanica Rukavishnikova, 1956: 123; pl. 1, figs 6–9 from Kopalinski Horizon (Llanvirn), Kstau-sai, Chu-Ili Mountains, Kazakhstan, USSR.

Aporthophyla perelegans Liu, 1976: 144; pl. 2, figs 1–9 from lower formation of Jiacun Group (U. Arenig–Llanvirn), Jiacun, Nielamu County, S. Xizang (Tibet), China (probably also includes '*Dactylogonia* sp.' of Liu 1976: 149; pl. 2, figs 10–11 from the same locality).

Aporthophyla stoermeri Neuman, *in* Neuman & Bruton 1974: 86, figs 4, 9, 10 from siltstone block of Llanvirn age, Trotland Farm, Hølonda, Norway.

Aporthophyla superstes Ross & James, 1987: 84; pl. 2, fig. 18; pl. 3, figs 1–4 from Table Point Formation (Llanvirn), Table Head, Newfoundland.

Aporthophyla tianjingshanensis Fu, 1982: 115; pl. 34, figs 2–6 from the Tianjingshan Formation (U. Arenig), Tianjingshan, Zhongwei, Ningxia Province, N. China.

Aporthophyla typa Ulrich & Cooper, 1936: 625 from the Upper Pogonip Group (Llanvirn), Ikes Canyon, Nevada, USA (revised Ulrich & Cooper, 1938: 183; pl. 37, figs 1–3, 5, 7, 8, 10, 11).

SPECIES QUESTIONABLY ASSIGNED

Aporthophyla ordensis Klenina, 1984: 64; pl. 5, figs 16, 18, 19; pl. 6, figs 7, 10, 14 from Abaevskaya Formation (Llanvirn–Llandeilo), SE Ordatas Hill, Pre-Chinghiz Mountains, Kazakhstan, USSR (no interiors illustrated).

Aporthophyla sp. of Liu *et al.* 1983: 273; pl. 92, figs 18–20 from Majiagou Formation (Llanvirn), Xiaoxian County, Anhui Province, China (no interiors known).

APORTHOPHYLINA Liu, 1976

1976 *Aporthophylina* Liu: 144

TYPE SPECIES. *Aporthophylina intermedia* Liu, 1976.

DIAGNOSIS. Like *Aporthophyla* but lacking dental plates in pedicle valve.

REMARKS. According to Liu (1976: 144), *Aporthophylina* differs from *Aporthophyla* in its socket ridges, in a cardinal process which becomes stronger posteriorly, in a long strong median ridge in the brachial valve, and in the lack of dental plates in the pedicle valve. We do not consider the first three characters to be of generic importance, but continue to separate the two genera on the absence of dental plates.

SPECIES ASSIGNED

Aporthophylina intermedia Liu, 1976: 145; pl. 2, figs 12–15 from lower formation of Jiacun Group (U. Arenig–Llanvirn), Chaya, Dingri County, Xizang (Tibet), China.

TAFFIA Butts, 1926
Figs 24, 25

1926 *Taffia* Ulrich MS *in* Butts: 99
1938 *Taffia* Ulrich & Cooper: 180
1956 *Taffia* Cooper: 697
1965 *Taffia* Williams: H372
1977 *Taffia* Neuman: 34

TYPE SPECIES. *Taffia planoconvexa* Butts, 1926.

DIAGNOSIS. Usually without simple cardinal process (but may be rarely present). Large pseudodeltidium, small chilidium also present.

REMARKS. Earlier authors (Ulrich & Cooper 1936, 1938, Williams 1965) stressed the absence of a cardinal process as part of their diagnosis of *Taffia*, but Neuman (1977: 34) described great variation in this respect; in a population of 12 specimens from the Odenville Limestone of Alabama, 3 have a low but definite simple cardinal process whilst in 9 the floor of the notothyrial platform is smooth. Until the occasional presence of a cardinal process is demonstrated in some other population of *Taffia* we think that it is better to keep *Taffia* and *Aporthophyla* as distinct genera.

SPECIES ASSIGNED

Taffia anomala Benedetto & Herrera 1986: 117; pl. 3, figs 1–13 from U. San Juan Formation (M. Arenig–L. Llanvirn), Quebradas Honda, San Juan Province, Argentina.

Taffia planoconvexa Butts, 1926: 100; pl. 18, figs 13–17 from the Odenville Formation (L. Arenig), Odenville, Alabama, USA (revised Ulrich & Cooper, 1938: 181; pl. 37, figs 12–18).

Taffia westgatei Ulrich & Cooper, 1936: 625 (figd Ulrich & Cooper 1938: pl. 37, figs 4, 6, 9) from Yellow Hill Formation (Arenig–Llanvirn), Ely Springs Range, Nevada, USA.

Taffia ? sp. of Neuman 1977: 34; pl. 7, figs 16–21; pl. 8, fig. 2 from Llanvirn rocks, Virgin Arm, Newfoundland, Canada.

TOURMAKEADIA Williams & Curry, 1985

1985 *Tourmakeadia* Williams & Curry: 252

TYPE SPECIES. *Tourmakeadia fimbriata* Williams & Curry, 1985.

DIAGNOSIS. With elevated and bilobed platform in pedicle valve.

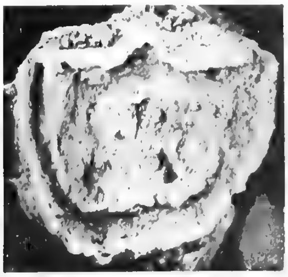
REMARKS. Even though the cardinal process is clearly that of a taffiid, nevertheless the rest of the morphology (apart from the interesting pedicle valve platform) is very close to *Leptellina* and its relatives in the Leptellinidae, and some form related to *Tourmakeadia* was probably the ancestor of *Leptellina*.

SPECIES ASSIGNED

Tourmakeadia fimbriata Williams & Curry, 1985: 253, figs 176–182 from Tourmakeady Limestone (U. Arenig), Tourmakeady, Co. Mayo, Ireland.

Subfamily **AHTIELLINAE** Öpik, 1933

1933 Ahtiellinae Öpik: 19
1953 Ahtiellinae Williams: 6
1965 Ahtiellinae Williams: H372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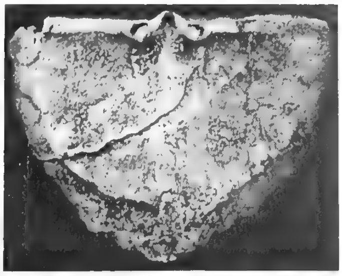
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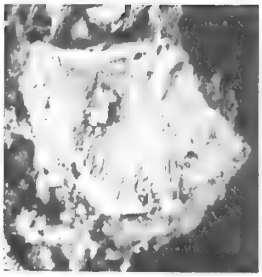
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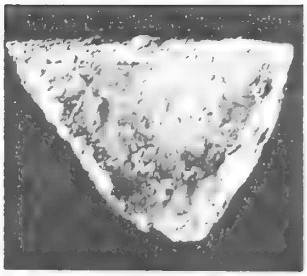
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Figs 31–34 *Borua modesta* Williams & Curry, 1985, from Tourmakeady Limestone (U. Arenig), stream 2 km SW of Srah Bridge, Co. Mayo, Ireland. Fig. 31, internal view of pedicle valve, paratype, the original of Williams & Curry 1985: fig. 171, BB 95532, × 3; Fig. 32, interior of brachial valve, holotype, the original of Williams & Curry 1985: fig. 171, BB 95531, × 3; Fig. 33, interior of brachial valve, the original of Williams & Curry 1985: fig. 173, BB 95533, × 3; Fig. 34, exterior of brachial valve, the original of Williams & Curry 1985: fig. 175, BB 95537, × 4.

DIAGNOSIS. Resupinate. With platform (or diaphragm).

REMARKS. Both Öpik (1933) and Williams (1965) included the Ahtiellinae as a subfamily within the Plectambonitidae, but we include the subfamily within the Taffiidae owing to the absence of side septa.

GENERA ASSIGNED. *Ahtiella* Öpik, 1932; *Borua* Williams & Curry, 1985; *Guttasella* Neuman, 1977; *Inversella* (*Inversella*) Öpik, 1933; *Inversella* (*Reinversella*) Bates, 1968; *Rutrumella* Harper, 1981; *Sanjuanella* Benedetto & Herrera, 1987; *Schedophyla* Neuman, 1971.

RANGE. U. Arenig (*Ahtiella quadrata*) to Llanvirn–Llandeilo (*Ahtiella lirata*).

AHTIELLA Öpik, 1932

1932 *Ahtiella* Öpik: 37
1933 *Ahtiella* Öpik: 19
1965 *Ahtiella* Williams: H372

TYPE SPECIES. *Ahtiella lirata* Öpik, 1932.

DIAGNOSIS. With brachial valve median septum and with impersistent rugae and simple geniculation. Relatively small socket plates.

REMARKS. *Ahtiella* may be distinguished from *Inversella* by the presence of a brachial valve median septum and impersistent rugae. *Guttasella* differs in its double geniculation and in lacking both a brachial valve median septum and also rugae. Hessland (1949) lists the various ornamental differences which he considered important in distinguishing species; however, a further revision might show that many of the names listed below should properly be synonymized with each other.

SPECIES ASSIGNED

Ahtiella arenaria Öpik, 1933: 19; pl. 4, figs 7, 8 from Rogö Lime-Sandstone (Llanvirn), Little Rogö Island, Estonia, USSR.

Ahtiella argentina Benedetto & Herrera, 1986: 114; pl. 1, figs 4–21 from U. San Juan Formation (L. Llanvirn), Quebradas Los Gatos y Honda, San Juan province, Argentina.

Ahtiella baltica Öpik, 1932: 42; pl. 2, fig. 12; pl. 5, fig. 1, from Rogö Sandstone, $B_{\text{iii}\gamma}$ (Llanvirn), Paldiski, Estonia, USSR.

Ahtiella concava Bates, 1968: 167; pl. 7, figs 12–22 from Bod Deiniol Formation (Llanvirn), Bod Deiniol, Anglesey, Wales.

Ahtiella jaanussoni Hessland, 1949: 523; pl. 1, fig. 2 from *raniceps* Zone Beds (Llanvirn), Hälluden, Öland, Sweden.

Ahtiella lirata Öpik, 1932: 39; pl. 3, figs 14–21; pl. 5, fig. 31; pl. 8, figs 36–37 from C_1 Beds (Llanvirn–Llandeilo), Tsitri, Estonia, USSR.

Ahtiella paucirugosa Neuman, 1977: 30; pl. 3, figs 24–37; pl. 8, fig. 1 from Llanvirn rocks, Virgin Arm, Newfoundland, Canada.

Ahtiella quadrata Bates, 1968: 166; pl. 8, figs 1–9 from Torllwyn Formation (Arenig), Ogof Gynfor, Anglesey, Wales.

SPECIES QUESTIONABLY ASSIGNED

Ahtiella dalecarlia Hessland, 1949: 520; pl. 1, figs 3–5 from 3 m above *limbata* Limestone (Llanvirn), Leskusänget, Orsa, Dalarna, Sweden (no interiors figured).

Leptaena gemella Eichwald, 1860: 861; pl. 36, fig. 6 from Lower Ordovician beds, Pulkowa, nr Leningrad, USSR (no interiors figured).

Strophomena jentzschi Gagel, 1980: 44; pl. 5 fig. 26 from glacial erratics in N. Germany of unknown age (assigned to *Ahtiella* by Hessland (1949: 518; pl. 1, figs 1, 2) and Sokolskaya (1960: pl. 27, figs 9, 10) but no interiors figured).

Ahtiella oelandica Hessland, 1949: 521; pl. 2, figs 1, 3, 4 from *raniceps* Zone Beds (Llanvirn), Stenasa, Öland, Sweden (no interiors figured).

Ahtiella plana Hessland, 1949: 524; pl. 1, figs 6, 7 from *raniceps* Zone beds (Llanvirn), Hälluden, Öland, Sweden (no interiors figured).

SPECIES REJECTED

Ahtiella ? *portlocki* Reed, 1952: 48; pl. 2, fig. 5 from Killey Bridge Formation (L. Ashgill), Pomeroy, County Tyrone, Northern Ireland (revised Mitchell 1977: 114; pl. 26, figs 1–13 and assigned to *Brachyprion*; reassigned to *Pholidostrophia* (*Eopholidostrophia*) by Cocks 1978: 129).

BORUA Williams & Curry, 1985
Figs 31–34

1985 *Borua* Williams & Curry: 250

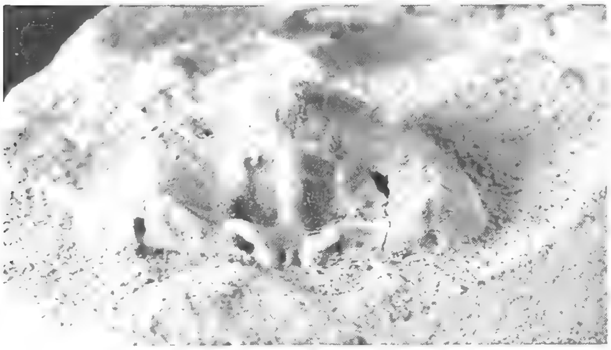
TYPE SPECIES. *Borua modesta* Williams & Curry, 1985

DIAGNOSIS. Smooth apart from faint peripheral parvicostellae and occasional impersistent rugae in some specimens. Short


35a


35b


36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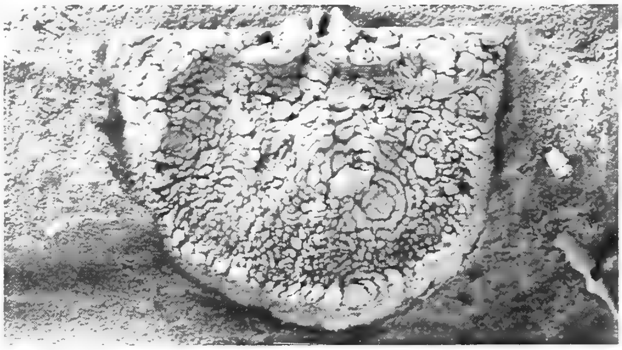
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37b

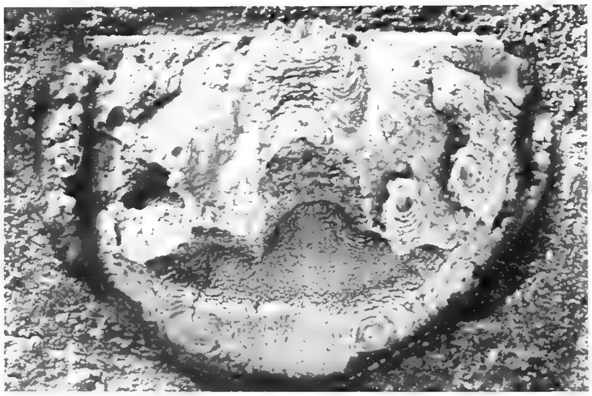
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Fig. 35 *Inversella* (*Reinversella*) *monensis* Bates, 1968, exterior and counterpart interior moulds of brachial valve, holotype, the original of Bates 1968: pl. 8, figs 10–12, BB 30574, from Treiorwerth Formation (Arenig), 300 yards SE of Ffynnon-y-mab, Trefor, Anglesey, Wales, × 2.

Figs 36–39 *Spanodonta hoskingiae* Prendergast, 1935, topotypes from Gap Creek Formation (Middle Ordovician), south side of Gap Spring, Price's Creek, Emmanuel Range, Western Australia. Fig. 36, lateral view of pedicle valve, BC 10604, × 3·5; Fig. 37, a brachial valve interior viewed obliquely from the posterior and straight down, BC 10605, × 3 and × 3·5; Fig. 38, brachial valve interior, BC 7238, × 4; Fig. 39, conjoined valves partly exfoliated to show the pedicle valve muscle field and part of the brachial valve platform, BC 7242, × 4.

myophragm in brachial valve, but no brachial valve median septum.

REMARKS. The smooth shell surface (apart from peripheral parvicostellae and occasional rugae) is not known elsewhere in the family. It may be the result of silicification processes in the only known specimens, but if original then the cause is unknown, as is the function of parvicostellae generally.

SPECIES ASSIGNED

Borua modesta Williams & Curry, 1985: 250, figs 169–175 from Tourmakeady Limestone (U. Arenig), Tourmakeady, Co. Mayo, Ireland.

GUTTASELLA Neuman, 1977

1977 *Guttasella* Neuman: 31

TYPE SPECIES. *Guttasella gutta* Neuman, 1977.

DIAGNOSIS. No rugae. No brachial valve median septum. Doubly geniculate like *Inversella* (*Reinversella*).

REMARKS. *Guttasella* is similar to *Reinversella* and differs externally in the lack of rugae. The cardinalia and shell shape indicate the placing of this genus within the Ahtiellinae. However, one of Neuman's illustrations (1977: pl. 5, fig. 4) indicates the slight trace of a bema, a feature which is generally absent in the Taffiidae; nevertheless we prefer to assign the genus here.

SPECIES ASSIGNED

Guttasella gutta Neuman, 1977: 31; pl. 5, figs 1–5 from Llanvirn age rocks, Virgin Arm, Newfoundland, Canada.

INVERSELLA (INVERSELLA) Öpik, 1933

1933 *Inversella* Öpik: 21
1965 *Inversella* Williams: H372

TYPE SPECIES. *Inversella borealis* Öpik, 1933.

DIAGNOSIS. No median septum in brachial valve. Persistent rugae over valve and strongly geniculate in a ventral direction.

SPECIES ASSIGNED

Inversella angulata Öpik, 1933: 23; pl. 3, fig. 3 from $B_{iii\beta}$ (L. Llanvirn), Toila, Estonia, USSR.

Inversella borealis Öpik, 1933: 23 (figured as *Palaeostrophomena concava* by Öpik 1932: pl. 4, fig. 24) from the Echinosphaeriten Limestone $C_{i}a$ (U. Llanvirn), Eesti, Estonia, USSR.

Inversella sp. of Neuman 1977: 34; pl. 6, figs 1–4 from Llanvirn age rocks, Virgin Arm, New World Island, Canada.

SPECIES QUESTIONABLY ASSIGNED

Inversella perundosa Öpik, 1939: 128; pl. 5, fig. 6 from the Expansus Shale (L. Llanvirn) of Rokstadasen, Hedenstad, Norway (only pedicle valve exterior illustrated – the species could be a leptaenid).

INVERSELLA (REINVERSELLA) Bates, 1968

Fig. 35

1968 *Reinversella* Bates: 169

TYPE SPECIES. *Reinversella monensis* Bates, 1968.

DIAGNOSIS. Like *Inversella* (*Inversella*) with second deflection of the anterior and lateral borders. With continuous rugae.

REMARKS. The close similarity between *Inversella* and *Reinversella* leads us to place the latter as a subgenus within the former.

SPECIES ASSIGNED

Reinversella arancibiai Herrera & Benedetto, 1987: 78, figs 2a–c from upper part of San Juan Formation (Llanvirn), Quebrada Los Gatos, west flank of Cerro Viejo, San Juan, Argentina.

Reinversella monensis Bates, 1968: 169; pl. 8, figs 10–17 from Treiorwerth Formation (Arenig), Ffynnon-y-mab, Anglesey, Wales.

RUTRUMELLA Harper, 1981

1981 *Rutrumella* Harper *in* Bruton & Harper 1981: 163

TYPE SPECIES. *Rutrumella implexa* Harper, 1981.

DIAGNOSIS. Resupinate. Differs from *Schedophyla* in having discontinuous rugae, not geniculate. Relatively large socket plates.

REMARKS. This resupinate genus has a distinctive ornament of discontinuous rugae. No pedicle valves and only three brachial valves are known, all as internal moulds with no definite proof of a pseudopunctate shell structure. The only cardinal process illustrated is similar to other taffiids, although it appears incomplete posteriorly. The muscle scars shown (Bruton & Harper 1981: pl. 2, figs 12, 13) are very indistinct, but appear similar to some contemporary Orthacea and Clitambonitacea. The genus is described as lacking radial ornamentation, but the preservation appears too coarse to exclude its possibility. Thus the plectambonitacean affinities of this genus are uncertain, although the genus is placed here in the Ahtiellinae.

SPECIES ASSIGNED

Rutrumella implexa Harper, *in* Bruton & Harper 1981: 164; pl. 2, figs 9, 12, 15 from Otta Conglomerate (Llanvirn), Otta, Norway.

SANJUANELLA Benedetto & Herrera, 1987

1987 *Sanjuanella* Benedetto & Herrera: 103

TYPE SPECIES. *Sanjuanella plicata* Benedetto & Herrera, 1987.

DIAGNOSIS. Myophragm but no brachial valve median septum. Relatively small pedicle valve muscle field and small socket plates in brachial valve. Like *Borua* but with marked parvicostellate ornament.

REMARKS. Although the material is somewhat scrappy, the two illustrated brachial valve interiors show the simple cardinal process and lack of side septa clearly, making the new genus definitely attributable to the Taffiidae, rather than to the Plectambonitidae where it was placed by its authors.

SPECIES ASSIGNED

Sanjuanella plicata Benedetto & Herrera, 1987: 104; pl. 1, figs 1–14 from upper part of San Juan Formation (Llanvirn), Quebrada Honda, west flank of Cerro Viejo, San Juan Province, Argentina.

SCHEDOPHYLA Neuman, 1971

1971 *Schedophyla* Neuman: 120
1984 *Schedophyla* Xu & Liu: 200

TYPE SPECIES. *Schedophyla potteri* Neuman, 1971.

DIAGNOSIS. Very similar to *Aporthophyla* but resupinate. Differs from *Rutrumella* in having radial ornamentation and no rugae.

REMARKS. The shell structure has not been determined since the New Brunswick material consists entirely of moulds; it is possible that the genus is an orthid. Neuman (1971:120) considered the genus to be 'most similar to *Ahtiella*' but this is true only of the valve form; the remaining characters appear identical to *Aporthophyla*, in particular the ventral muscle field and the cardinalia.

SPECIES ASSIGNED

Schedophyla minor Xu & Liu, 1984: 202; pl. 14, figs 15, 16, 21 from Meitan Formation (Arenig), Nanzhang, W. Hubei, China.

Schedophyla potteri Neuman, 1971: 122; pl. 2, figs 1–11 from Tuffaceous sandstone (Llanvirn?), middle Haydon Brook, York County, New Brunswick, Canada.

- *'Hesperonomia' striata* Xu, Rong & Liu, 1974: 144; pl. 64, figs 29–31 from Lower Meitan Formation (L. Arenig), Sinan, NE Guizhou, China.
- *Schedophyla subquadrata* Xu & Liu, 1984: 201 *pars*; pl. 14, figs 30, 31, *non* fig. 20; pl. 15, figs 6–8, 20 from Lower Meitan Formation (L. Arenig), Yanhe, NE Guizhou, China.

SPECIES QUESTIONABLY ASSIGNED

- *Schedophyla interrupta* Xu, *in* Liu *et al*. 1983: 276; pl. 92, figs 10–12 from U. Dawan Formation (U. Arenig), Nanjing, Jiangsu Province, China (no interiors known).
- *Schedophyla* sp. of Xu & Liu 1984: 202; pl. 15, fig. 9 from Lower Meitan Formation (Arenig), Yanhe, NE Guizhou, China (no brachial valve interior known).

Subfamily **PELONOMIINAE** nov.

DIAGNOSIS. Not resupinate, although fairly flat. No platform.

REMARKS. *Pelonomia* is difficult to place, except that it is undoubtedly a plectambonitacean. It is close to the Taffiinae, but has no platform and we therefore erect a new subfamily for the genus.

GENUS ASSIGNED. *Pelonomia* Cooper, 1956.

RANGE. Llanvirn.

PELONOMIA Cooper, 1956

1956 *Pelonomia* Cooper: 699
1965 *Pelonomia* Williams: H372

TYPE SPECIES. *Orthis delicatula* Billings, 1865.

DIAGNOSIS. Slight fold in pedicle valve with corresponding sulcus in brachial valve. Larger pseudopunctae seen on dorsal sulcus.

REMARKS. The only species is small, but it is distinctive and difficult to place systematically. Pseudopunctae are clearly visible and there is a simple single cardinal process, and so it is undoubtedly a plectambonitacean. However, the specimens illustrated so well by Cooper (1956: pl. 223) are not the original type specimens of Billings, and until the latter are revised, there must remain some doubt as to the identity of the species and genus.

SPECIES ASSIGNED

- *Orthis delicatula* Billings, 1865: 217 (revised by Cooper 1956: 699; pl. 223, figs 8–10) from the Table Head Formation (Llanvirn) near Table Head, Newfoundland, Canada.

Subfamily **SPANODONTINAE** nov.

DIAGNOSIS. Normal convexity. Distinctive 'dalmanelloid' brachial valve muscle field. With chilidium. With platform.

DISCUSSION. The distinctive 'dalmanelloid' brachial valve muscle field, with the transverse ridge separating the two pairs of muscle scars, is unique among the Plectambonitacea (except possibly for the unplaced genus *Rutrumella*). This feature alone certainly merits subfamilial recognition to separate it from the rest of the Taffiidae. *Spanodonta* is only known from silicified specimens, and thus its strophomenoid assignment is only based on a general similarity to the taffiids and other plectambonitaceans. It also bears some resemblance to *Eostrophomena* Walcott, 1905, from the latest Tremadoc of Sweden, which has been assigned to the Orthidiellidae by Williams (1965: H309–310), and whose shell composition is also undocumented.

GENUS ASSIGNED. *Spanodonta* Prendergast, 1935.

RANGE. Llanvirn–Llandeilo.

SPANODONTA Prendergast, 1935
Figs 36–40

1935 *Spanodonta* Prendergast: 12
1965 *Spanodonta* Williams: H375
1987 *Spanodonta* Laurie: 44

TYPE SPECIES. *Spanodonta hoskingiae* Prendergast, 1935.

DIAGNOSIS. As for subfamily. The cardinal process is not trilobed (*contra* Williams 1965: H375) and consists of a simple ridge.

Fig. 40 *Spanodonta hoskingiae* Prendergast, 1935, from Gap Creek Formation (Middle Ordovician), south side of Gap Spring, Price's Creek, Emmanuel Range, Western Australia, interior of brachial valve, based on BC 7238 and BC 10605, × 5.

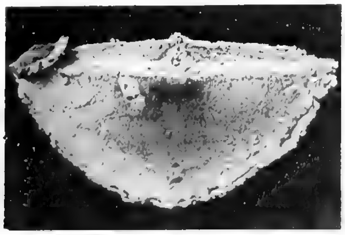
REMARKS. *Spanodonta* was originally described as a productacean from the Carboniferous of Western Australia, but was reassigned to the Plectambonitacea when the Ordovician age of the beds became known. A good new collection of topotype material made by the British Museum (Natural History) expedition to Western Australia in 1966 enables us to illustrate the genus properly (Figs 36–40) as has Laurie (1987). We agree with Laurie's assignment of the genus to the Taffiidae, but do not think that it was so closely related to *Aporthophyla* as he thought (1987: 44, figs 2, 3).

SPECIES ASSIGNED

- *Spanodonta hoskingiae* Prendergast, 1935: 13; pl. 3, figs 1–3 from Gap Creek Formation (Lower to Middle Ordovician), Price's Creek, Kimberley, Western Australia (revised Laurie 1987: 44, figs 2–3).

SPECIES REJECTED

- *Spanodonta tingriensis* Liu, 1976: 146; pl. 2, figs 24-31 from a pebble of Ordovician age, Bensai, Dingri County, Xizang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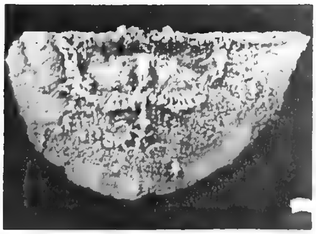
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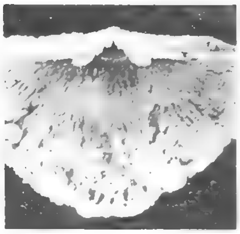
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Figs 41–44 *Leptella musculosa* Williams & Curry, 1985, topotypes from Tourmakeady Limestone (U. Arenig), stream 2 km SW of Srah Bridge, Co. Mayo, Ireland. Fig. 41, conjoined valves, holotype, the original of Williams & Curry 1985: fig. 183, BB 95546, × 5; Fig. 42, brachial valve interior, the original of Williams & Curry 1985: fig. 188, BB 95547, × 5; Fig. 43, brachial valve interior, the original of Williams & Curry 1985: fig. 184, BB 95549, × 5; Fig. 44, central part of pedicle valve interior, the original of Williams & Curry 1985: fig. 186, BB 95548, × 5.

(Tibet), China (because of the trifid cardinal process this species should be placed within the Leptellinidae, but the true genus is uncertain).

Subfamily **LEPTELLINAE** Williams, 1965

1936 Leptellininae Ulrich & Cooper: 626 *pars*
1938 Leptellininae Ulrich & Cooper: 187 *pars*
1965 Leptellinae Williams: H376

Diagnosis. Leptellinidae without cardinal process.

Remarks. Both nominal genera in the subfamily possess a platform and they are united here as subgenera within a single genus. Obviously, since they lack a cardinal process, their assignment to the Taffiidae must then remain a little doubtful. However, *Leptella* and *Petroria* are otherwise very similar to *Taffia* and its relatives, which causes us to place the Leptellinae within the Taffiidae. This differs from Williams (1965) in the *Treatise on Paleontology*, who placed the Leptellinae within the Leptellinidae; however *Leptella* and *Petroria* are so much older than the rest of the Leptellinidae that they would seem very unlikely to be either the direct ancestors or descendants of forms with trifid cardinal processes.

Genera assigned. *Leptella* (*Leptella*) Hall & Clarke, 1892; *Leptella* (*Petroria*) Wilson, 1926.

Range. Possibly Tremadoc (*Leptella exigua*) but definitely L. Arenig (*Leptella hubeiensis*) to Arenig–Llanvirn boundary beds (*Leptella sordida*).

LEPTELLA (LEPTELLA) Hall & Clarke, 1892

Figs 41–44

1892 *Leptella* Hall & Clarke: 293
1938 *Leptella* Ulrich & Cooper: 187
1965 *Leptella* Williams: H377

Type species. *Leptaena sordida* Billings, 1862.

Diagnosis. Median septum not anterior of the platform in the brachial valve.

Species assigned

Leptella grandis Xu, Rong & Liu, 1974: 149; pl. 65, figs 14–17 from Lower Meitan Formation (L. Arenig), Sinan, Sinan County, NE Guizhou, China.

Leptella hubeiensis Zeng, 1977: 57; pl. 20, figs 1–3 from L. Dawan Formation (M. Arenig), Fenxian, Yichang County, W. Hubei Province, China.

Leptella musculosa Williams & Curry 1985: 254, figs 183–189 from Tourmakeady Limestone (U. Arenig), Tourmakeady, Co. Mayo, Ireland.

Leptaena sordida Billings, 1862: 74, fig 66 from Limestone No 2 (Arenig–Llanvirn Boundary), Point Lévis, Quebec, Canada (revised Ulrich & Cooper 1938: 189; pl. 39, figs 17–21, 23–33).

Species questionably assigned

Leptella? *exigua* Clark, 1924: 84; pl. 8, fig. 13 from *Shumardia* Zone of Beekmantown Series (Tremadoc), Lévis, Quebec, Canada (no interiors figured).

Leptella nevadensis Ulrich & Cooper, 1938: 189; pl. 39, figs 16, 22 from Billingsura Zone of U. Pogonip (Llanvirn), Antelope Range, Nevada, USA (no interiors known).

LEPTELLA (PETRORIA) Wilson, 1926

1926 *Petroria* Wilson, 1926
1956 *Petroria* Cooper, 746
1965 *Petroria* Williams: H378
1987 *Petroria* Ross & James: 84

Type species. *Petroria rugosa* Wilson, 1926.

Diagnosis. Like *Leptella* (*Leptella*) but with median septum continuing anteriorly of the platform in brachial valve.

Remarks. The type species was originally described as from the Beaverfoot Formation which is of Ashgill age, but Cooper (1956: 746) suggests that the specimens are more probably of Arenig age. This was confirmed by Norford (1969: 37), who reassigned the type locality to the Lower Ordovician Skoki Formation. We are most grateful to Dr B. S. Norford, who has provided us with copies of his unpublished notes and illustrations of *P. rugosa*. These confirm that the genus is closely related to *Leptella*, but differs in the length of the median septum in the brachial valve.

Species assigned

Petroria rugosa acuta Benedetto & Herrera, 1986: 115; pl. 2, figs 1–4, 8–17 from U. San Juan Formation (M. Arenig to L. Llanvirn), Quebradas Los Gatos, San Juan Province, Argentina; also subspecies *elevata* Benedetto & Herrera, 1986: 116; pl. 2, figs 5–7, 18–19 from U. San Juan Formation (L. Llanvirn), Quebradas Ancha, San Juan Province, Argentina.

Fig. 45 *Bimuria superba* Ulrich & Cooper, 1942, from Arline Formation (Llandeilo), half mile east of Friendsville, Tennessee, USA, posterior and anterior views of the cardinal process area, based on BC 7269, × 6.

- *Petroria rugosa* Wilson, 1926: 27; pl. 5, figs 15–18 from *Orthidiella* Zone, Skoki Formation (M.–U. Arenig), Palliser Pass, British Columbia, Canada (revised Cooper 1956: pl. 221, figs 29–36).
- *Petroria* cf. *P. austrina* of Ross & James 1987: 85; pl. 4, figs 1–5 from Shallow Bay Formation (U. Arenig), Cow Head, Newfoundland, Canada.

SPECIES TENTATIVELY ASSIGNED

- *Petroria ? austrina* Ross, 1972: 27; pl. 11, figs 1–5 from bioherm of Arenig age, Meiklejohn Peak, Nevada, USA (no interiors known).

SPECIES REJECTED

- *Petroria lata* Xu & Liu, 1984: 203; pl. 13, figs 19–26 from Dawan Formation (M.–U. Arenig), Yichang, Hubei Province, China (no platform in brachial valve, undercut cardinal process; genus uncertain but probably subfamily Chonetoideinae).

Family **BIMURIIDAE** Cooper, 1956

1956 Bimuriidae Cooper: 764 (pars)
1965 Bimuriidae Williams: H383 (pars)

DIAGNOSIS. Cardinal process simple, not undercut. With bema. With side septa.

REMARKS. Cooper (1956) and Williams (1965) united the two genera *Bimuria* and *Craspedelia* as the sole genera within the Bimuriidae chiefly on account of their smooth surface and side septa. However, we divide these two genera into separate families on the fundamental basis of their cardinal process. True *Bimuria* has a simple cardinal process, whilst that of *Craspedelia* (and some species formerly attributed to *Bimuria*, but attributed to the new genus *Cooperea* here) is undercut and thus assigned to the Sowerbyellidae.

GENUS ASSIGNED. *Bimuria* Ulrich & Cooper, 1942.

RANGE. Llandeilo (*B. superba*) to U. Caradoc (*B. youngiana*).

BIMURIA Ulrich & Cooper, 1942
Figs 45–47

1942 *Bimuria* Ulrich & Cooper: 622
1956 *Bimuria* Cooper: 764 *pars*
1965 *Bimuria* Williams: H383

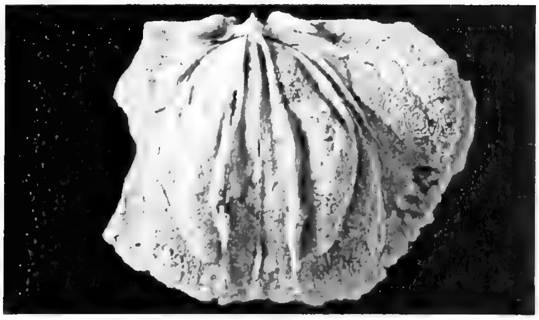
TYPE SPECIES. *Bimuria superba* Ulrich & Cooper, 1942.

DIAGNOSIS. No ornament. Comae sometimes developed. Elongate and divided bema.

REMARKS. Within the species assigned to *Bimuria* by Cooper (1956) we can recognize two types, firstly a group (which includes the type species) with a simple cardinal process and elongate divided bema, and a second group, represented by *B. siphonata*, which has undercut cardinal processes and a transverse divided bema, for which we are erecting a new genus within the Craspedeliinae.

SPECIES ASSIGNED

- *Bimuria bugrischichiensis* Severgina, *in* Petrunina & Severgina 1962: 91; pl. 4, figs 1, 2 from Khankharin Formation (U. Llandeilo), Uskychevka River, Gornoi Altai, USSR.
- *Bimuria buttsi* Cooper, 1956: 765; pl. 212, figs 11–31 from Little Oak Formation (U. Llandeilo–L. Caradoc), Pelham, Alabama, USA.
- *Christiania lamellosa* Bassler, 1919: 257; pl. 49, figs 3–10 from Oranda Formation (L. Caradoc), Strasburg, Virginia, USA.
- *Bimuria parvula* Cooper, 1956: 769; pl. 184, fig. 4; pl. 210, figs 1–4 from Chatham Hill Formation (L. Caradoc), Sharon Springs, Virginia, USA.
- *Bimuria peregrina* Jaanusson, 1962: 5; pl. 1, figs 1–10 from Dalby Limestone (M. Caradoc), Siljan District, Sweden.
- *Bimuria superba* Ulrich & Cooper, 1942: 623; pl. 90, figs 13–18 from Middle Arline Formation (Llandeilo), SE of Friendsville, Tennessee, USA.
- *Leptaena transversalis* var. *youngiana* Davidson, 1871: 320; pl. 47, figs 19, 20 from Craighead Limestone (U. Caradoc), Craighead, Girvan, Scotland (revised Williams 1962: 175; pl. 16, figs 38–41; pl. 17, figs 1–3); also subspecies *recta* Williams, 1962: 175; pl. 17, figs 4–7 from Balclatchie Mudstones (L. Caradoc), Penwhapple Burn, Girvan, Scotland.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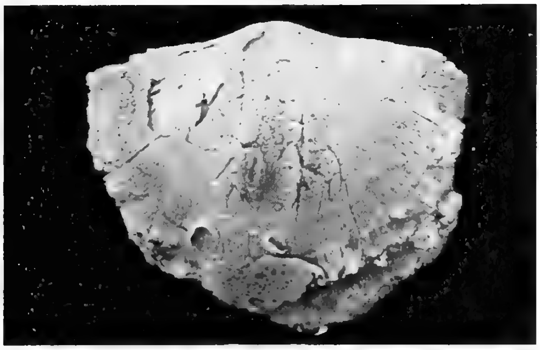
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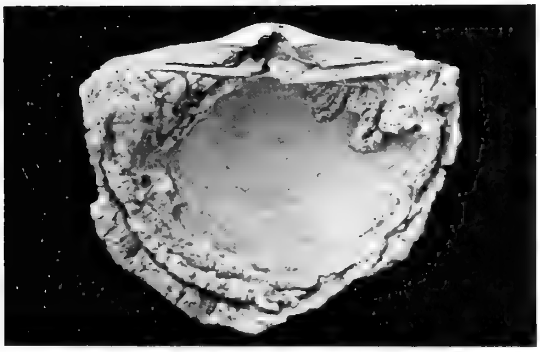
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Figs 46–47 *Bimuria superba* Ulrich & Cooper, 1942, from Arline Formation (Llandeilo), half mile east of Friendsville, Tennessee, USA. Fig. 46, straight down, posterior and lateral views of brachial valve interior, BC 7269, × 3; Fig. 47, two views of a pair of conjoined valves showing comae, BC 7270, × 2.

Bimuria triquetra Nikitin & Popov, 1984: 150; pl. 18, figs 6, 8, 11, 12 from Bestamakskaya Formation (U. Llandeilo–L. Caradoc), Novaya Archali Hill, Chinghiz Mountains, Kazakhstan, USSR.

SPECIES QUESTIONABLY ASSIGNED

Bimuria? *apsaclinata* Su, 1980: 273; pl. 115, figs 1–4 from Guanniaohe Formation (M. Ordovician), Lower Guanniao river, Nenjiang County, Heilongjiang Province, NE China (no interiors figured).

Bimuria dyfiensis Lockley, 1980: 215; figs 60–62, 64, 65 from Gelli-grîn Formation (U. Caradoc), Rhiw March, Llanystwmdwy, Powys, Wales (no brachial interior known).

Bimuria ? *matutina* Cooper, 1956: 768; pl. 210, figs 6–10 from boulder in Mystic conglomerate (Llanvirn ?), Stanbridge, Quebec, Canada (no interiors figured).

Bimuria sp. 1 of Cooper, 1956: 772; pl. 210, figs 12–14 from Eureka Quartzite (Llanvirn), Martins Ridge, Nevada, USA (no interior figured).

SPECIES REJECTED

Bimuria immatura Cooper, 1956: 766; pl. 211, figs 1–3 from Effna Rich Valley Formation (L. Caradoc), Porterfield Quarry, Virginia, USA (transferred to *Cooperea* gen. nov.).

Bimuria siphonata Cooper, 1956: 770; pl. 210, figs 17–24 from Pratt Ferry Formation (Llandeilo), Pratt Ferry, Alabama, USA (transferred to *Cooperea* gen. nov.).

Bimuria sp. of Liu *et al.* 1983: 277; pl. 92, fig. 17 from Tangtou Formation (L. Ashgill), Chuxian County, Anhui Province, China (probably *Christiania*).

Family **SYNDIELASMATIDAE** Cooper, 1956

1956	Leptestiinae Cooper: 700 *pars*
1956	Syndielasmatidae Cooper: 742
1965	Isophragmatinae Williams: H375 *pars*

DIAGNOSIS. Trifid cardinal process. No bema. Side septa usually developed.

REMARKS. *Syndielasma* and *Sowerbyites* are morphologically quite close to *Isophragma* and *Taphrodonta* but differ in their possession of a trifid rather than simple cardinal process, and in having true side septa rather than a double median septum.

GENERA ASSIGNED. *Sowerbyites* Teichert, 1937; *Syndielasma* Cooper, 1956.

RANGE. Llanvirn (*Syndielasma biseptatum*) to Upper Caradoc (*Sowerbyites* spp.).

SOWERBYITES Teichert, 1937

1937	*Sowerbyites* Teichert: 66
1956	*Sowerbyites* Cooper: 723
1965	*Sowerbyites* Williams: H373

TYPE SPECIES. *Sowerbyites medioseptatus* Teichert, 1937.

DIAGNOSIS. Like *Syndielasma*, but median septum present in the brachial valve. Cardinal process fused with brachiophore bases. Side septa variably developed.

REMARKS. Only one specimen showing the interior of the brachial valve of the type species has ever been illustrated

(Teichert 1937: pl. 12, fig. 17) and thus the variability of this species is difficult to assess. That specimen shows a strong median septum which posteriorly is low and has a slight groove in its centre, and anteriorly is higher, with no groove to be seen. Of the six other species attributed by Cooper (1956) to this genus and listed below, none shows an identical septal form, although all possess a brachial valve median septum.

SPECIES ASSIGNED

Sowerbyites delicatus Cooper, 1956: 725; pl. 179, figs 7–20 from L. Sevier Shale (L. Caradoc), Athens, Tennessee, USA.

Sowerbyites gildersleevei Cooper, 1956: 725; pl. 183, figs 1–16 from Lincolnshire Limestone (U. Llandeilo), Strasburg, Virginia, USA.

Sowerbyites hami Cooper, 1956: 727; pl. 181, figs 19–33 from U. Bromide Formation (L. Caradoc), Gilsonite, Oklahoma, USA.

Sowerbyites hibernicus Mitchell, 1977: 69; pl. 12, figs 5–18 from Bardahessiagh Formation (M. Caradoc), Pomeroy, Co. Tyrone, Northern Ireland.

Sowerbyites lamellosus Cooper, 1956: 728; pl. 180, figs 17–25; pl. 181, figs 10–18; pl. 184, figs 23–27 from L. Bromide Formation (L. Caradoc), Carter County, Oklahoma, USA.

Sowerbyites [incertus] mongolicus Rozman, 1981: 129; pl. 31, figs 4–10 from Bairimski beds (U. Caradoc), Agach-Ula hills region, Mongolia (certainly *Sowerbyites*, but not a subspecies of *Titanambonites*? *incertus* Williams).

Sowerbyites medioseptatus Teichert, 1937: 66; pl. 12, figs 16, 17 from Upper Ordovician Limestone, Ignertoq, east coast of Melville Peninsula, Arctic Canada.

Sowerbyites subnasutus Cooper, 1956: 729; pl. 182, figs 1–11 from Lincolnshire Limestone (U. Llandeilo), Gate City, Virginia, USA.

Plectambonites triseptatus Willard, 1928: 277; pl. 2, figs 7, 8 from Holston Formation (L. Caradoc), Goodwins Ferry, New River, Virginia, USA (revised Cooper 1956: 730; pl. 169, figs 10–12; pl. 180, figs 1–13; pl. 182, figs 12–29; pl. 183, figs 17, 18; pl. 209, figs 4–7).

SPECIES REJECTED

Sowerbyites vesciseptus Percival, 1979: 106; fig. 7B.1–13 from Goonumbla Volcanics (L. Caradoc), Gunningbland, New South Wales, Australia (with bema, no side septa, transferred to *Bilobia*).

SYNDIELASMA Cooper, 1956

1956 *Syndielasma* Cooper: 742
1965 *Syndielasma* Williams: H376

TYPE SPECIES. *Syndielasma biseptatum* Cooper, 1956.

DIAGNOSIS. Like *Sowerbyites* but with no median septum. Two long side septa. Cardinal process not fused anterolaterally to brachiophore bases.

REMARKS. This genus is known only from its original description by Cooper (1956), who found fourteen specimens attributable to the type species. Four brachial valve internals are illustrated by Cooper, none of which shows a median septum, although it should be remembered that the presence or absence of a median septum can be a variable feature in some plectambonitacean genera such as *Sowerbyella*.

SPECIES ASSIGNED

Syndielasma biseptatum Cooper, 1956: 734; pl. 185, figs 14–29 from Upper Pogonip Group (Llanvirn), Ikes Canyon, Nevada, USA.

Family **LEPTELLINIDAE** Ulrich & Cooper, 1936

1936 Leptellininae Ulrich & Cooper: 626 *pars*
1938 Leptellininae Ulrich & Cooper: 187 *pars*
1956 Leptellinidae Cooper: 744 *pars*
1965 Leptellinidae Williams: H376 *pars*
1965 Leptestiidae Williams: H372 *pars*
1967 Leptellinidae Havlíček: 26
1970 Leptellinidae Cocks: 155 *pars*
1984 Leptellinidae Klenina: 66

DIAGNOSIS. All with trifid cardinal process (not undercut). No side septa present. No bema present (although clear muscle bounding ridges occasionally seen).

REMARKS. This family is easily divided into two natural groups – the large group of the Leptellininae and the smaller group of the Palaeostrophomeninae in which the pedicle valve muscle field is so much more expanded and longer by comparison with the Leptellininae. It is interesting to note that the genera in the Palaeostrophomeninae have deeply impressed pallial markings: we cannot explain this.

SUBFAMILIES ASSIGNED. Leptellininae Ulrich & Cooper, 1936; Palaeostrophomeninae subfam. nov.

RANGE. Llanvirn to U. Llandovery.

Subfamily **LEPTELLININAE** Ulrich & Cooper, 1936

1936 Leptellininae Ulrich & Cooper: 626 *pars*
1956 Leptelloidinae Cooper: 763
1965 Leptellininae Williams: H376 *pars*
1970 Leptellininae Cocks: 155

DIAGNOSIS. With trifid cardinal process. Restricted pedicle valve muscle field.

REMARKS. This subfamily flourished in Middle Ordovician times, providing the dominant brachiopod species at many localities. However, the subfamily endured a cryptic extinction in the Middle Ashgill – there are no records between the Middle Ashgill *Qianjiangella* of Kazakhstan and south China and the late Llandovery records of *Merciella* in south China and the Welsh Borderland.

GENERA ASSIGNED. *Acculina* Misius, 1977; *Dulankarella* Rukavishnikova, 1956 (including *Shlyginia* Nikitin & Popov, 1983); *Kajnaria* Nikitin & Popov, 1984; *Leptellina* (*Leptellina*) Ulrich & Cooper, 1936 (including *Benignites* Havlíček, 1952, *Mabella* Klenina, 1984, *Qianjiangella* Liang, 1983 and *Urbimena* Havlíček, 1976); *Leptellina* (*Merciella*) Lamont & Gilbert, 1945; *Leptelloidea* Jones, 1928; *Reversella* Liang, 1983.

RANGE. Llanvirn (*Leptellina* spp.) to U. Llandovery (*Merciella vesper*).

ACCULINA Misius, 1977

1977 *Acculina* Misius *in* Misius & Ushatinskaya: 113
1986 *Acculina* Misius: 143

TYPE SPECIES. *Acculina acculica* Misius, 1977.

DIAGNOSIS. Resupinate. Brachial valve like *Reversella*. Pedicle muscle field not enclosed anteriorly; no pedicle valve median septum.

REMARKS. Only *Acculina* and *Reversella* are resupinate within the Leptellinidae. Comparison is difficult since the type species of *Acculina* is small (maximum width 20 mm), whilst the only known species of *Reversella* is large, with valves about 50 mm wide. Although the two genera have very similar brachial valve interiors, *Reversella trigonoformis* has distinctive pedicle valve muscle bounding ridges, and so we provisionally keep the two genera distinct here; however, further work might indicate them to be congeneric. *Reversella* also has strong geniculation.

SPECIES ASSIGNED

Acculina acculica Misius, *in* Misius & Ushatinskaya 1977: 114; pl. 26, figs 21–24 from the Tabilgatinsk Formation (Middle Ordovician), northern slope of Moldo-Too mountains, northern Kirgiziya, USSR.

Acculina villosa Nikitina, 1985: pl. 1, figs 14–19 from the Rgayta Formation (Llandeilo), Talapta, southwestern Kendyktas Mountains, southern Kazakhstan, USSR.

DULANKARELLA Rukavishnikova, 1956

1956 *Dulankarella* Rukavishnikova: 135 *pars*
1965 *Leptestiina* Williams: H378 *pars*
1979 *Dulankarella* Percival: 103
1983 *Shlyginia* Nikitin & Popov: 238
1984 *Dulankarella* Klenina: 73

TYPE SPECIES. *Dulankarella magna* Rukavishnikova, 1956. Type species of *Shlyginia* is *Shlyginia declivis* Nikitin & Popov, 1983.

DIAGNOSIS. Normal convexity. Differs from *Leptellina* in large muscle field in pedicle valve to about half valve length or more. Adductor muscle scars usually enclosed by diductor scars in pedicle valve. Cardinal process projecting slightly or not at all posteriorly from the hinge line like *Leptellina*.

REMARKS. This genus, although erected in 1956, was essentially overlooked and unrevised until the paper by Percival (1979), although the brachial valve interior was not originally illustrated by Rukavishnikova. Nikitin & Popov (1983) erected *Shlyginia* separately from *Dulankarella* on the absence of dental plates and on a small septum or shell thickening anterior to the muscle field in the middle of the pedicle valve. Both these features are very variable in the published illustrations of both *Dulankarella* and *Shlyginia* and in any case are not features we can trust for generic differentiation (cf. *Leangella* and *Diambonia*), and we consider the two nominal genera to be the same.

SPECIES ASSIGNED

Leptellina carinata Yadrenkina, 1965: 12; pl. 2, figs 13–22 from Baksan Horizon, Mangazei Stage (Caradoc), Podkammenayar Tunguska River, Kuzimovk, NW Siberia, USSR.

Shlyginia declivis Nikitin & Popov, 1983: 238; pl. 3, figs 1–5 from Andrushenskaya Formation (Caradoc), Ishim River, near Kyprianovska, Kazakhstan, USSR.

Dulankarella extraordinaria Rukavishnikova, 1956: 138; pl. 3, figs 1–3 from Dulankarinski Horizon (U. Caradoc), Degeresski beds, Kopali-Sai, Chu-Ili Mountains, Kazakhstan, USSR.

Dulankarella magna Rukavishnikova, 1956: 139; pl. 3, figs 4–9 from Otarsky Horizon (Caradoc), Dzhartas hill, Dulankara, Chu-Ili Mountains, Kazakhstan, USSR.

Dulankarella namasensis Klenina, 1984: 75; pl. 6, figs 1, 20–24 from Anderkenski Horizon (Caradoc), east of River Hamas, Chinghiz Mountains, Kazakhstan, USSR.

Shlyginia solida Nikitin & Popov, 1984: 146; pl. 16, figs 10, 12–16 from Erkebidaikski Horizon, Upper Bestamakski Formation (U. Llandeilo–basal Caradoc), Chagan River, Chinghiz Mountains, Kazakhstan, USSR.

Dulankarella subquadrata Klenina, 1984: 76; pl. 6, figs 3, 12, 13, 16, 18, 19, 25 from Anderkenski Horizon (Caradoc), east of River Hamas, Chinghiz Mountains, Kazakhstan, USSR (probably a synonym of *D. namasensis*).

SPECIES REJECTED

Dulankarella fragilis Rukavishnikova: 136; pl. 2, figs 15–22 from the Anderkenski horizon (Caradoc), Kopali-sai, Chu-Ili Mountains, Kazakhstan, USSR. (Nikitin & Popov (1983: 237) appear wrong to attribute this species to *Shlyginia*, since pl. 2, figs 19–21 of Rukavishnikova 1956 show that *S. fragilis* possesses a bema; however, the interior of Rukavishnikova's holotype (1956: pl. 2, fig. 15) is unknown and more than one species may be involved).

Dulankarella ? partita Percival, 1979: 103; figs 5C.1–7, 6 from Goonumbla Volcanics (U. Caradoc), Gunningbland, New South Wales, Australia (the cardinalia is not leptellinid and is similar to *Sowerbyites*).

KAJNARIA Nikitin & Popov, 1984

1984 *Kajnaria* Nikitin & Popov: 144

TYPE SPECIES. *Kajnaria derupta* Nikitin & Popov, 1984.

DIAGNOSIS. Strong muscle bounding ridges in pedicle valve, with anteriorly to them two curved ridges (the 'diaphragm' of Nikitin & Popov 1984). Variably developed pedicle valve myophragm.

REMARKS. Within the Plectambonitacea we have not seen elsewhere any structure exactly like that in the pedicle valve of *Kajnaria*. Its function is unknown, it is certainly not part of the muscle field and in the two shells illustrated (Nikitin & Popov 1984: pl. 18, figs 14, 15) it varies in the completion anteriorly of the curved ridge. The genus is assigned to the Leptellininae because of the internal structure of the brachial valve, which is similar to *Leptellina*.

SPECIES ASSIGNED

Kajnaria derupta Nikitin & Popov, 1984: 145; pl. 18, figs 10, 13–16 from Bed bs$_{iii}$, U. Bestamakskaya Formation, Erkebidaikski horizon (M. Ordovician), south of New Archal Hill, Chinghiz Mountains, Kazakhstan, USSR.

LEPTELLINA (LEPTELLINA) Ulrich & Cooper, 1936

Figs 48, 49

1936 *Leptellina* Ulrich & Cooper: 626
1938 *Leptellina* Ulrich & Cooper: 190

Fig. 48 *Leptellina* (*Leptellina*) *tennesseensis* Ulrich & Cooper, 1936, from Lenoir Formation (Llandeilo), quarter mile west of Friendsville, Tennessee, USA, interior of brachial valve, based on BB 1228, × 5.

1952 *Benignites* Havlíček: 13
1965 *Leptellina* Williams: H376
1965 *Merciella* Williams: H376 *pars*
1967 *Leptellina* Havlíček: 27 *pars*
1976 *Urbimena* Havlíček: 367
1976 *Benignites* Havlíček: 368
1983 *Qianjiangella* Liang *in* Liu *et al.*: 274
1984 *Leptellina* (*Mabella*) Klenina: 69

TYPE SPECIES. *Leptellina tennesseensis* Ulrich & Cooper, 1936. Type species of *Benignites* is *Strophomena primula* Barrande, 1879; of *Mabella* is *Leptellina* (*Mabella*) *semiovalis* Klenina, 1984; of *Qianjiangella* is *Q. quianjiangensis* Liang, 1983 and of *Urbimena* is *U. mareki* Havlíček, 1976.

DIAGNOSIS. Normal convexity. With platform. Pedicle valve muscle field small (usually less than quarter valve length). Thin central ridge to cardinal process with lateral components less prominent (only thin central process projecting posteriorly from hinge line, and even this is sometimes entirely anterior to the hinge line).

REMARKS. The muscle field in the pedicle valve shows some variation. In most species, including the type species, it is small and does not extend more than a quarter of the valve length, and the adductor scars are usually open anteriorly. However, in *L.* (*Merciella*) the adductor scars are enclosed anteriorly by the diductor scars. This genus was very common in Llanvirn to Ashgill times, and in many cases dominated the community in which it occurred. Further research might recognize more features worthy of subgeneric recognition, but we have been unable to recognize any (apart from those of *Merciella*), and so we group here all the species hitherto attributed to *Leptellina*, *Benignites*, *Mabella*, *Qianjiangella* and *Urbimena* into a single undivided *Leptellina* (*Leptellina*). *Benignites* is said by Havlíček (1976: 368) to differ from *Leptellina* 'in having a slender adductor scar narrowing to the front of the ventral muscle field', but we do not think this important, and indeed the muscle scars of *Leptellina* are very variable and include '*Benignites*'-like forms. The perforated platform margin is also sometimes continuous, and other plectambonitaceans, such as *Merciella*, also show this occasionally (Cocks 1970: pl. 1, figs 2, 4).

According to Havlíček (1976: 367), *Urbimena* differs from *Leptellina* in lacking dental plates, in having a very narrow adductor scar in the pedicle muscle field and in having a very weak 'submarginal rim' (what we would term a platform) in the brachial valve. In fact there are weak dental plates in *Urbimena* (Havlíček 1976: pl. 1, fig. 2), the narrow adductor scar is a variably developed feature in all plectambonitaceans, and the weakness of the platform is merely because the specimens of *U. mareki* are all very small (less than 8 mm wide). We consider the two genera as synonyms. It is true that the strength of the platform is very much weaker in the type species of *Benignites* and *Urbimena* than in other species of *Leptellina*, but we have seen all intergrades between a barely continuous row of septules and a very strong platform and we cannot therefore separate these genera on that criterion. When Klenina (1984) erected *Mabella* she did it on the basis of the forked anterior end of the brachial valve median septum. This is a common phenomenon within the Leptellininae and other members of the Plectambonitacea and is simply a median modification of the platform which forms the septum: for example, it is seen in *Merciella striata* (Rong & Yang 1981: pl. 2, figs 4, 5) and in *Leptellina pulchra* Cooper (1956: pl. 189, figs 21–23). Otherwise *Mabella* is similar to *Qianjiangella* and the two are placed in synonymy here with *Leptellina*.

SPECIES ASSIGNED

Leptellina bella Cooper, 1956: 748; pl. 186, figs 1–8; pl. 190, figs 1–4 from Whitesburg Formation (L. Caradoc), Bulls Gap, Tennessee, USA.

Leptellina deminuta Liu, 1976: 147; pl. 2, figs 20–23 from Jiacun Group (Llanvirn–Llandeilo), Mount Jolmo Lungma area, Tibet, China.

Leptellina kirgizica Misius, 1986: 140; pl. 11, figs 29–36; pl. 12, figs 1–10 from M. Tabulgat Formation (U. Llandeilo–L. Caradoc), R. Tabulgat, Moldo-Too, Kirgiziya, USSR.

Leptaena llandeiloensis Davidson, 1883: 171; pl. 12, fig. 26, *non* figs 27–29 from L. Ardwell Mudstone (M. Caradoc), Ardmillan Braes, Girvan, Scotland (revised Williams 1962: 164; pl. 15, figs 27–29, 32).

Urbimena mareki Havlíček, 1976: 368; pl. 1, figs 1–6 from Libeň Formation (L. Caradoc), Motol, Prague, Czechoslovakia (but his pl. 1, fig. 4 may not be the same species).

Leptelloidea multicostata Rukavishnikova, 1956: 132; pl. 2, figs 8–11 from Otarski Horizon (Caradoc), Bokkot River, Chu-Ili Mountains, Kazakhstan, USSR (revised Misius 1986: 133; pl. 12, figs 11–30; pl. 13, figs 1, 2).

Leptellina (*Mabella*) *obtusa* Klenina, 1984: 71; pl. 5, figs 5, 6; pl. 6, fig. 2 from Taldiboiskaya Formation (Ashgill), River Taldiboi, Chinghiz Mountains, Kazakhstan, USSR (same locality and horizon as *M. semiov* and may be a synonym).

Leptellina occidentalis Ulrich & Cooper, 1938: 191; pl. 39, figs 3, 7 from Upper Pogonip Formation (Llanvirn), Ikes Canyon, Nevada, USA.

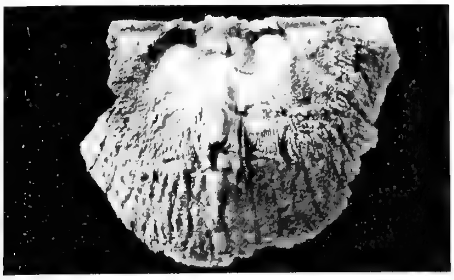
Leptellina primaria Cooper, 1956: 752; pl. 187, figs 1–7 from Crown Point Formation (Llanvirn–Llandeilo), Valcour Island, Lake Champlain, New York, USA.

Strophomena primula Barrande, 1879: pl. 52, fig. 3 from the Dobrotivá Shales (Llandeilo), Svata Dobrotivá, Czechoslovakia (revised Havlíček 1967: 27; pl. 1, figs 9–13).

Leptellina pulchra Cooper, 1956: 753; pl. 189, figs 1–23; pl. 195, figs 9–16; pl. 219, fig. 14 from Effna–Rich Valley Formations (Llandeilo), Porterfield Quarry, Virginia, USA.

Qianjiangella qianjiangensis Liang, *in* Liu *et al.* 1983: 275; pl. 95, figs 5–8 from Changwu Formation (M. Ashgill), Jianglütang village, Chunan County, W. Zhejiang, China.

Leptellina rhacta Williams, 1962: 164; pl. 15, figs 17–19, 21,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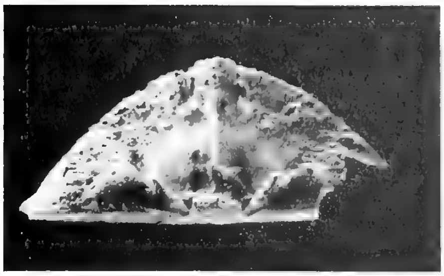
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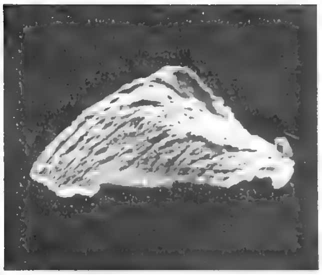
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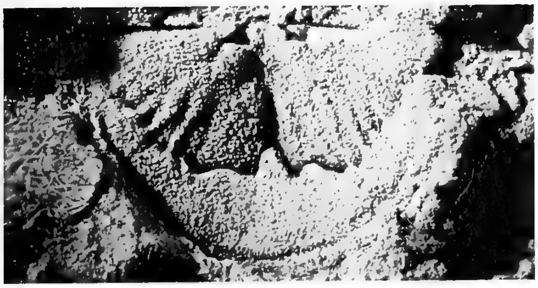
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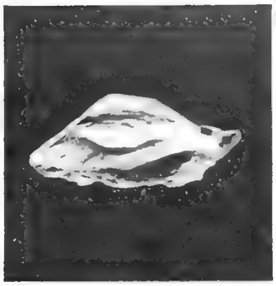
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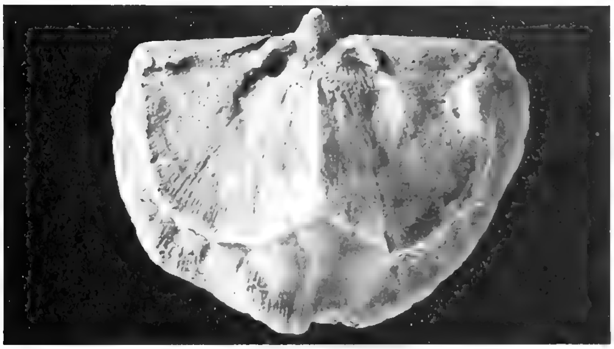
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Fig. 49 *Leptellina* (*Leptellina*) *tennesseensis* Ulrich & Cooper, 1936, from Lenoir Fromation (Llandeilo), quarter mile west of Friendsville, Tennessee, USA, downwards, posterior and lateral views of a brachial valve interior, BB 1228, × 4.

Figs 50, 51 *Leptellina* (*Merciella*) *vesper* (Lamont & Gilbert, 1945), from Wych Beds (U. Llandovery), Coneygore Coppice, near Alfrick, Worcestershire, England. Fig. 50, natural internal mould of brachial valve, BU 370, × 3; Fig. 51, latex cast of brachial valve interior, lectotype, the original of Lamont & Gilbert 1945: pl. 4, figs 10, 12, BU 369, × 3.

Fig. 52 *Leptelloidea leptelloides* (Bekker, 1922), topotype from Kukruse Formation (L. Caradoc), Kohtla-Järve, Estonia, USSR, lateral, posterior and downward views of the interior of a brachial valve, BB 5169; 52a, × 3; 52b, c, × 5.

22 from U. Stinchar Limestone (Llandeilo), Brockloch, Girvan, Scotland.

Leptellina seletensis Nikitin & Popov, 1983: 235; pl. 3, figs 6, 9, 11, 13–15 from Isobilnaya Formation, Tselinogradski Horizon (Middle Ordovician), Akzhar River basin, central Kazakhstan, USSR.

Leptellina semilunata Rozman, 1981 (*non* Williams, 1962): 132; pl. 24, figs 16–23 from *Christiania subquadrata* beds (Llandeilo), Agach-Ula, S. Mongolian Altai, Mongolia (same genus as *L. semilunata*, but different ornament).

Leptellina semilunata Williams, 1962: 164; pl. 15, figs 23–26 from Stinchar Limestone (Llandeilo), Brockloch, Girvan, Scotland.

Leptellina (Mabella) semiovalis Klenina, 1984: 69; pl. 5, figs 1, 3, 4; pl. 9, figs 4, 7 from Taldiboiskaya Formation (Ashgill), River Taldiboi, Chinghiz Mountains, Kazakhstan, USSR.

Leptella sinensis Xu, Rong & Liu, 1974: 152; pl. 66, figs 13, 17, 18 from Shihtzipu Formation (Llandeilo), Zunyi, Zunyi County, N. Guizhou, China.

Leptellina subcarinata Cooper, 1956: 754; pl. 190, figs 32–39 from Athens Formation (Llandeilo), Riceville, Tennessee, USA.

Leptellina sublamellosa Cooper, 1956: 755; pl. 188, figs 12, 15–24; pl. 190, figs 5–25 from Chatham Hill Formation (Llandeilo), Sharon Springs, Virginia, USA.

Leptellina tabylgatyensis Misius, 1986: 137; pl. 11, figs 1–28 from Tabulgat Formation (L. Caradoc), River Tabulgat, Moldo-Too, north Kirgiziya, USSR.

Leptellina tennesseensis Ulrich & Cooper, 1936: 626 (illustrated in Ulrich & Cooper, 1938: pl. 39, figs 1, 2, 4, 5) from the Lenoir Formation (Llandeilo), Friendsville, Tennessee, USA.

Leptellina transversa Cooper, 1956: 758; pl. 191, figs 1–8 from Arline Formation (Llanvirn–Llandeilo), Porterfield, Virginia, USA.

Leptellina sp. of Williams 1962: 167; pl. 16, figs 1, 2 from Balclatchie Conglomerate (L. Caradoc), Penwhapple Burn, Girvan, Scotland.

SPECIES QUESTIONABLY ASSIGNED

Leptellina abbreviata Cooper, 1956: 747; pl. 191, figs 23–31 from Oranda Formation (Llandeilo), Strasburg, Virginia, USA (pedicle valves look similar, but no brachial valve interiors figured).

Leptaena decipiens Billings, 1865: 74, fig 67 (reillustrated by Ulrich & Cooper, 1938: pl. 39, figs 13–15) from Limestone in Lévis Shale (Arenig), Lévis, Quebec, Canada (pedicle valves look similar, but no brachial valves now known).

Plectambonites delicatula Butts, 1926: 116; pl. 26, figs 20, 21 (also Cooper 1956: pl. 188, figs 13, 14; pl. 191, figs 32–39) from Little Oak Formation (Llandeilo), Pelham, Alabama, USA (pedicle valve looks similar, but no brachial valve interiors figured).

Sampo (*Leptellina*) *elevata* Spjeldnaes, 1957: 73; pl. 6, figs 11, 12 from 4b beds (M. Caradoc), Gomnes-Rud, Ringerike, Norway (no brachial interiors figured).

Leptellina huanghuaensis Chang, 1983: 476; pl. 1, fig. 1 from Miaopo Formation (U. Llandeilo–L. Caradoc), Huanghuachang, Yichang County, Hubei Province, China (no interiors known).

Leptellina incompta Cooper, 1956: 750; pl. 191, figs 9–22 from shale below Eureka Quartzite (Llanvirn?), Martins Ridge, Monitor Range, Nevada, USA (pedicle valve unlike *Leptellina*; brachial valve not figured in posterior region).

Leptellina (*Mabella*) *incurvata* Klenina, 1984: 72; pl. 5, fig. 2 from Taldiboiskaya Formation (Ashgill), River Taldiboi, Chinghiz Mountains, Kazakhstan, USSR (same locality and horizon as *M. semiovalis* but no interiors known).

Leptellina (*Leptellina*) *infrequens* Klenina, 1984: 68; pl. 7, fig. 1; pl. 8, fig. 7; pl. 9, fig. 5 from Abaevskaya Formation (Llanvirn–Llandeilo), SE Ordatas Hill, Pre-Chinghiz Mountains, Kazakhstan, USSR (no interiors illustrated).

Leptaena? *ledetensis* Reed, 1906: 54; pl. 4, figs 39–41 from Naunkangyi Formation (?L. Caradoc), Ledet, northern Shan States, Burma (no brachial valve interior figured, but pedicle valve with platform, cardinal process trifid).

Leptellina maxima Zhang, 1981: 89; pl. 40, figs 9, 10 from L. Kiziltesikea Formation (Ashgill), Jaboshaer, Fuyun County, Xinjiang Province, China (no interiors figured).

Leptellina platys Cooper, 1956: 751; pl. 186, figs 13, 14 from Benbolt Formation (L. Caradoc), Clinchport, Virginia, USA (no interiors known).

Orthis ? *productoides* M^cCoy, 1846: 32; pl. 3, fig. 15 (*non O. productoides* Murchison, 1840) from Tramore Limestone (Caradoc), Tramore, Co. Waterford, Ireland (discussed Cocks 1978: 93, no interior figured).

Leptellina sanyuanzhiensis Liu, *in* Liu *et al.* 1983: 273; pl. 93, figs 1–5 from Tangtou Formation (L. Ashgill), Chuxian County, Anhui Province, China (interiors poorly figured).

SPECIES REJECTED

Leptellina carinata Yadrenkina, 1965: 12; pl. 2, figs 13–22 from Baksan Horizon, Mangazei Stage (Caradoc), Podkamennayar Tunguska River, Kuzimovk, NW Siberia, USSR (large pedicle valve muscle field, so assigned to *Dulankarella*).

Benignites (*Leptestiina*) *prantli* Havlíček, 1952: 412 from Králův Dvůr Shales (Ashgill) of Králův Dvůr, Czechoslovakia (the type of *Leptestiina* – now a separate genus).

Leptellina sp. 1 of Cooper 1956: 759; pl. 187, fig. 8 from Edinburg Formation (Llandeilo), Strasburg, Virginia, USA (overhanging cardinal process).

LEPTELLINA (MERCIELLA) Lamont & Gilbert, 1945

Figs 50, 51

1945 *Leptella* (*Merciella*) Lamont & Gilbert: 655 *pars*
1965 *Merciella* Williams: H376 *pars*
1970 *Merciella* Cocks: 155
1981 *Merciella* Rong & Yang: 170

TYPE SPECIES. *Leptella* (*Merciella*) *vesper* Lamont & Gilbert, 1945.

DIAGNOSIS. Differs from *Leptellina* (*Leptellina*) in having a broader cardinal process, and in having a more elevated bema.

REMARKS. This is the only known Silurian representative of the Leptellininae. There is a gap in the stratigraphical record between the middle Ashgill records of *Leptellina* (*Leptellina*) and the late Llandovery records of *Leptellina* (*Merciella*). However, there is no doubt that the nominal genera are very close in morphology, which is why *Merciella* is relegated here to its original subgeneric status (although of course within a different genus).

SPECIES ASSIGNED

Merciella striata Rong, Xu & Yang, 1974: 198; pl. 93, figs 9, 10 from Lojoping Formation (U. Llandovery), Dazhongba, Yichang, W. Hubei, China.

Leptella (*Merciella*) *vesper* Lamont & Gilbert, 1945: 655; pl. 4, figs 7–12 from Wych Formation (Upper Llandovery), Alfrick, Worcestershire, England.

LEPTELLOIDEA Jones, 1928

Figs 52, 53

1928 *Leptelloidea* Jones: 475
1930 *Leptelloidea* Öpik: 133
1933 *Leptelloidea* Öpik: 30
1956 *Leptelloidea* Cooper: 763
1965 *Leptelloidea* Williams: H376

TYPE SPECIES. *Plectambonites schmidti* var. *leptelloides* Bekker, 1922.

DIAGNOSIS. Normal convexity, large strong cardinal process projecting posteriorly from hinge line, but cardinal process separate from socket plates. Large pedicle valve muscle scars extending to about half valve length (much longer than in *Leptellina* but not so wide as in *Dulankarella*): adductor scars enclosed by diductor scars. Distinctive articulation including pits and accessory teeth in the ends of the dental plates and corresponding structures in brachial valve.

REMARKS. Some specimes from the Lower Meitan Formation (L. Arenig) of SW China were identified and illustrated as *Leptelloidea leptelloides* (e.g. Wang *et al.* 1964: 181; pl. 26, figs 4–8), but these are now known to lack a cardinal process and have been reassigned to *Leptella grandis* (Xu *et al.* 1974: 149; pl. 65, figs 14–17). Despite the many nominal species at one time or another attributed to *Leptelloidea*, the distinctive articulation and musculature of *L. leptelloides* itself makes us place it as the only species within the genus.

SPECIES ASSIGNED

Plectambonites leptelloides Bekker, 1922: 68; pl. 3, fig. 16; pl. 4, fig. 12; pl. 5, figs 9–13 from Kukruse Formation (L. Caradoc), Kohtla-Järve, Estonia, USSR.

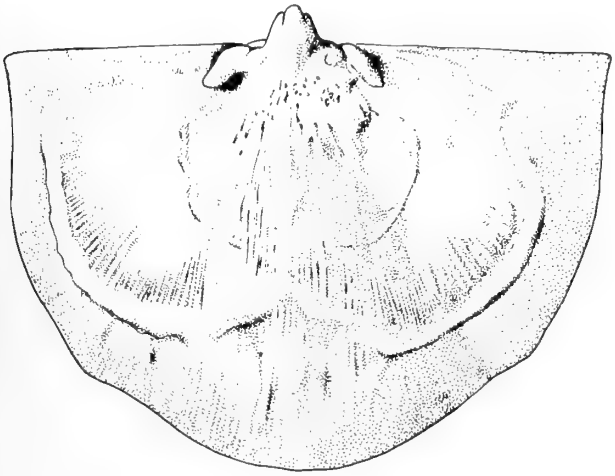


Fig. 53 *Leptelloidea leptelloides* (Bekker, 1922), from Kukruse Formation (L. Caradoc), Kohtla-Järve, Estonia, USSR, interior of brachial valve, based on BB 5169, × 6.

SPECIES QUESTIONABLY ASSIGNED

Leptelloidea campestris Reed, 1936: 42; pl. 3, figs 16, 17 from Naunkangyi Formation (?L. Caradoc), west of Yeosin, southern Shan States, Burma (no pedicle valve interior figured, so uncertain whether *Leptelloidea* or *Leptellina*, but brachial valve typical).

Leptelloidea (*Benignites*?) *heintzi* Spjeldnaes, 1957: 74; pl. 4, figs 10–11 from 4aα Beds (Llanvirn), Ravaldsjøelven, Sandsvaer, Norway (no brachial interiors known).

Leptelloidea yaxianensis Xu & Su, 1979: 108 from Middle Ordovician iron ores, Yaxian county, Hainan Island, China (brachial valve interior uncertain).

Leptelloidea yeosinensis Reed, 1932*b*: 196; pl. 3, figs 3–6 from Pindaya Formation (Caradoc?), Yeosin, southern Shan States, Burma (no pedicle valve interior figured, so uncertain whether *Leptelloidea* or *Leptellina*, but brachial valve typical).

SPECIES REJECTED

Leptelloidea derfelensis Jones, 1928: 479; pl. 25, figs 3–7 from Derfel Limestone (L. Caradoc), Nant Aber Derfel, Gwynedd, Wales (transferred to *Leptestiina* by Williams 1963: 430).

Leptelloidea multicostata [Borrissiak MS] Rukavishnikova, 1956: 132; pl. 2, figs 8–11 from Otarsky Horizon (Caradoc), Bokkot River, Chu-Ili Mountains, Kazakhstan, USSR (transferred to *Mabella* by Klenina 1984: 72).

Leptelloidea musca Öpik, 1930: 140; pl. 8, figs 95, 97–108 and subspecies *alata* Öpik, 1930: 144; pl. 8, fig. 96 both from Kukruse Formation (L. Caradoc), Kohtla-Järve, Estonia, USSR (transferred to *Bilobia* by Cooper 1956: 761; pl. 192, figs 21–24).

Leptelloidea rosendahli Spjeldnaes, 1957: 75; pl. 2, figs 4–5 from Coelosphaeridium Beds (M. Caradoc), Fangberget, Ringsaker, Norway (to *Bilobia*).

Leptelloidea sholeshookensis Jones, 1928: 488; pl. 25, fig. 19 from Slade and Redhill Mudstone Formation (M. Ashgill), Lower Cresswell, Dyfed, Wales (transferred to *Leangella*? by Cocks 1978: 96).

Leptelloidea subquadrata Rukavishnikova, 1956: 134; pl. 2, figs 12–14 from Kopalinski Horizon (Llanvirn), Kstau-sai, Chu-Ili Mountains, Kazakhstan, USSR (uncertain genus but Rukavishnikova 1956: 135 compares the species with *Bilobia musca* and *Leangella scissa*).

REVERSELLA Liang, 1983

1983 *Reversella* Liang *in* Liu *et al.*: 274

TYPE SPECIES. *Reversella trigonoformis* Liang, 1983.

DIAGNOSIS. Resupinate and strongly geniculate. Brachial valve like *Acculina*. Pedicle muscle field with strong bounding ridges, meeting anteriorly, and with central strong myophragm within the muscle field.

REMARKS. *Reversella* is close to *Acculina*, but its large valves show strong geniculation by comparison with *Acculina*, which lacks geniculation and in addition has the muscle bounding ridges in the pedicle valve.

SPECIES ASSIGNED

Reversella trigonoformis Liang, *in* Liu *et al.* 1983: 274; pl. 98, figs 1–5 from Changwu Formation (M. Ashgill), Jianglütang, Chunan County, W. Zhejiang, China.

Subfamily **PALAEOSTROPHOMENINAE** nov.

DIAGNOSIS. With trifid cardinal process. Large open pedicle valve muscle field. Usually with deeply impressed pallial markings in both valves.

REMARKS. This group of plectambonitaceans, which are often of very large size for the superfamily and confused in early works with strophomenaceans, has been classified in different families and subfamilies in the past. In fact the genera below form a close-knit group, which has caused us to suppress *Titanambonites* and *Ishimia* in favour of *Apatomorpha* and *Toquimia* respectively. The subfamily is included within the Leptellinidae on the basis of the trifid cardinal processes, which are not undercut, and on the lack of bema or side septa.

GENERA ASSIGNED. *Apatomorpha* Cooper, 1956 (including *Titanambonites* Cooper, 1956); *Glyptambonites* Cooper, 1956; *Palaeostrophomena* Holtedahl, 1916; *Toquimia* Ulrich & Cooper, 1936 (including *Ishimia* Nikitin, 1974).

RANGE. Llanvirn (*Toquimia kirki*) to U. Caradoc (*Toquimia sumsarica*).

APATOMORPHA Cooper, 1956

1956 *Apatomorpha* Cooper: 709
1956 *Titanambonites* Cooper: 717
1963 *Titanambonites* Williams: 160
1965 *Apatomorpha* Williams: H373
1965 *Titanambonites* Williams: H375

TYPE SPECIES. *Rafinesquinia pulchella* Raymond, 1928. Type species of *Titanambonites* is *T. medius* Cooper, 1956.

DIAGNOSIS. Brachial valve like *Glyptambonites* but pedicle valve differs in wider muscle field with shorter muscle bounding ridges. No platform.

REMARKS. We can find no substantial differences between *Apatomorpha* and *Titanambonites* except that of size, and described but not illustrated differences in the articulation, both of which are regarded here as intrageneric variation. *Glyptambonites* is also very similar (see below), but still regarded as separate in this paper.

SPECIES ASSIGNED

Plectambonites amplus Raymond, 1928: 297; pl. 2, fig 9; pl. 3, fig. 12 from Lenoir Formation (U. Llandeilo), 6 miles SE of Knoxville, Tennessee, USA (revised Cooper 1956: 718; pl. 177 &c.).

Titanambonites medius Cooper, 1956: 721; pl. 178, figs 9–21; pl. 185, figs 11–15 from base of Athens Formation (U. Llandeilo–L. Caradoc), Christiansburg, Tennessee, USA.

Titanambonites praecursor Cooper, 1956: 722; pl. 184, figs 6–12 from the Lenoir Formation (Llandeilo), Friendsville, Tennessee, USA.

Rafinesquina pulchella Raymond, 1928: 296; pl. 3, fig. 10 from Athens Formation (U. Llandeilo–L. Caradoc), Tennessee, USA (revised Cooper 1956: 709; pl. 166, figs 1–20).

SPECIES QUESTIONABLY ASSIGNED

Titanambonites convexus Cooper: 719; pl. 178, figs 1–8 from Little Oak Formation (Llandeilo–Caradoc), Newhope, Alabama, USA (brachial interior not known).

Titanambonites sp. 1 of Cooper, 1956: 723; pl. 177, fig. 11 from Lenoir Formation (Llandeilo), Pratt Ferry, Alabama, USA (no interior known).

SPECIES REJECTED

Apatomorpha altaicus Severgina, 1960: 406; pl. 0–17, figs 19–21 from Khankharin Formation (U. Llandeilo), River Ebogon, Gornoi Altai, USSR (with platform, so to *Toquimia*).

Titanambonites incertus Williams, 1962: 160; pl. 14, figs 36–38; pl. 15, figs 1–4, 6 from Balclatchie Mudstones (L. Caradoc), Girvan, Scotland (genus uncertain: pedicle valve with inclined dental plates like a leptellinid, brachial valve interior not well known).

Titanambonites magnus Nikitin, 1974: 56; pl. 5, figs 1–5 from Andryshenskaya Formation (U. Llanvirn?), Ishim River, Kazakhstan, USSR (with platform, transferred to *Toquimia*).

Titanambonites planus Rozman, 1964: 148; pl. 13, figs 1–7 from U. Kalychan Formation (M. Ordovician), River Kalychan, Selenniakh Mountains, NE USSR (platform present, so assigned to *Toquimia*).

GLYPTAMBONITES Cooper, 1956
Figs 54–56

1956 *Glyptambonites* Cooper: 712
1965 *Glyptambonites* Williams: H373

TYPE SPECIES. *Glyptambonites musculosus* Cooper, 1956.

DIAGNOSIS. No platform seen (although no entire brachial valve yet illustrated). Like *Apatomorpha* but with pedicle valve muscle field narrower and with longer muscle bounding ridges.

REMARKS. *Glyptambonites* is extremely close in morphology to *Apatomorpha* (and its synonym *Titanambonites*), differing generically in our view only in the relative narrowness of the pedicle valve muscle field and perhaps also the longer bounding ridges of the two pedicle valves of *G. musculosus* yet illustrated. Other species of *Glyptambonites* assigned by Cooper (1956), e.g. *G. glyptus*, have wider and shorter muscle bounding ridges and delicate cardinal processes when compared with the bulbous process of *G. musculosus*, and may thus belong to a separate taxon, perhaps a subgenus. The rugae and concentric ornament seen variably in *G. musculosus* and other species are not, in our view, helpful in generic differentiation.

SPECIES ASSIGNED

Glyptambonites musculosus Cooper, 1956: 715; pl. 171, fig. 15; pl. 175, figs 9–13; pl. 176, figs 1–5 from Oranda Formation (L. Caradoc), Linville Station, Virginia, USA.

SPECIES QUESTIONABLY ASSIGNED

Glyptambonites glyptus Cooper, 1956: 713; pl. 168, figs 1, 2; pl. 173, figs 13–23; pl. 175, figs 1–8 from Effna–Rich Valley Formation (L. Caradoc), Porterfield Quarry, Virginia, USA.

Glyptambonites aff. *glyptus* Cooper; Williams, 1962: 160; pl. 14, figs 33–35 from Lower Stinchar Limestone (Llanvirn–Llandeilo), Tormitchell, Girvan, Scotland.

Sowerbyella platys Butts, 1940: 200; 1942: 109; pl. 95, fig. 17 probably from Edinburg Formation (L. Caradoc), Strasburg, Virginia (see Cooper, 1956: 716).

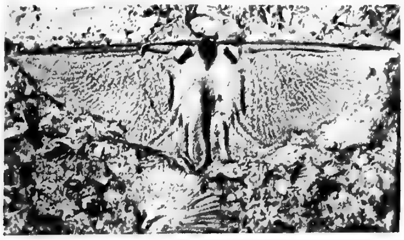
PALAEOSTROPHOMENA Holtedahl, 1916
Figs 57, 58

1916 *Palaeostrophomena* Holtedahl: 43
non 1932 *Palaeostrophomena* Öpik: 35 (rejected by Öpik, 1933)
1933 *Palaeostrophomena* Öpik: 24
1956 *Palaeostrophomena* Cooper: 700
1965 *Palaeostrophomena* Williams: H373

TYPE SPECIES. *Strophomena concava* Schmidt, 1858.

DIAGNOSIS. Resupinate.

REMARKS. No brachial valve interiors of *P. concava* are known although from Öpik's (1933: pl. 4, fig. 1) illustration of the exterior, it is certain that the cardinal process is trifid. It is the only member of the subfamily which is resupinate. None of the North American species described by Cooper (1956), which are listed below, possess a platform, and a new genus would be required for them if a platform was subsequently discovered in *P. concava*. All the North American specimens are resupinate and also possess a trifid cardinal process.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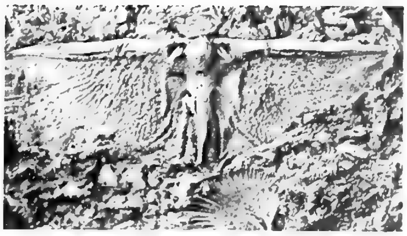
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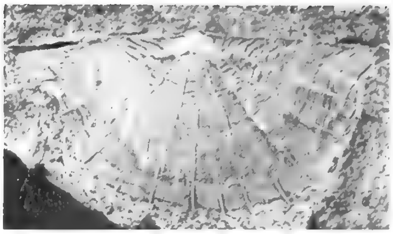
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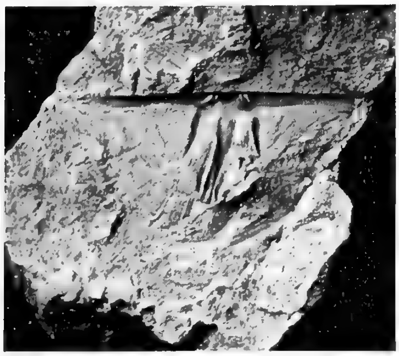
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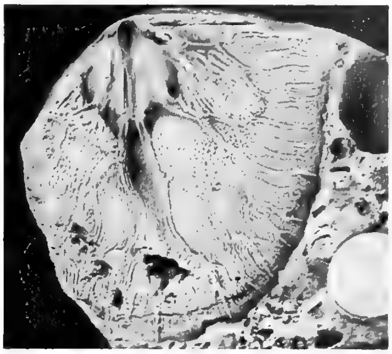
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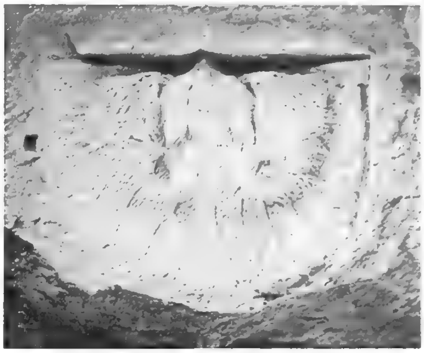
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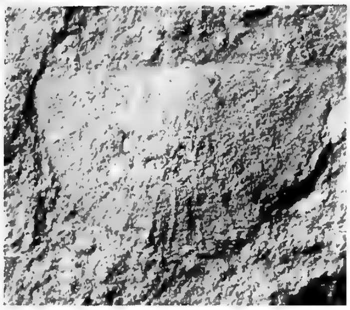
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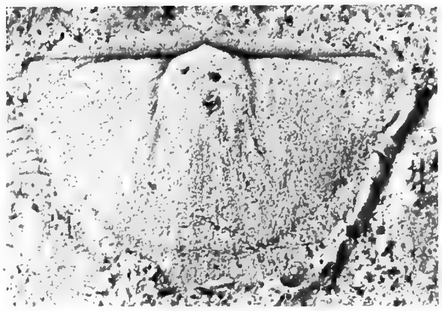
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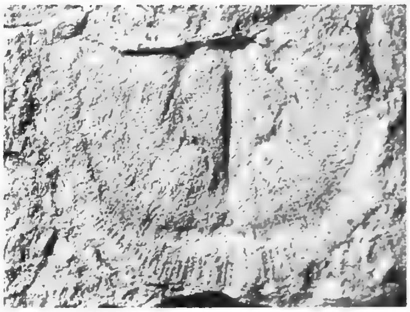
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Fig. 54 *Glyptambonites musculosus* Cooper, 1956, paratype from Oranda Formation (L. Caradoc), 0·6 miles NW of Linville Station, Virginia, USA, natural internal mould of brachial valve and latex cast of it, the original of Cooper 1956: pl. 176, figs 4, 5, USNM 117388c, × 2.

Figs 55, 56 *Glyptambonites* sp. from Balclatchie Mudstones (L. Caradoc), Penwhapple, Girvan, Strathclyde, Scotland, the originals of Williams 1962: pl. 14, figs 25, 31. Fig. 55, pedicle valve exterior, BB 15140, × 3; Fig. 56, internal mould of brachial valve, BB 15141, × 3.

Figs 57, 58 *Palaeostrophomena kilbuchoensis* (Davidson, 1883), from beds of Caradoc age, near Kilbucho Church, 3 km west of Cutler, Peebleshire, Scotland. Fig. 57, natural internal mould of brachial valve, the original of Davidson 1883: pl. 13, fig. 2, GSE 6625, × 3; Fig. 58, natural internal mould of pedicle valve, the original of Davidson 1883: pl. 13, fig. 1, lectotype selected Cocks 1978: 92, GSE 359, × 2.

Figs 59–61 *Toquimia aranea* (Salter, 1865), from Lower Ordovician beds, Niti, NW India. Fig. 59, partly exfoliated pedicle valve exterior from Damchen, B 4102, × 2; Fig. 60, natural internal mould of pedicle valve from Upper Rimkin, the original of Salter *in* Salter & Blanford 1865: pl. 3, fig. 11, and selected here as the **lectotype** of *Strophomena nubigena* Salter, B 15804, × 1·5; Fig. 61, natural internal mould of brachial valve from Damchen, the original of Salter *in* Salter & Blanford 1865: pl. 3, fig. 10 (right) and selected here as the **lectotype** of *Strophomena aranea* Salter, BC 10606, × 1·5.

Species assigned

Palaeostrophomena angulata Cooper, 1956: 702; pl. 168, figs 3–10; pl. 194, figs 19–22 from the Botetourt Formation (L. Caradoc), Catawba, Virginia, USA.

Palaeostrophomena canalis Lockley, 1980: 210; figs 47–52 from Gelli-grîn Formation (U. Caradoc), Gelli-grîn, Powys, Wales.

Strophomena concava Schmidt, 1858: 215 from Uhaku Formation (Llandeilo), Ärra, Estonia, USSR (revised Öpik, 1933: 25; pl. 2, figs 1–4; pl. 3, fig. 1; pl. 4, fig. 1; pl. 8, fig. 2).

Orthis vel *Strophomena*? *kilbuchoensis* Davidson, 1883: pl. 13, figs 1, 2 from beds of Caradoc age, Kilbucho, Peebleshire, Scotland (revised Williams 1962: 157; pl. 14, figs 22–25, 27, 28, 31).

Palaeostrophomena magnifica Williams *in* Whittington & Williams 1955: 414; pl. 39, figs 64–70 from Derfel Limestone (L. Caradoc), Pont Aberderfel, Gwynedd, Wales.

Palaeostrophomena necopina Popov, 1980*b*: 145; pl. 1, figs 8–11 from Anderkenski Horizon (U. Llandeilo–L. Caradoc), Katnak Mountain, Chu-Ili Mountains, Kazakhstan, USSR.

Palaeostrophomena resupinata Cooper, 1956: 704; pl. 167, figs 1–28 from Lower Benbolt Formation (L. Caradoc), Cedar Point, Hilton, Virginia, USA.

Stropheodonta (*Leptostrophia*) *subfilosa* Reed, 1917: 893; pl. 17, figs 9–12 from Craighead Limestone (U. Caradoc), Craighead, Girvan, Scotland (revised Williams 1962: 158; pl. 14, figs 26, 29, 30, 32).

Palaeostrophomena superba Cooper, 1956: 707; pl. 169, figs

13–29; pl. 184, figs 13–18 from M. Arline Formation (L. Caradoc), Friendsville, Tennessee, USA.

Palaeostrophomena subtransversa Cooper, 1956: 707; pl. 168, figs 11–13 from Arline Formation (L. Caradoc), Porterfield Quarry, Virginia, USA.

SPECIES QUESTIONABLY ASSIGNED

Palaeostrophomena? *majori* Spjeldnaes, 1957: 64; pl. 1, fig. 13 from Bryozoan Zone (Caradoc), Saltboden, Freierfjorden, Langesund–Gjerpen district, Norway (no brachial valve internal known).

Palaeostrophomena? *rugosa* Cooper, 1956: 705; pl. 176, figs 6–12 from Botetourt Formation (L. Caradoc), Lexington, Virginia, USA (rugate).

TOQUIMIA Ulrich & Cooper, 1936
Figs 59–61

1936	*Toquimia* Ulrich & Cooper: 626
1938	*Toquimia* Ulrich & Cooper: 183
1956	*Toquimia* Cooper: 698
1965	*Toquimia* Williams: H372
1970	*Toquimia* Ross: 63
1974	*Ishimia* Nikitin: 59

TYPE SPECIES. *Toquimia kirki* Ulrich & Cooper. Type species of *Ishimia* is *I. ishimensis* Nikitin, 1974.

DIAGNOSIS. Large flabellate pedicle valve muscle field. Bulbous cardinal process with massive central component and small lateral processes. Large pseudodeltidium, small chilidium variably developed. Like *Apatomorpha* but with platform.

REMARKS. *Toquimia* is transferred from the Taffiidae (where it has always been classified) because it possesses a trifid, not a simple cardinal process, as seen in Cooper 1956: 698; pl. 164, figs 11, 13. Ross (1970: 64; pl. 8, fig. 17) has found some bilobed structures on sectioning some specimens, but he and Cooper are not certain from this sectioned material whether *Toquimia* has a bilobed cardinal process or not. Of course if it had, then the genus would be classified as an early member of the Strophomenacea, but from the pictures of Cooper (1956: pl. 164) we believe *Toquimia* to be correctly placed within the Leptellinidae. In fact, there is some variability in the external form of the cardinal process, but no generic differences between *T. kirki* and *I. ishimensis*. We agree with Nikitin (1974: 61) in his comment that *Ishimia* is very close to *Titanambonites*, and that it would be possible to unite them within the Leptellinidae, even though his concept of the Leptellinidae differs from ours in the systematic value of the possession of a platform. The brachial valve of *Ishimia* and *Titanambonites* are virtually identical, apart from the platform in *Ishimia*. Some excellent specimens of *Toquimia aranea* are available to us from old collections made by Strachey in the western Himalayas (Indo-Chinese border area) in the 1840s (Figs 59–61).

SPECIES ASSIGNED

Apatomorpha altaicus Severgina, 1960: 406; pl. 0–17, figs 19–21 from Khankharin Formation (U. Llandeilo), River Ebogon, Gornoi Altai, USSR.

Strophomena aranea Salter, *in* Salter & Blanford 1865: 36; pl. 3, fig. 10 from Lower Ordovician beds, Damchen, Niti, NW India, and its synonym *Strophomena nubigena* Salter, *in* Salter & Blanford 1865: 37; pl. 3, fig. 11 from similar beds at Upper Rimkin, Niti.

Plectambonites crassus Willard, 1928: 278; pl. 3, fig. 10 from Effna Formation (L. Caradoc), Bland, Virginia (revised by Cooper, 1956: 720; pl. 181, figs 1–9 as *Titanambonites crassus* but has platform).

Ishimia humilis Nikitin, 1974: 62; pl. 6, figs 1–3 from Bestamak Formation, Yekebidaik Horizon (M. Caradoc), Sakbay, Chinghiz Mountains, Kazakhstan, USSR.

Ishimia ishimensis Nikitin, 1974: 61; pl. 5, figs 10–16 from Andryshenskaya Formation (U. Llanvirn?), Ishim River, Kazakhstan, USSR.

Toquimia kirki Ulrich & Cooper, 1936: 626; from U. Pogonip (Llanvirn), Ikes Canyon, Nevada, USA (also Cooper, 1956: 698; pl. 164, figs 4–14; pl. 195, fig. 32; Ross 1970: pl. 8, figs 16, 18).

Titanambonites magnus Nikitin, 1974: 56; pl. 5, figs 1–5 (from same locality and horizon as *I. ishimensis* and probably a synonym).

Ishimia mediasiaticia Misius, 1986: 145; pl. 9, figs 18–24; pl. 10, figs 1–23 from Tabilgat Formation (U. Llandeilo), River Tabilgat, Moldo-Too, N. Kirgiziya, USSR.

Titanambonites planus Rozman, 1964: 148; pl. 13, figs 1–7 from U. Kalychan Formation (M. Ordovician), River Kalychan, Selenniakh Mountains, NE USSR.

Ishimia radiata Nikitin, 1974: 64; pl. 6, figs 7–10 (from same locality and horizons as *I. ishimensis* and probably a synonym).

Ishimia sumsarica Rozman, 1978: 88; pl. 14, figs 9–12 from Obikalon Beds (U. Caradoc), Shakhriomon, Tian-Shan, USSR.

NOMEN NUDUM. *Ishimia*? *triangula* Nikitin, 1974: 59.

SPECIES QUESTIONABLY ASSIGNED

Toquimia? *asiatica* Borissiak, 1972: 182; pl. 49, figs 1–3 from *Catenipora* Beds (Ashgill), Abaktiigen River, Tarbagatau Mountains, E. Kazakhstan, USSR (no brachial valve interior illustrated).

Ishimia narulgensis Nikitin, 1974: 63; pl. 6, figs 4–6 from Tselinograd Horizon (Llandeilo–L. Caradoc), Narulgen,

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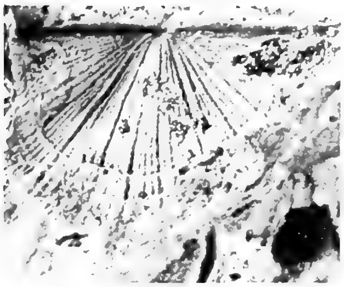
Figs 62, 63 *Calyptolepta diaphragma* Neuman, 1976, paratypes from Virgin Arm Tuffs (Llanvirn), east side of Virgin Arm, New World Island, Newfoundland, Canada. Fig. 62, downward and posterior views of latex cast and oblique and downward views of natural internal mould of brachial valve, the original of Neuman 1976: pl. 6, figs 8, 9, GSC 35068a, × 5, × 4, × 6, × 4; Fig. 63, external mould of brachial valve, the original of Neuman 1976: pl. 6, fig. 7, GSC 35068b, × 4.

Figs 64–67 *Grorudia grorudi* Spjeldnaes, 1957, from Zone 4aβ (L. Caradoc), east of Tåsen Station, Oslo, Norway. Fig. 64, natural mould and latex cast of brachial valve interior, holotype, the original of Spjeldnaes 1957: pl. 1, fig. 10, PMO 66939, × 8; Fig. 65, natural mould and latex cast of brachial valve interior, figured by Spjeldnaes 1957: pl. 1, fig. 9 as *Alwynella osloensis*, PMO 66931/69931, × 8; Fig. 66, latex cast of brachial valve exterior, the original of Spjeldnaes 1957: pl. 1, fig. 5 (upper), PMO 66940, × 8; Fig. 67, latex cast of brachial valve interior, figured by Spjeldnaes 1957: pl. 1, fig. 5 (lower) as the holotype of *Alwynella osloensis*, PMO 66940, × 8.


62a


62b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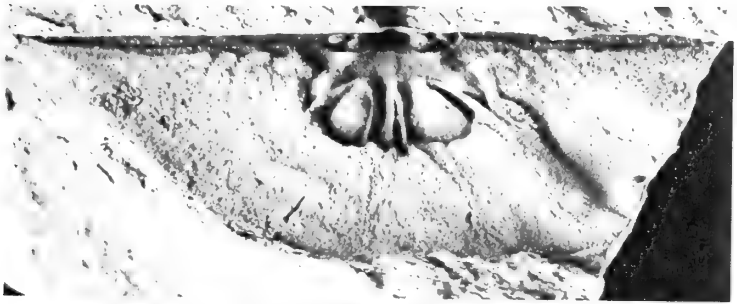
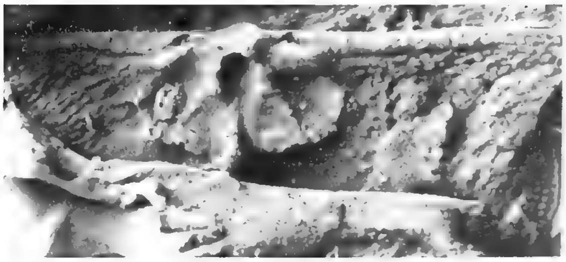
62c

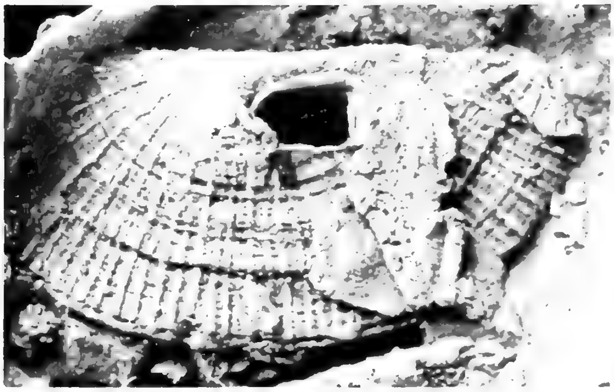

62d


64a


64b


65a


65b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67

Kazakhstan, USSR (no brachial internal figured – could be *Titanambonites*).

Family **GRORUDIIDAE** nov.

DIAGNOSIS. Cardinal process trifid, not undercut. Bema present. Side septa present, but sometimes weakly developed. Platform variably developed.

REMARKS. We have placed *Yuanbaella* in synonymy with *Calyptolepta*. When better collections of all the forms are available then *Calyptolepta* and perhaps *Anechophragma* might properly be regarded as synonyms of *Tetraodontella* itself. *Grorudia* is revised here and now includes *Alwynella*; it is the only member of the family without a platform.

GENERA ASSIGNED. *Anechophragma* Neuman, 1977; *Calyptolepta* Neuman, 1977 (including *Yuanbaella* Fu, 1982); *Grorudia* Spjeldnaes, 1957 (including *Alwynella* Spjeldnaes, 1957); *Tetraodontella* Jaanusson, 1962.

RANGE. L. Llanvirn (*Tetraodontella* spp.) to M.–U. Caradoc (*Tetraodontella transversa*).

ANECHOPHRAGMA Neuman, 1977

1977	*Anechophragma* Neuman: 37
non 1984	*Anechophragma* Xu & Liu: 204

TYPE SPECIES. *Anechophragma rarum* Neuman, 1977.

DIAGNOSIS. Like *Calyptolepta* but with very wide teeth and no dental plates.

REMARKS. The type specimens of the aptly-named *Anechophragma rarum* have been checked by us and they have very wide teeth (see Neuman 1977: pl. 5, fig. 22) and no dental plates, in contrast to the narrow teeth with short dental plates of *Calyptolepta diaphragma* which occurs in the same bed. In addition there are a pair of very thin structures projecting anteriorly from the bema of *Anechophragma* which may be interpreted simply as an exaggerated part of the bema itself or alternatively as thin and short side septa. We are undecided whether or not the two species (and therefore the two genera) are in fact separate or really variants of each other. They provisionally remain separate here until further material is available (see also below under *Calyptolepta*).

SPECIES ASSIGNED

Anechophragma rarum Neuman, 1977: 38; pl. 5, figs 22–25 from tuffs of Llanvirn age, Virgin Arm, New World Island, Newfoundland, Canada.

CALYPTOLEPTA Neuman, 1977
Figs 62, 63

1977	*Calyptolepta* Neuman: 35
1982	*Yuanbaella* Fu: 116
1984	*Anechophragma* Xu & Liu: 204

TYPE SPECIES. *Calyptolepta diaphragma* Neuman, 1977. Type species of *Yuanbaella* is *Tetraodontella truncata* Fu, 1975.

DIAGNOSIS. Like *Tetraodontella* but with two distinct side septa in the median part of the brachial valve, no median septum. Platform present.

REMARKS. When Neuman erected *Calyptolepta* and *Anechophragma* he did not compare them with each other and also did not compare them with *Tetraodontella*, to which they are closely related. In fact the type species of the two genera are very similar (except that there are no dental plates in *Anechophragma*) and in particular include very distinctive partly united side septa in the brachial valve extending beyond the bema and a distinctive small median septum in the central region of the pedicle valve. Neuman (1977: 35) described only a 'median ridge' in *Calyptolepta*, but his photographs, including the holotype (pl. 6, figs 5, 6), clearly show that it is in fact a double septum and not a single ridge. When Fu (1982) established *Yuanbaella*, he did not compare it with *Calyptolepta* or *Anechophragma*, although he did say how it differed from *Tetraodontella*. All three nominal taxa have a very distinctive pedicle valve structure in common, with a small central median septum to either side of which are two recesses into which fitted the two side septa of the brachial valve. Certainly *Yuanbaella* should be considered as a junior synonym of *Calyptolepta*, but we have only questionably assigned *Anechophragma* in this paper because no dental plates can be seen in the sparse type material. Further investigation is needed, although original material of *Calyptolepta diaphragma* is illustrated here.

SPECIES ASSIGNED

Tetraodontella chengkouensis Xu, Rong & Liu, 1974: 149; pl. 65, figs 21–23 from Houping Formation (Llanvirn), Chengkou, N. Sichuan Province, China (also '*Anechophragma chengkouensis* sp. nov.' of Xu & Liu 1984: 205; pl. 13, figs 15–18 described on the same specimens).

Calyptolepta diaphragma Neuman, 1977: 36; pl. 6, figs 5–16 (? *non* figs 17, 18 which may be a leptellinid) from tuffs of Llanvirn age, Virgin Arm, Newfoundland, Canada.

Tetraodontella truncata Fu, 1975: 108; pl. 12, figs 12–18 from Xiliangsi Formation (L. Llanvirn), Dangmengou, Yuanba, Nanzheng County, S. Shaanxi Province, China.

GRORUDIA Spjeldnaes, 1957
Figs 64–67

1957	*Grorudia* Spjeldnaes: 61
1957	*Alwynella* Spjeldnaes: 85
1965	*Grorudia* Williams: H373
1965	*Alwynella* Williams: H381

TYPE SPECIES. *Grorudia grorudi* Spjeldnaes, 1957. Type species of *Alwynella* is *Alwynella osloensis* Spjeldnaes, 1957.

DIAGNOSIS. Like *Tetraodontella* and *Calyptolepta* but with no platform and side septa not extending beyond bema. Short median septum also present.

REMARKS. This genus has not been revised since its original erection by Spjeldnaes (1957), and a larger collection of topotype material illustrating the interior would be desirable. However, the original types, reillustrated here, have been examined by us. There are three brachial valve interiors from Tåsen, the common type locality of both the type species of *Grorudia* and *Alwynella*. All three show a very similar cardinal process which is not truly undercut but which has a small depression anteriorly to it in the valve floor. There is no doubt that all three specimens (which include the holotypes of *Grorudia grorudi* and *Alwynella osloensis*) belong to the same species – all have a very characteristic small median septum with a swollen knob at the anterior end and interesting small semicircular bemas. Two of the three specimens (PMO 66931, Fig. 65 and PMO 66939, Fig. 64) have distinct side septa confined within the bema, the third (PMO 66940, Fig. 66) has side septa only faintly developed, but appears to represent a younger growth stage. There is some doubt on the nature of the hinge line; Spjeldnaes describes *Grorudia* as having a smooth hinge line (1957: 61) but *Alwynella* as possessing crenulations (1957: 86). All the specimens we have seen have smooth hinge lines apart from PMO 66931 (Fig. 65) which has some small structures on the hinge line, but these appear too irregular to be termed denticulations.

SPECIES ASSIGNED

Grorudia ? glabrata Spjeldnaes, 1957: 63; pl. 1, figs 4, 8, 18 from Zone 4aβ–4bα (L. Caradoc), Blindern, Oslo, Norway.

Grorudia grorudi Spjeldnaes, 1957: 62; pl. 1, figs 7, 10, 11 from Zone 4aβ (L. Caradoc), Tåsen, Oslo, Norway, and its junior synonym *Alwynella osloensis* Spjeldnaes, 1957: 86; pl. 1, figs 5, 14, ?fig 9 from the same horizon and locality.

TETRAODONTELLA Jaanusson, 1962
Fig. 68

1962 *Tetraodontella* Jaanusson: 1
1965 *Tetraodontella* Williams: H376

TYPE SPECIES. *Tetraodontella biseptata* Jaanusson, 1962.

DIAGNOSIS. Like *Calyptolepta* but with double median septum, united posteriorly and centrally. Weak platform present.

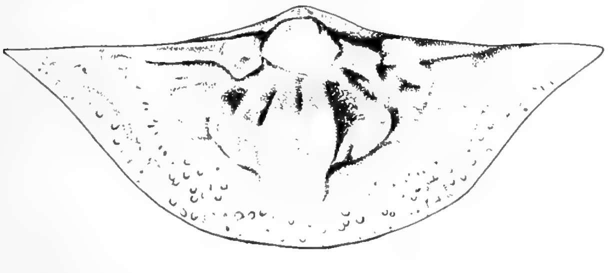


Fig. 68 *Tetraodontella biseptata* Jaanusson, 1962, from Dalby Limestone (M. Caradoc), Sweden, brachial valve interior (based on Williams 1965: fig. 240.2c), × 6·5.

REMARKS. Only two brachial valve interiors of the type species have been illustrated; one (Jaanusson 1962: pl. 1, figs 14–16) has a slim central shaft to the cardinal process, whilst the other (Williams 1965: fig. 240, 2c) has a large bulbous cardinal process (Fig. 68). Thus further collection, analysis and illustration of topotype specimens is clearly desirable, since these two illustrated specimens seem so different from each other.

SPECIES ASSIGNED

Tetraodontella biseptata Jaanusson, 1962: 3; pl. 1, figs 11–18 from Dalby Limestone (M. Caradoc), Böda Hamn borehole, Öland, Sweden.

SPECIES QUESTIONABLY ASSIGNED

Tetraodontella aquiloides Fu, 1975: 109; pl. 12, fig. 19 from Xiliangsi Formation (L. Llanvirn), Liangshan, Nanzheng County, S. Shaanxi Province, China (no interiors illustrated).

Tetraodontella transversa Chen, *in* Fu 1982: 116; pl. 34, fig. 12 from Pagoda Limestone (M.–U. Caradoc), Liangshan, Nanzheng County, S. Shaanxi Province, China (no interiors illustrated).

SPECIES REJECTED

Tetraodontella chengkouensis Xu, Rong & Liu, 1974: 149; pl. 65, figs 21–23 from Houping Formation (Llanvirn), Chengkou, N. Sichuan Province, China (to *Calyptolepta*).

Tetraodontella truncata Fu, 1975: 108; pl. 12, figs 12–18 from Xiliangsi Formation (L. Llanvirn), Dangmengou, Yuanba, Nanzheng County, S. Shaanxi Province, China (to *Calyptolepta*).

Family **LEPTESTIIDAE** Öpik, 1933 *emend.*

1933 Leptestiinae Öpik: 24 *pars*
1953 Leptestiidae Williams: 6 *pars*
1956 Leptestiidae Cooper: 700 *pars*
1961 Leptestiinidae Havlíček: 447
1965 Leptestiidae Williams: H372 *pars*
1965 Leptellinidae Williams: H376 *pars*
1967 Leptestiinidae Havlíček: 29 *pars*
1970 Leptestiininae Cocks: 156

DIAGNOSIS. With bema, no side septa. Trifid cardinal process not undercut.

REMARKS. We have completely changed the concept of the Leptestiidae from that of both Öpik (1933) and also Williams (1965). In fact our concept of the family closely corresponds to that of the Subfamily Leptestiininae of Havlíček (1961) and Williams (1965), with the addition of *Leptestia* itself. We do not know of any basis or justification for splitting this natural group into subfamilies. However, there are three types of bema, the first elongate (as in *Leptestia*), the second transverse (as in our new genus *Rurambonites*) and the third divided (as in *Bilobia*). Although most of the leptestiid genera can be allocated unequivocally to one of these groups, nevertheless there is some variation (especially between the second and third groups) and thus we do not divide the genera into separate subfamilies. Two genera, *Sampo* and *Rurambonites*, have denticulate hinge lines; the rest do not.

GENERA ASSIGNED. *Bilobia* Cooper, 1956; *Leangella* (*Leangella*) Öpik, 1933, including *Diambonia* Cooper & Kindle, 1936, *Tufoleptina* Havlíček, 1961 and *Leangella* (*Opikella*) Amsden, 1968; *Leangella* (*Leptestiina*) Havlíček, 1952; *Leptestia* Bekker, 1922; *Rurambonites* gen. nov.; *Sampo* Öpik, 1933.

RANGE. L. Caradoc (*Bilobia* spp.) to L. Ludlow (*Leangella segmentum*).

BILOBIA Cooper, 1956
Figs. 69–71

1956 *Bilobia* Cooper: 759
1965 *Bilobia* Williams: H378

TYPE SPECIES. *Bilobia hemisphaerica* Cooper, 1956.

DIAGNOSIS. Strongly convex, divided bema, small platform.

REMARKS. There is variability in the shape of the bema, for example the specimen of *Bilobia musca* illustrated by Cooper (1956: pl. 192, fig. 23) has a bema which is united for most of its length whereas the specimen illustrated here (Fig. 70) has a bema united posteriorly for half its length and divided

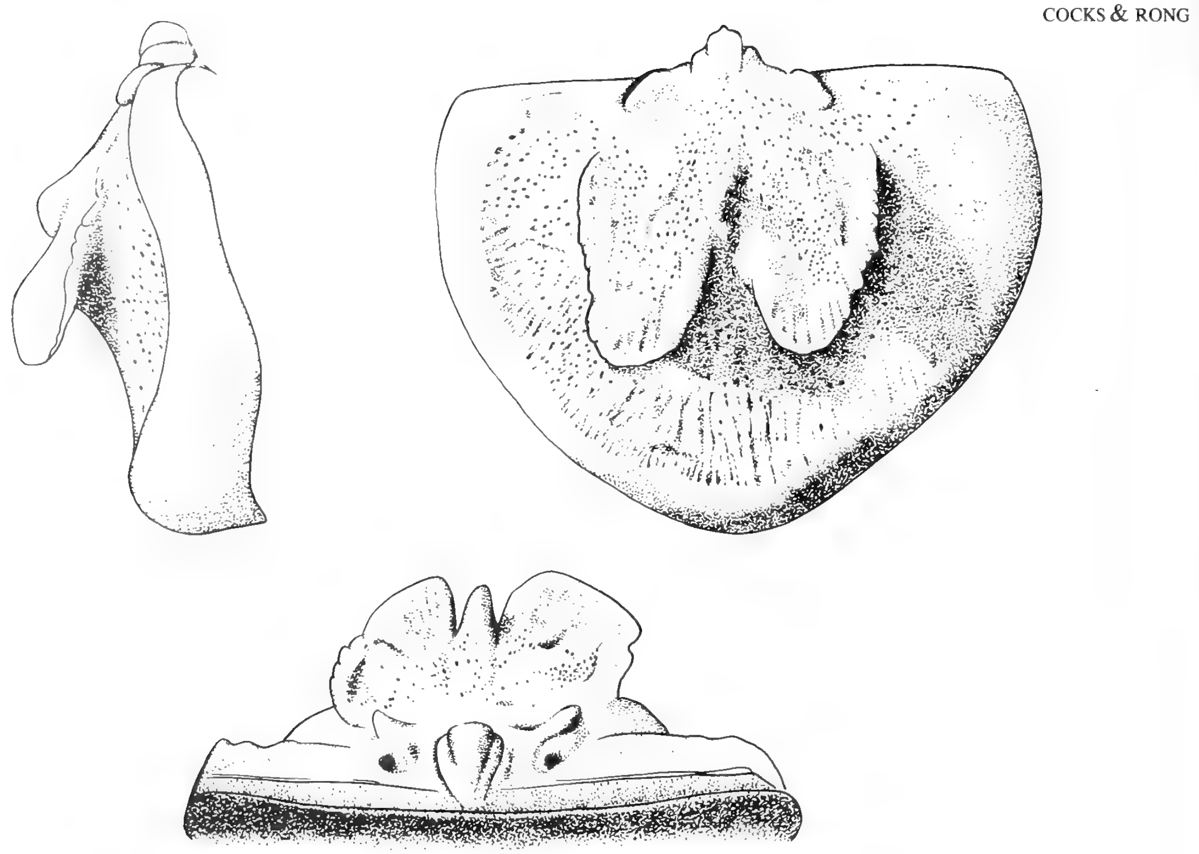


Fig. 69 *Bilobia musca* (Öpik, 1930), from Kukruse Formation (L. Caradoc), Kohtla-Järve, Estonia, USSR, interior of brachial valve showing the very elevated bema (based on BB 5202), × 12.

anteriorly, which is why *musca* is assigned to *Bilobia* rather than given its own new genus.

SPECIES ASSIGNED

Leptaena etheridgei Davidson, 1883: 170; pl. 12, figs 11, 12 from Craighead Limestone (U. Caradoc), Craighead, Girvan, Scotland, and subspecies *B. etheridgei acuta* Williams, 1962: 168; pl. 16, figs 3–7 from L. Ardwell Mudstones (M. Caradoc), Ardmillan Braes, Girvan, Scotland.

Bilobia hemisphaerica Cooper, 1956: 760; pl. 192, figs 16–20; pl. 193, figs 10–36; pl. 194, figs 31–36 from Oranda Formation (L. Caradoc), Strasburg, Virginia, USA.

Bilobia huanghuaensis Chang, 1983: 477; pl. 1, fig. 22 from U. Miaopo Formation (L. Caradoc), Huanghuachang, Yichang, Hubei, China.

Sampo indentata Spjeldnaes, 1957: 69; pl. 2, figs 15–16; pl. 4, fig. 8 from 4bγ beds (M. Caradoc), west of Billingstad Station, Asker, Norway (revised Harper & Owen 1984: 29; pl. 3, figs 10, 12–15, 17–19, 21, 22, 24, 26, as *Leptestiina indentata*).

Leptelloidea musca Öpik, 1930: 140; pl. 8, figs 95, 97–108 from Idavere Formation (M. Caradoc), Kohtla, near Tallinn, Estonia, USSR.

Leptelloidea rosendahli Spjeldnaes, 1957: 75; pl. 2, figs 4, 5 from *Coelosphaeridium* Beds (M. Caradoc), Fangberget, Ringsaker, Norway.

Sowerbyites vesciseptus Percival, 1979: 106; fig. 7B.1–13 from Goonumbla Volcanics (L. Caradoc), Gunningbland, New South Wales, Australia.

Bilobia virginiensis Cooper, 1956: 762; pl. 192, figs 1–15; pl. 195, figs 6–8 from Edinburg Formation (L. Caradoc), Strasburg, Virginia, USA.

SPECIES QUESTIONABLY ASSIGNED

Plectambonites pisum Ruedemann, 1901: 19; pl. 1, figs 8–20 from Rysedorf Conglomerate (M. Ordovician), Rysedorf, Rensselaer County, New York, USA (difficult figures, but assigned to *Bilobia* by Cooper 1956: 762).

LEANGELLA (LEANGELLA) Öpik, 1933

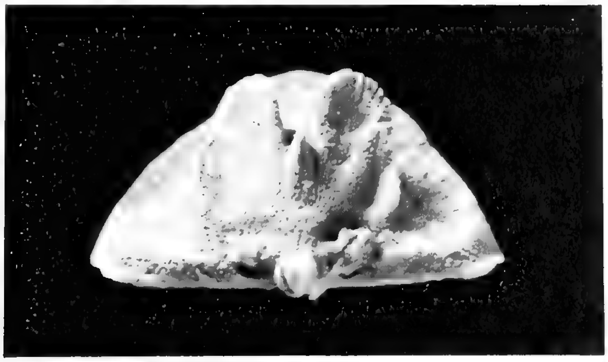
Figs 72–77

1933	*Leangella* Öpik: 42
1936	*Diambonia* Cooper & Kindle: 356
1961	*Tufoleptina* Havlíček: 447
1965	*Leangella* Williams: H378
1967	*Tufoleptina* Havlíček: 33
1968	*Leangella* (*Opikella*) Amsden: 48
1970	*Leangella* Cocks: 156

TYPE SPECIES. *Plectambonites scissa* var. *triangularis* Holtedahl, 1916, a junior subjective synonym of *Leptaena scissa* Davidson, 1871. Type species of *Diambonia* is *Plectambonites gibbosa* Winchell & Schuchert, 1892. Type species of *Tufoleptina* is *T. tufogena* Havlíček, 1961 and type species of *Opikella* is *L. (O.) dissiticostella* Amsden, 1968.

DIAGNOSIS. Bema bilobed anteriorly. Platform near valve margin.

REMARKS. The structure we term a platform near the valve margin of *Leangella* has also sometimes been termed a peripheral rim (Fig. 1, p. 79). We are certain that it is a true platform in, for example, *Leangella segmentum* (Cocks 1970: pl. 3, fig. 1); however, in many species, including the type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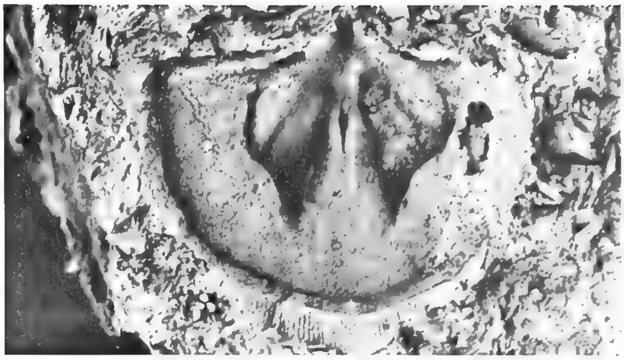
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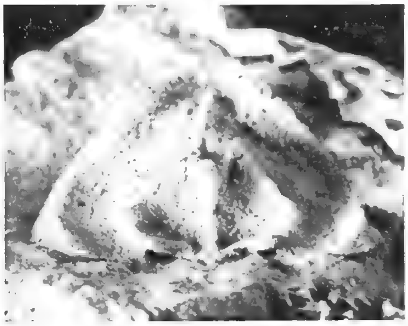
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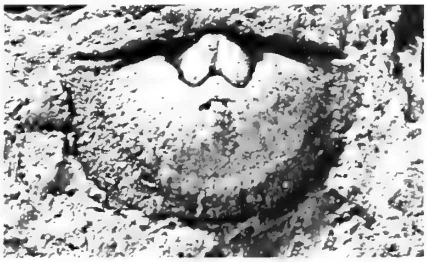
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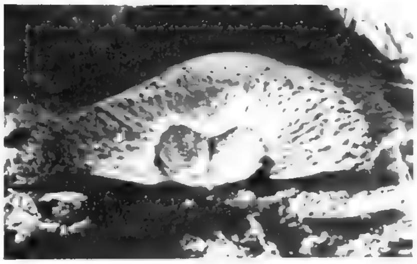
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Fig. 70 *Bilobia musca* (Öpik, 1930), from Kukruse Formation (L. Caradoc), Kohtla-Järve, Estonia, USSR, posterior, exterior and lateral views of brachial valve, topotype, BB 5202, × 7 (70a) and × 5 (70b, c).

Fig. 71 *Bilobia hemisphaerica* Cooper, 1956, paratype from Oranda Formation (L. Caradoc), Guilford Springs, 2·5 miles SW of Chambersburg, Pennsylvania, USA, internal mould of brachial valve, the original of Cooper 1956: pl. 193, figs 34, 35, USNM 111087c, × 5

Fig. 72 *Leangella* (*Leangella*) *gibbosa* (Winchell & Schuchert, 1892), from Stewartville Formation (L. Ashgill), between Stewartville and Chatville, Minnesota, USA, silicified interior of brachial valve, BC 7272, × 5.

Fig. 73 *Leangella* (*Leangella*) *scissa* (Davidson, 1871), topotype from U. Haverford Mudstone Formation (L. Llandovery), Gasworks, Haverfordwest, Dyfed, Wales, natural internal mould and downwards and posterior views of latex cast of brachial valve, BB 32167, × 6.

Figs 74–76 *Leangella* (*Leangella*) *tufogena* (Havlíček, 1961), topotypes from Liteň Formation (U. Wenlock), Hlinik, Svaty Jan Pod Skalou, Bohemia, Czechoslovakia. Fig. 74, natural internal mould of brachial valve, BB 71535, × 8; Fig. 75, natural internal mould of pedicle valve, BB 71530, × 6; Fig. 76, natural internal mould of pedicle valve viewed obliquely from the posterior, BB 71536, × 8.

species, this platform is not developed so strongly and its function is less certain. There is some variation in the median septum in the brachial valve – this is usually a double septum, sometimes a single septum and in some specimens no septum at all can be seen. Likewise the median septum in the pedicle valve is also variably developed; in some populations (e.g. that figured in Mitchell 1977: pl. 15) the septum is present in some specimens and absent in others, and for this reason we do not separately recognize *Diambonia* as a valid genus. In addition, the brachial valves of '*Leangella*' and '*Diambonia*' are identical. Havlíček erected *Tufoleptina* on the basis of the extra presence of a submarginal ridge in the pedicle valve, but Cocks (1970: 157) has demonstrated the variable occurrence of this ridge in several *Leangella* populations and so we do not accept *Tufoleptina* as valid. *Opikella* differs from *Leangella* only in lacking the finer radial ornament; however, it still possesses normal costellae and we do not think the differences merit more than specific separation; we do not use the term for a separate subgenus or genus.

SPECIES ASSIGNED

Leangella anaclyta Havlíček, 1981: 21; pl. 7, figs 19–27 from M.–U. Caradoc, La Grange-du-Pin, Montagne Noire, France (revised Villas 1985: 85; pl. 18, figs 13–14; pl. 19, figs 1–15).

Diambonia anatoli Spjeldnaes, 1957: 80; pl. 2, figs 6–8 from Zone 4bα (M. Caradoc), Nesøya, Oslo, Norway.

Leangella auritus Su, 1980: 271; pl. 116, figs 11–14 from Huanghuagou Formation (M. Llandovery), east side of Luohe River, Aihui County, Heilongjiang Province, NE China.

Plectambonites quinquecostata var. *cylindrica* (= *Leangella cylindrica*) Reed, 1917: 878; pl. 14, figs 11, 14–17 *non* figs 12, 13 from Shalloch Formation (L. Ashgill), Shalloch Mill, Girvan, Scotland.

Leangella discuneata Lamont, 1935: 315; pl. 7, figs 17–19 from Auld Thorns Conglomerate (L. Ashgill), Auld Thorns, Girvan, Scotland (revised Mitchell 1977: 78; pl. 15, figs 10–25).

Leangella (*Opikella*) *dissiticostella* Amsden, 1968: 48; pl. 5, figs 1a–q; pl. 16, figs 1a–e; pl. 19, figs 2a–b from St Clair Limestone (L. Wenlock), Batesville, Arkansas, USA.

Plectambonites gibbosa Winchell & Schuchert, 1892: 288 from Caradoc beds, Mantorville, Old Concord, Tennessee, USA.

Leangella hamari Spjeldnaes, 1957: 81; pl. 2, figs 1–3 from Cyclocrinus Shale (M. Caradoc), Furuberget, Hamar-Nes district, Norway.

Leangella ino Öpik, 1953: 13; pl. 2, figs 5–11; pl. 3, figs 12–15 from the Illaenus Band (U.Llandovery), Heathcote, Victoria, Australia.

Leptaena scissa Davidson, 1871: 325 *pars*; pl. 47, figs 21–23 *non* figs 24, 25 from U. Haverford Mudstone Formation (L. Llandovery), Haverfordwest, Dyfed, Wales, a senior subjective synonym of *Plectambonites segmentum* var. *woodlandensis* Reed, 1917: 881; pl. 14, figs 36–41 from Woodland Formation (L. Llandovery), Woodland Point, Girvan, Scotland, and *Plectambonites scissa* var. *triangularis* Holtedahl, 1916: 84; pl. 15, figs 5–6 from Solvik Formation (L. Llandovery), Asker, Norway (all revised Cocks 1970: 158; pl. 1, figs 11–14; pl. 2, figs 1–14; pl. 3, figs 2–14; pl. 4, figs 1–4 and Temple 1987: 55; pl.5, figs 1–8).

Leptaena segmentum Lindström, 1861: 374 from Mulde Beds (U. Wenlock), Djupvik, Gotland, Sweden (revised Cocks 1970: 162; pl. 3, fig. 1; pl. 4, figs 7–12).

Leptelloidea septata Cooper, *in* Schuchert & Cooper 1930: 272; pl. 1, figs 9–13 from U. Ashgill Beds, Grande Coupe, Percé, Quebec, Canada.

Leptelloidea sholeshookensis Jones, 1928: 488; pl. 25, fig. 19 from Slade and Redhill Mudstones (M. Ashgill), Lower Cresswell, Dyfed, Wales.

Plectambonites tennesseensis Foerste, 1903: 708 from Waldron Shale (Wenlock), Clifton, Tennessee, USA.

Tufoleptina tufogena Havlíček, 1961: 449; pl. 1, figs 1–6 from U. Liten Shale (U. Wenlock), Svaty Jan pod Skalou, Bohemia, Czechoslovakia (revised Havlíček 1967: 33; pl. 1, figs 1–7).

SPECIES QUESTIONABLY ASSIGNED

Sowerbyella transversalis brevis Northrop, 1939: 176; pl. 15, figs 11–14 from Clemville Formation (L. Wenlock), Clemville, Gaspé, Quebec, Canada (no interiors known, but by its shape almost certainly a *Leangella*).

Leangella hubeiensis Chang, 1983: 478; pl. 1, figs 27–31 from Miaopo Formation (U. Llandeilo–L. Caradoc), Huanghuachang, Yichang County, Hubei Province, China (no brachial valve known).

Leptelloidea (*Leangella?*) *lamellata* Reed, 1936: 44; pl. 4, figs 22–23 from Naunkangyi Formation (L. Caradoc), hill behind Taunggyi, Southern Shan States, Burma (no brachial valve interior figured, but pedicle valve interior looks more like a sowerbyellid).

Diambonia ? *leifi* Spjeldnaes, 1957: 79; pl. 2, figs 9–11 from *Mastopora* Zone (Caradoc), Stranda, Langesund-Gjerpen district, Norway (interior poorly figured).

Orthis quinquecostata M^{c}Coy, 1846: 33; pl. 3, fig. 8 from U. Llandovery rocks of Coolin or Kilbride, Co. Galway, Ireland (no interiors figured; discussed Cocks, 1978: 95).

Leangella yichangensis Chang, 1983: 478; pl. 1, figs 32–34 from Miaopo Formation (U. Llandeilo–L. Caradoc), Huanghuachang, Yichang County, Hubei Province, China (no brachial interior known).

SPECIES REJECTED

Leangella magna Ushatinskaya, *in* Misius & Ushatinskaya 1977: 115; pl. 27, figs 1, 2 from Saribypakskaya bed (M. Llandovery), Jhelesken Hill, Kazakhstan, USSR (genus uncertain, brachial valve lacks platform).

Diambonia miaopoensis Chang, 1983: 477; pl. 1, figs 12, 17 from Miaopo Formation (U. Llandeilo–L. Caradoc), Huanghuachang, Yichang County, Hubei, China (genus uncertain).

LEANGELLA (LEPTESTIINA) Havlíček, 1952

1952 *Benignites* (*Leptestiina*) Havlíček: 412
1965 *Leptestiina* Williams: H378 *pars* (*non Dulankarella*)

TYPE SPECIES. *Benignites* (*Leptestiina*) *prantli* Havlíček, 1952.

DIAGNOSIS. Like *Leangella* (*Leangella*) except that the 'platform' is made up anteriorly of discrete septules which are not merged to form a typical continuous platform.

REMARKS. From the type species of *Leptestiina* (e.g. Havlíček 1967: pl. 2, fig. 18) it is clear that a typical platform is absent. However, the row of discontinuous septules where a platform might be is clear indication of the very close relationship between *Leangella* and *Leptestiina*. This is further reinforced by the populations illustrated by Melou (1971: pls 1 and 2) in which a true platform is weakly developed laterally, but not anteriorly, where only septules are found; and the same is true of the population figured by Sheehan (1973: pl. 1).

SPECIES ASSIGNED

Leptestiina aonensis Melou, 1971: 95; pl. 1, figs 1–6; pl. 2, figs 1–3 from Rosan Tuffs (L.–M. Ashgill), Ster ar Poul Men, Brittany, France (transitional to *Leangella* (*Leangella*)).

Leptelloidea derfelensis Jones, 1928: 479; pl. 25, figs 3–7

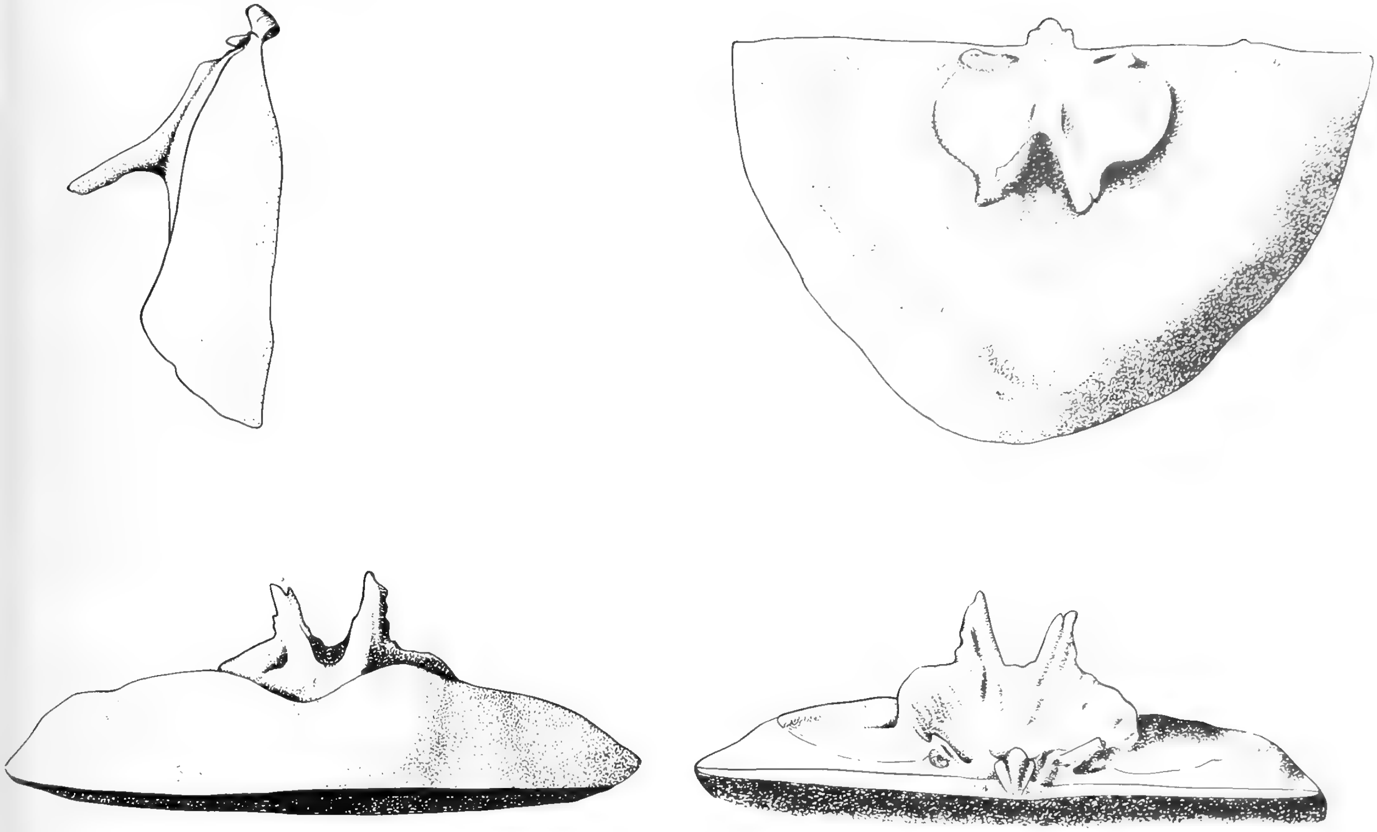


Fig. 77 *Leangella* (*Leangella*) *gibbosa* (Winchell & Schuchert, 1892), from Stewartville Formation (L. Ashgill), between Stewartville and Chatville, Minnesota, USA, lateral downward, anterior and posterior views of a brachial valve interior, based on BC 7272, × 9.

(revised Melou 1971: 99; pl. 2, figs 4–9) from Derfel Limestone (L. Caradoc), Derfel Gorge, Wales.

Leptestiina meloui Havlíček, 1981: 20; pl. 7, figs 1–10 from M.–U. Caradoc rocks, Gabian, Montagne Noire, France.

Sampo oepiki Whittington, 1938: 255; pl. 10, figs 15–16; pl. 11, fig. 10 from Longvillian beds (M. Caradoc), Bryngwyn Hill, Llanfyllin, Powys, Wales (revised Williams, 1963: 428; pl. 10, figs 15, 16, 19–21).

Benignites (*Leptestiina*) *prantli* Havlíček, 1952: 412; text–fig. 1 from Králův Dvůr Shales (M. Ashgill), Králův Dvůr, Bohemia, Czechoslovakia (revised Havlíček 1967: 30; pl. 2, figs 16, 18).

Leptestiina sp. of Hurst 1979: 276; figs 399, 403, 407, 408 from Acton Scott Formation (U. Caradoc), Acton Scott, Shropshire, England.

SPECIES QUESTIONABLY ASSIGNED

Leptestiina longxianensis Fu, 1982: 117; pl. 34, figs 13–16 from U. Pingliang Formation (L. Caradoc), Shiguancun, Longxian County, Shaanxi Province, China (no adequate interior known for generic assignment).

LEPTESTIA Bekker, 1922

Figs 78, 79

1922 *Leptestia* Bekker: 362
1930 *Leptestia* Öpik: 123
1965 *Leptestia* Williams: H373

TYPE SPECIES. *Leptestia musculosa* Bekker, 1922.

DIAGNOSIS. With elongate bema. With platform.

REMARKS. This is the only genus within this family which has an elongate bema (apart from the denticulate *Sampo*) and is therefore easy to recognize.

SPECIES ASSIGNED

Strophomena jukesii Davidson, 1869: 296; pl. 37, figs 23–26 from beds of Caradoc age, Grangegeeth, Co. Meath, Ireland.

Leptestia musculosa Bekker, 1922: 363; text-figs 1–4 from L.-M. Kuckruse Formation (L. Caradoc), Kohtla-Järve, near Tallinn, Estonia, USSR.

SPECIES QUESTIONABLY ASSIGNED

Leptestia cita Rukavishnikova, 1956: 130; pl. 2, figs 4–7 from Kopalinsky Horizon (Llanvirn), Kyandysai, Chu-Ili Mountains, Kazakhstan, USSR (interiors poorly known).

Leptestia diaphanes Öpik, 1930: 130; pl. 7, fig. 80 from L.–M. Kuckers Formation (L. Caradoc), Kohtla, near Tallinn, Estonia, USSR (only pedicle valve figured – may be synonym of *L. musculosa*).

Leptestia sp. of Bekker 1922: 364; text-fig. 5 from Rakvere Formation (Caradoc–Ashgill), Rakvere, Estonia, USSR (only pedicle valve known).

Leptestia sp. of Xu & Liu 1984: 204; pl. 14, figs 12–14 from U. Meitan Formation (U. Arenig), Tongzi County, N. Guizhou, China (no platform visible).

SPECIES REJECTED

Leptestia (*Leptoptilum*) *bekkeri* Öpik, 1930: 131; pl. 8, fig. 81 from U. Kukruse Formation (L. Caradoc), Kohtla, near Tallinn, Estonia, USSR (see *Leptoptilum*).

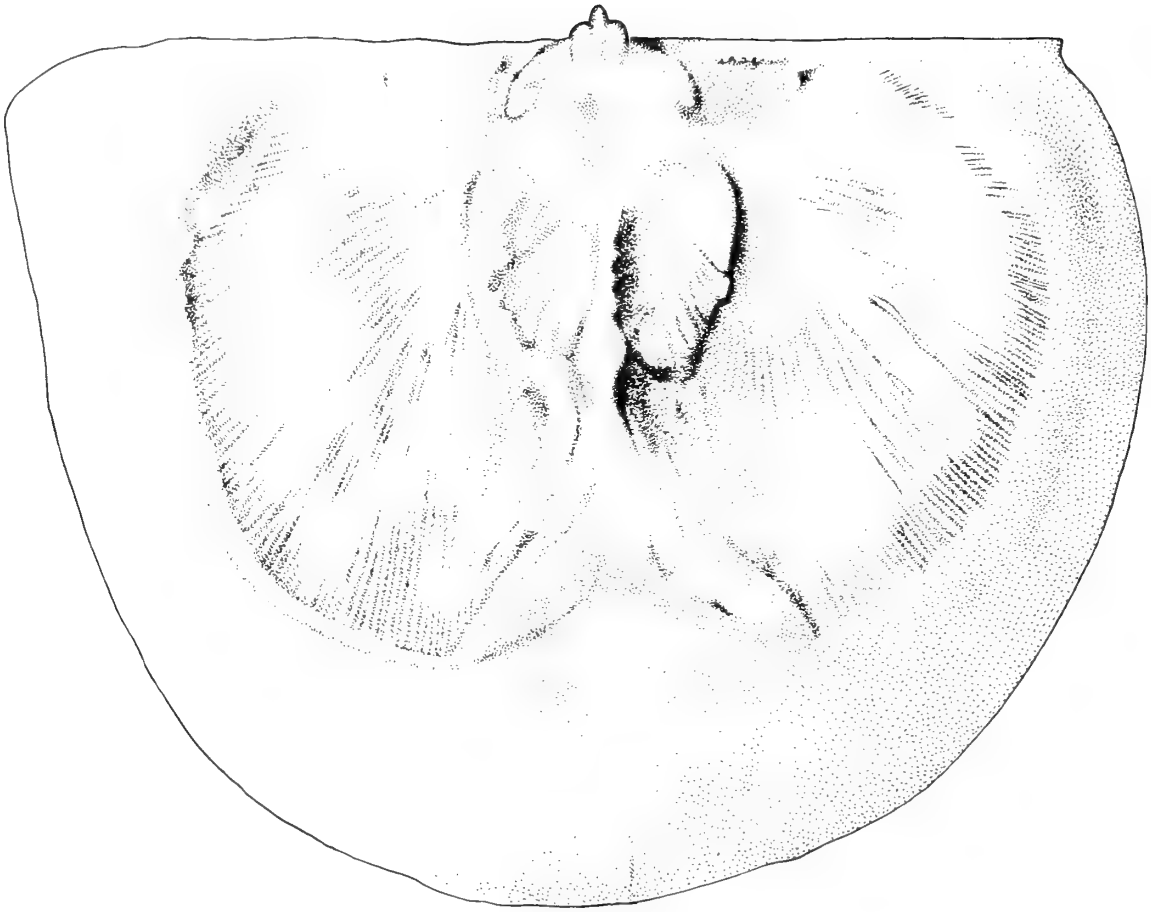


Fig. 78 *Leptestia musculosa* Bekker, 1922, from Kukruse Formation (L. Caradoc), Kohtla-Järve, Estonia, USSR, brachial valve interior, based on BB 5189, × 6.

RURAMBONITES gen. nov.

Figs 80–84

TYPE SPECIES. *Plectambonites ruralis* Reed, 1917.

DIAGNOSIS. Bema transverse and not bilobed, in contrast to the bilobed elongate bema of *Sampo*. Denticulate hinge line.

REMARKS. Öpik (1933) and others have placed *ruralis* within *Sampo*. However, we feel that the shapes of the bemas in the two genera are so different that generic separation is appropriate. We illustrate here the lectotype and additional topotype specimens (Figs 80–84). The denticles are on the pedicle valve and the pits on the brachial valve, as in *Sowerbyella (Eochonetes)*.

SPECIES ASSIGNED

Sampo hiiuensis Öpik, 1933: 36 *pars*; pl. 8, fig. 5 only from F_1 Beds (U. Caradoc–L. Ashgill), Korgessaare, Hiiumaa, Estonia, USSR.

Sampo molodovensis Tsegelniuk, 1976: 60; pl. 8, figs 4–9 from Subochskaya Formation (U. Ordovician), Komarov, Podolia, Ukraine, USSR.

Plectambonites ruralis Reed, 1917: 879; pl. 14, figs 25–33 from Upper Drummuck Group (U. Ashgill), Starfish Bed, Girvan, Scotland.

SAMPO Öpik, 1933

1933 *Sampo* Öpik: 35
1965 *Sampo* Williams: H378

TYPE SPECIES. *Sampo hiiuensis* Öpik, 1933.

DIAGNOSIS. Bema elongate and bilobed. Like *Bilobia* but with denticulate hinge line.

REMARKS. In both brachial valves illustrated by Öpik (1933: pl. 7, fig. 3 and pl. 8, fig. 4) the anterior end of the bema finishes irregularly, with two main calcite platforms and additional straggly septules. It is difficult both to describe these structures unambiguously and also to assess properly their systematic significance. New collections of topotype *Sampo hiiuensis* are needed to assess properly the true variation of the bema. The disposition of the denticles is the same as in *Rurambonites*.

SPECIES ASSIGNED

Sampo hiiuensis Öpik, 1933 *pars*: 36; pl. 6, figs 4, 5; pl. 7, figs 1–3; pl. 8, fig. 4, *non* fig. 5 from Nabala Beds (U. Caradoc–L. Ashgill), Moe, Estonia, USSR.

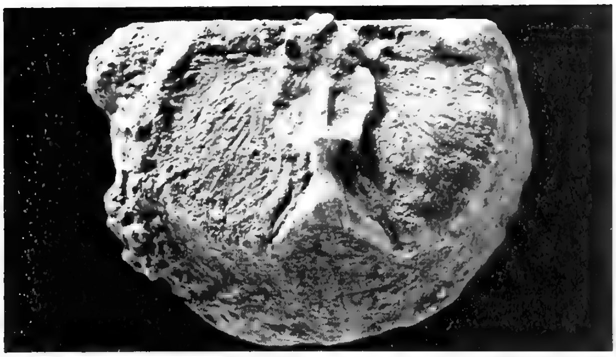
SPECIES QUESTIONABLY ASSIGNED

Sampo hiiuensis var. *mucronata* Öpik, 1933: 39; fig. 2E from Rakvere Formation (U. Caradoc), Pühalepa, Hiiumaa, Estonia, USSR (no interiors known).

Sampo hiiuensis var. *nasuta* Öpik, 1933: 39; pl. 8, fig. 3 from Vormsi Formation (L. Ashgill), Korgessaare, Estonia, USSR (only exterior known).

SPECIES REJECTED

Sampo indentata Spjeldnaes, 1957: 69; pl. 2, figs 15–16; pl. 4, fig. 8 from 4bγ beds (M. Caradoc), west of Billingstad, Asker, Norway (to *Bilobia*).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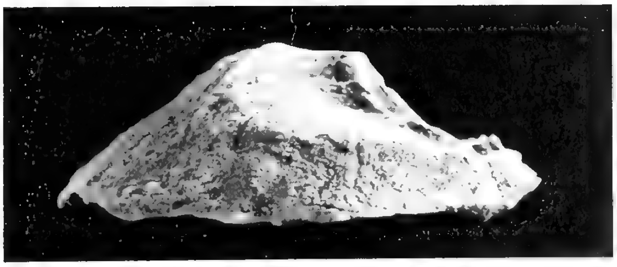
79b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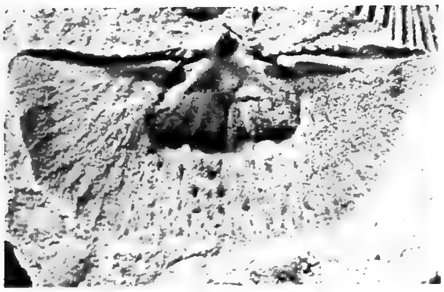
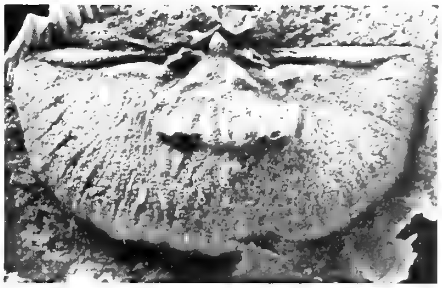

81a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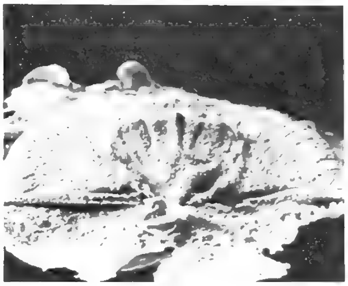
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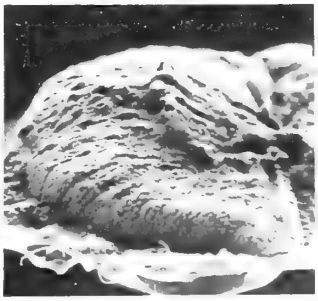
82a


82b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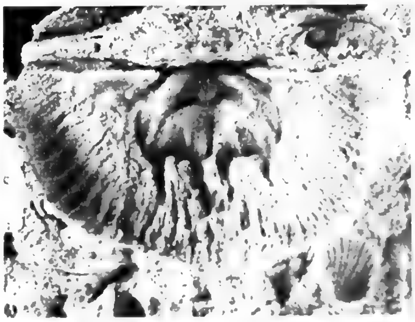
83a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83c

Fig. 79 *Leptestia musculosa* Bekker, 1922, topotype from Kukruse Formation (L. Caradoc), Kohtla-Järve, Estonia, USSR, downward, posterior and lateral views of brachial valve, BB 5189, × 3.

Figs 80–83 *Rurambonites ruralis* (Reed, 1917) gen. nov., topotypes from Starfish Bed, South Threave Formation (Ashgill: U. Rawtheyan), 650 m ENE of South Threave Farmhouse, Girvan, Strathclyde, Scotland. Fig. 80, natural internal mould of pedicle valve, BC 7202, × 3·5; Fig. 81 natural internal mould and three views of a latex cast of a brachial valve, BC 7200, × 3; Fig. 82, natural internal mould and latex cast of a brachial valve, BC 7201, × 4; Fig. 83, latex cast, natural internal mould and posterior view of latex cast of a brachial valve interior, BC 7204, × 4

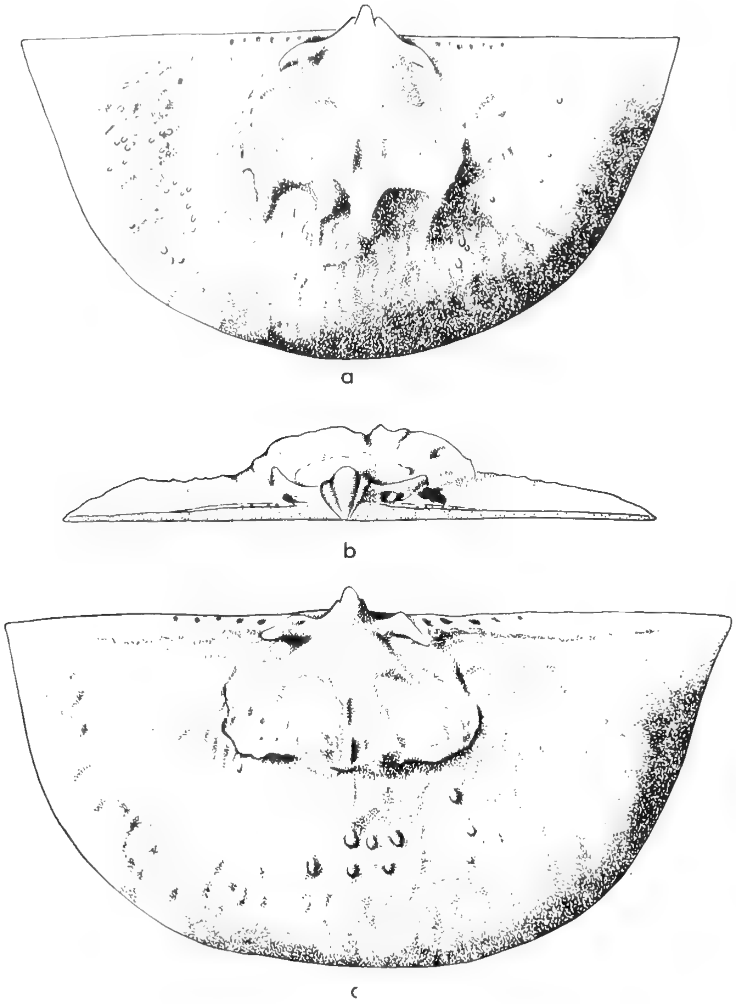


Fig. 84 *Rurambonites ruralis* (Reed, 1917) gen. nov., from Starfish Bed, South Threave Formation (Ashgill: U. Rawtheyan), Girvan, Strathclyde, Scotland, showing the bema variation in the interiors of two brachial valves (a, b after BC 7204, c after BC 7200), × 5.

Sampo oepiki Whittington, 1938: 255; pl. 10, figs 15, 16; pl. 11, fig. 10 from beds of Longvillian (M. Caradoc) age, Bryngwyn Hill, Llanfyllin, Powys, Wales (to *Leptestiina*).

Family **XENAMBONITIDAE** Cooper, 1956

1956	Xenambonitinae Cooper: 813
1965	Xenambonitinae Williams: H381
1965	Aegiromeninae Williams: H381 *pars*
1967	Sowerbyellidae Havlíček: 37 *pars*

Diagnosis. Cardinal process undercut. With variably developed bema. No side septa.

Remarks. Cooper's subfamily is elevated here to familial level to differentiate the group from the Sowerbyellidae, which possess side septa. The Xenambonitidae is divided into two subfamilies based on the elevated bema of the Xenambonitinae as opposed to the weak bema of the Aegiromeninae, which sometimes consists only of disconnected septules, and the presence or absence of a platform.

Subfamilies assigned. Xenambonitinae Cooper, 1956; Aegiromeninae Havlíček, 1964.

Range. Llandeilo–Pridoli.

Subfamily **XENAMBONITINAE** Cooper, 1956

1956	Xenambonitinae Cooper: 813
1965	Xenambonitinae Williams: H381

Diagnosis. Like Aegiromeninae, but with platform. Bema elevated.

Remarks. At first glance, xenambonitinines are apparently rather different from aegiromenines in possessing a strong platform (absent in aegiromenines) and an elevated bema, rather than the weak and never elevated bema seen in aegiromenines. However, we put both within the same family because of the presence in both groups of an undercut cardinal process and a bema and because of the absence of side septa.

Genus assigned. *Xenambonites* Cooper, 1956.

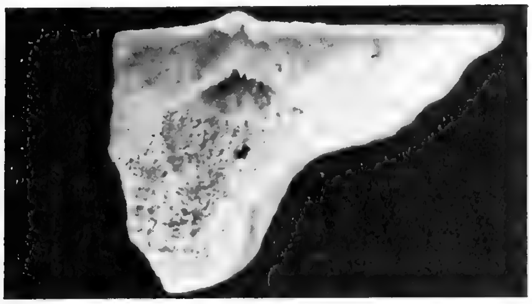
Range. Llandeilo–Caradoc.

XENAMBONITES Cooper, 1956

Figs 85, 86

1956	*Xenambonites* Cooper: 813
1965	*Xenambonites* Williams: H381

Type species. *Xenambonites undosus* Cooper, 1956.



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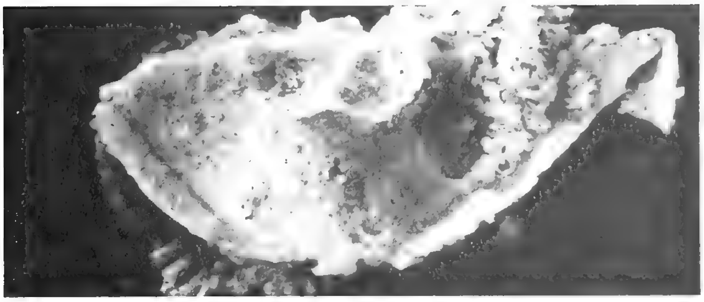

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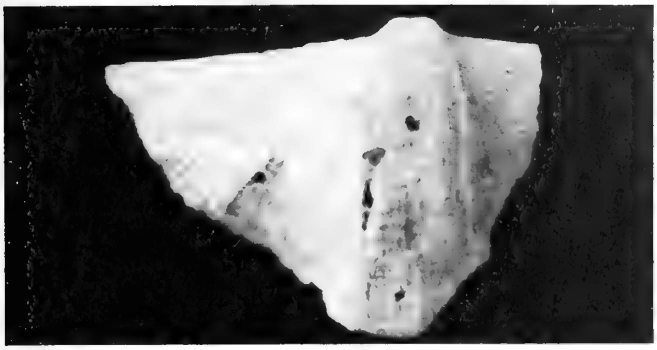

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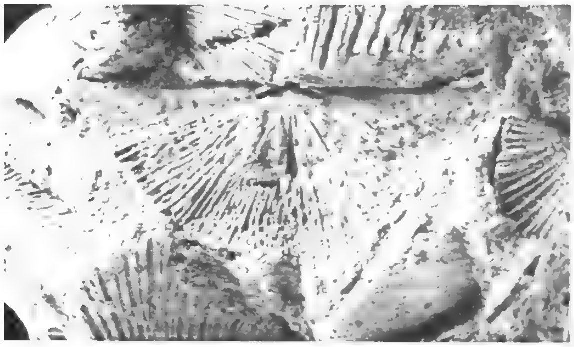

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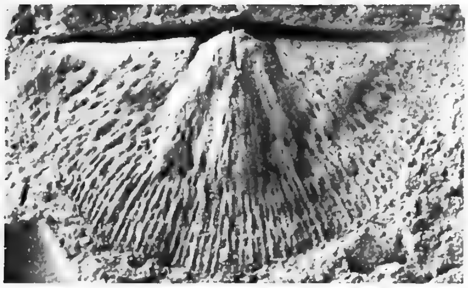

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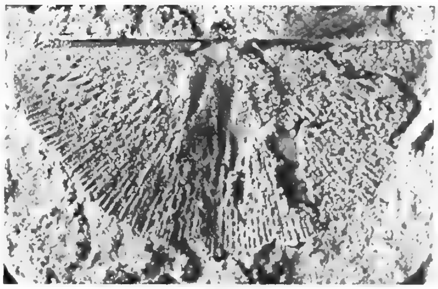

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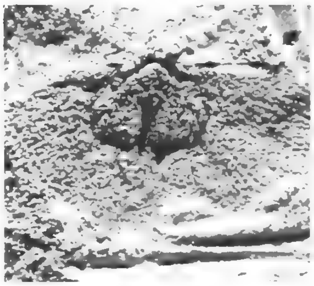

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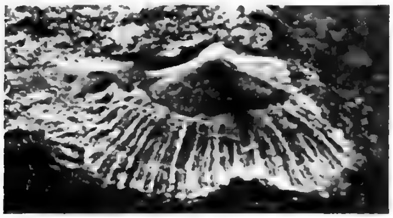

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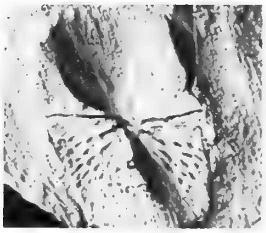

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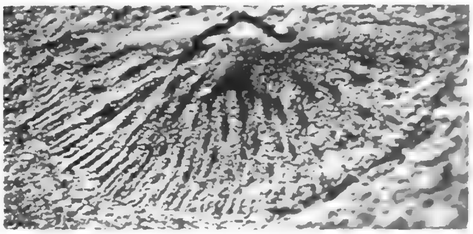

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Figs 85, 86 *Xenambonites undosus* Cooper, 1956, topotypes from Pratt Ferry Formation (Llandeilo), SE of Pratt Ferry, Blocton, Alabama, USA. Fig. 85, interior and exterior views of a silicified pedicle valve, BC 10293, × 12; Fig. 86, interior of a silicified brachial valve, BC 10292, × 9.

Figs 87–89 *Aegiria* (*Aegiria*) *aquila aquila* (Barrande, 1848), from Zahorany Formation (M. Caradoc), Bohemia, Czechoslovakia. Fig. 87, natural internal mould of brachial valve from Palmovka, Praha-Libeň, BC 7212, × 4; Fig. 88, natural internal mould of pedicle valve from Beroun, BB 13658, × 5; Fig. 89, natural internal mould of brachial valve from Sporilov, Prague, BB 33341, × 5.

Fig. 90 *Aegiria* (*Aegiria*) *aquila praecursor* Havlíček, 1952, from Letná Formation (L. Caradoc), Blyskava Hill, near Chrustenice, Czechoslovakia, natural internal mould of brachial valve, BC 6831, × 6.

Fig. 91 *Aegiria* (*Aegiria*) *garthensis* (Jones, 1928), topotype from Lower Llandovery beds, north of Garth, Powys, Wales, natural internal mould of brachial valve, GSM 50418, × 7.

Figs 92, 93 *Chonetoidea papillosa* (Reed, 1905), from Slade and Redhill Mudstone Formation (M. Ashgill), Upper Slade, near Haverfordwest, Dyfed, Wales. Fig. 92, natural internal moulds of conjoined valves, SMA 11313, × 4; Fig. 93, lectotype (selected Cocks 1970: 194), the original of Reed 1905: pl. 23, fig. 13, natural internal mould of a brachial valve, SMA 11311, × 10.

DIAGNOSIS. As for family. With ventral fold and dorsal sulcus. Geniculate anteriorly towards pedicle valve.

REMARKS. *Xenambonites* is a very distinctive plectambonitacean and is given a subfamily of its own here, although we believe that the geniculation by itself is a generic rather than a familial character.

SPECIES ASSIGNED

Xenambonites revelatus Williams, 1962: 191; pl. 18, figs 21–23 from Balclatchie Conglomerate (L. Caradoc), Penwhapple Burn, Girvan, Scotland.

Xenambonites cf. *X. revelatus* of Ross & Dutro 1966: 16; pl. 2, figs 21–26 from beds of Caradoc age, Hard Luck Creek, Alaska, USA.

Xenambonites undosus Cooper, 1956: 815; pl. 195, figs 17–31; pl. 268, figs 25–38 from Pratt Ferry Formation (Llandeilo), Pratt Ferry, Alabama, USA.

Subfamily **AEGIROMENINAE** Havlíček, 1961

1961 Aegiromeninae Havlíček: 450
1965 Aegiromeninae Williams: H381
1967 Aegiromeninae Havlíček: 37

DIAGNOSIS. Like Xenambonitinae, but without platform. Variably developed bema, but never elevated.

REMARKS. The lack of platform differentiates this subfamily from the Xenambonitinae and the Hesperomenidae, to which the Aegiromeninae is, nevertheless, closely related. Although the absence of a bema would generally make us assign some specimens or populations of *Chonetoidea* and *Jonesea* to another family such as the Hesperomenidae, there is no doubt that the occasional loss of the bema is a secondary characteristic in the family and for this reason these forms are classified unhesitatingly within the Aegiromeninae. Even though *Aegiromena* is here considered a junior synonym of *Aegiria*, the subfamily name Aegiromeninae still stands.

GENERA ASSIGNED. *Aegiria* (*Aegiria*) Öpik, 1933, including *Aegiromena* Havlíček, 1961; *Aegiria* (*Aegironetes*) Havlíček, 1967; *Aegiria* (*Epelidoaegiria*) Strusz, 1982; *Chonetoidea* Jones, 1928, including *Sentolunia* Havlíček, 1967 and *Sericoidea* Lindström, 1953; *Jonesea* gen. nov.; *Mezounia* Havlíček, 1967.

RANGE. Llandeilo (*Aegironetes minuta*) to Pridoli (*Jonesea mariaformis*).

AEGIRIA (AEGIRIA) Öpik, 1933
Figs 87–91, 94

1933 *Aegiria* Öpik: 55
1961 *Aegiromena* Havlíček: 450
1965 *Aegiria* Williams: H381
1967 *Aegiromena* Havlíček: 39
1970 *Aegiria* Cocks: 195

TYPE SPECIES. *Aegiria norvegica* Öpik, 1933. The type species of *Aegiromena* is *Leptaena aquila* Barrande, 1848.

DIAGNOSIS Differs from *Mezounia* in the transverse bema, which is not bilobed anteriorly. Bema always present.

DISCUSSION. Now that the distinctive species centering around '*Aegiria*' *grayi* are now distinguished as a separate genus, *Jonesea* gen. nov. herein (p. 127), it is very clear that the type species of *Aegiria*, *A. norvegica*, cannot usefully be distinguished generically from *Aegiromena*, and so the two genera are placed in synonymy here. Havlíček (e.g. 1967: 39) separated the two genera on the relative strengths of what we term the bema, but in our opinion there is continuous variation in bema strength, both between species and even in the same population (e.g. *A. descendens* figured by Havlíček 1967: pl. 4) and we cannot separate them generically (see also Rong & Yang 1981: 171).

SPECIES ASSIGNED

Leptaena aquila Barrande, 1848: 228; pl. 22, figs 15, 16 from Zahoraný Formation (M. Caradoc), Praskolesy, Bohemia, Czechoslovakia (revised Havlíček 1967: 39; pl. 3, figs 1–14) and subspecies *Aegiria aquila praecursor* Havlíček, 1952: 401; pl. 1, figs 3, 4, 8 from Letná Formation (L. Caradoc), Chrustenice, Czechoslovakia (revised Havlíček 1967: 42; pl. 4, figs 1–6).

Aegiromena convexa Chang, 1981: 562; pl. 1, fig 28 from Kuanyinchiao Bed, U. Wufeng Formation (U. Ashgill), Huanghuachang, Yichang, W. Hubei Province, China (revised Rong 1984: 148; pl. 11, figs 1–9).

Aegiromena corolla Havlíček & Branisa, 1980: pl. 2, figs 1–6 from Llanvirn Sandstone, Tuctapari, Bolivia.

Aegiria descendens Havlíček, 1952: 402; pl. 2, figs 1–9 from Bohdalec Formation (U. Caradoc), Velká Chuchle, Czechoslovakia (revised Havlíček 1967: 43; pl. 4, figs 7–16).

Chonetoidea garthensis Jones, 1928: 500; pl. 25, figs 25, 26 from Lower Llandovery beds, north of Garth, Dyfed, Wales (revised Cocks 1970: 195; pl. 17, figs 4–7 and Temple 1987: 70; pl. 5, figs 16–21).

Aegiria grayi [*non A. grayi* (Davidson)] Rong, Xu & Yang, 1974: 203; pl. 95, figs 30–31 from U. Xiushan Formation (U. Llandovery), Leijiatun, Shiqian County, NE Guizhou, China (a new species also figured Yang & Rong 1982: 423; pl. 1, figs 17–23 from the same locality).

Aegiromena guichenensis Melou, 1973: 259; pl. 36, fig. 7 from ? Llandeilo schists, Traveusot, Brittany, France.

Aegiromena ? *mariana* Drot, *in* Chauvel *et al.* 1970: 618; pl. 13, figs 14, 14a (revised Melou 1973: 254; pl. 33, figs 1–5; pl. 34, figs 1–8; pl. 35, figs 1–9; pl. 36, figs 1–3) from Bed 13 (Llandeilo–Caradoc), El Centenillo, Sierra Morena, Spain (also refigured Villas 1985: 91; pl. 20, figs 11–18).

Orthis (*Dalmanella*) *meneghiniana* Vinassa, 1927: 461; pl. 2, figs 28–35 (revised Havlíček 1981: 22, pl. 7, figs 11–18) from Portixeddu Formation (U. Caradoc), Gùtturu màndara o punta Giovasanna, Sardinia, Italy.

Aegironetes minuta Xu, Rong & Liu, 1974: 152; pl. 66, figs 9–12 from Shihtzipu Formation (Llandeilo), Zunyi, N. Guizhou Province, China.

Aegiria norvegica Öpik, 1933: 55; pl. 10, figs 1–5; pl. 11, figs 3–5 from the Solvik Formation (L. Llandovery), Leangen, Asker, Norway.

Aegiria shiqianensis Yang & Rong, 1982: 423; pl. 1, figs 7–16 from U. Xiushan Formation (U. Llandovery), Leijiatun, Shiqian County, NE Guizhou, China.

SPECIES QUESTIONABLY ASSIGNED

Aegiria noriiskensis Lopushinskaya, 1976: 38; pl. 3, figs 9–14 from *Dalmanella neocrassa* beds (M. Llandovery), S. Pyasinskaya, N. Siberia, USSR (no interiors figured).

SPECIES REJECTED

Aegiromena durbenensis Nikitin, *in* Nikitin *et al.* 1980: 52; pl. 13, figs 16–22 from Durben Formation (U. Ashgill), Durben, Chu-Ili Mountains, Kazakhstan, USSR (to *Jonesea* gen. nov.).

Aegiromena incerta Wan, 1982: 41; pl. 11, figs 19, 20 from Shihniulan Formation (U. Llandovery), Guanyinqiao, Qijiang County, Sichuan Province, SW China (to *Jonesea* gen. nov.).

Aegiria mariaformis Lenz, 1977*a*: 67; pl. 8, figs 6–9, 12–21 from L. Road River Formation (Pridoli), Royal Creek, Yukon, Canada (to *Jonesea* gen. nov.).

Aegiromena praeultima Mikuláš, 1983: 5; pl. 1, figs 1–9 from Podolí iron ore horizon of Králův Dvůr Formation (L.–M. Ashgill), Vlnitá ulice, Praha-Braník, Czechoslovakia (to *Jonesea* gen. nov.).

Aegiromena ultima Marek & Havlíček, 1967: 281; pl. 3, figs 9–12 from Kosov Formation (U. Ashgill), Bechovice, Czechoslovakia (to *Jonesea* gen. nov.).

Aegiromena urbana Havlíček, 1967: 44; pl. 4, figs 24–26 from Králův Dvůr Formation (L.–M. Ashgill), Praha-Podoli, Czechoslovakia (to *Jonesea* gen. nov.).

Aegiria thomasi Talent, 1965: 24; pl. 6, figs 1, 3, 5–7 from Dargile Formation (Ludlow), Heathcote, Victoria, Australia (to *Jonesea* gen. nov.).

Aegiromena yanheensis Rong & Yang, 1981: 171; pl. 2, figs 17–25 from Leijaitung Formation (U. Llandovery), Ganxi, Yanhe County, NE Guizhou Province, China (to *Jonesea* gen. nov.).

AEGIRIA (AEGIRONETES) Havlíček, 1967

1967	*Aegironetes* Havlíček: 46

TYPE SPECIES. *Strophomena tristis* Barrande, 1879.

DIAGNOSIS. Like *Aegiria* (*Aegiria*), but lacking dental plates.

REMARKS. Havlíček (1967: 47) lists the differences between *Aegiromena* (which we now include in *Aegiria*) and *Aegironetes*. Four of the five differences are either non-existant or only of specific importance, but the absence of dental plates in *Aegironetes*, as opposed to the 'short, divergent' dental plates of *Aegiromena* we consider important enough to warrant subgeneric distinction.

SPECIES ASSIGNED

Aegironetes minuta Xu, Rong & Liu, 1974: 152; pl. 66, figs 9–12, from Shihtzipu Formation (Llandeilo), Zunyi, N. Guizhou Province, China.

Strophomena tristis Barrande, 1879, *pars*: pl. 70, figs 6:1 (*non* figs 6:2–4) from Králův Dvůr Formation (L.–M. Ashgill), Kosov, Czechoslovakia (revised Havlíček 1967: 47; pl. 4, figs 17–23).

AEGIRIA (EPELIDOAEGIRIA) Strusz, 1982

1982	*Aegiria* (*Epelidoaegiria*) Strusz: 115

TYPE SPECIES. *Aegiria* (*Epelidoaegiria*) *chilidifera* Strusz, 1982.

DIAGNOSIS. Like *Aegiria* (*Aegiria*) but with hinge line denticulate. Small chilidium present.

REMARKS. Strusz (1982: 115) distinguished *Epelidoaegiria* from *Aegiria* in (a) possessing unequally parvicostellate ornament, (b) possessing a chilidium and (c) in being denticulate. We find that the ornament among plectambonitaceans can be very variable, even within the same subgenus, and discount that feature. The 'chilidium' in *Epelidoaegiria* may better be termed chilidial plates (Strusz 1982: fig. 9 A3) and also occurs in '*Aegiromena*' (Havlíček 1967: 39). However, we regard *Epelidoaegiria* as a valid subgenus of *Aegiria* because of its denticulate hinge line.

SPECIES ASSIGNED

Aegiria (*Epelidoaegiria*) *chilidifera* Strusz, 1982: 116; fig. 9 A–G, 10 A–H from Walker Volcanics (Wenlock), Canberra, Australia.

Stropheodonta minuta Mitchell, 1923: 470; pl. 41, figs 22–25 from Lower Trilobite Bed of Hume Series (Ludlow?), Bowning, New South Wales, Australia.

Aegiria sugiyamai Tachibana, 1976: 37; pl. 5, figs 1–24; pl. 6, figs 3–6; pl. 7, fig. 3 from Kawanchi Series (Wenlock–Ludlow), Kusayami-zawa, Ofunato, Japan.

CHONETOIDEA Jones, 1928
Figs 92, 93, 95

1928	*Chonetoidea Jones: 393*
1933	*Chonetoidea* Öpik: 51
1953	*Sericoidea* Lindström: 134
1957	*Chonetoidea* Spjeldnaes: 104
1965	*Chonetoidea* Williams: H383
1965	*Sericoidea* Williams: H383
1967	*Chonetoidea* Havlíček: 48
1967	*Sericoidea* Havlíček: 51
?1967	*Sentolunia* Havlíček: 53
1970	*Chonetoidea* Cocks: 192
1977	*Chonetoidea* Mitchell: 93
1979	*Sericoidea* Percival: 113
1979	*Sericoidea* Hurst: 280

TYPE SPECIES. *Plectambonites papillosa* Reed, 1905. Type species of *Sericoidea* is *Leptaena sericea* var. *restricta* Hadding, 1913. Type species of *Sentolunia* is *S. senta* Havlíček 1967, a probable subjective junior synonym of *Chonetes radiatula* Barrande, 1879.

DIAGNOSIS. As for family. Like *Jonesea* gen. nov. but with elongated septules rather than circular papillae. Bema usually absent.

REMARKS. Lindström (1953: 134) differentiated *Sericoidea* from *Chonetoidea* on the basis of 'a slit-like adductor scar' in the pedicle valve which 'has not, as far as I know, been observed in *Chonetoidea*'; however, the adductor scars in *Chonetoidea* are the same when developed. Lindström and Williams (1962: 189; 1965: H383) also separated the two genera on the differentiated ornament of *Sericoidea* as compared with the equal parvicostellae of *Chonetoidea*. However, we have found considerable variation in the ornament, as has Mitchell (1977: 93–94), and also Hurst (1979: 281) 'felt that *Sericoidea* may prove to be a synonym of *Chonetoidea*'. In general there are fewer internal tubercles in *Sericoidea* than *Chonetoidea*, but there is tremendous variation in that character and we cannot separate the two genera. For example, in the population of *Chonetoidea radiatula* figured by Mitchell (1977: pl. 18) the juvenile in fig. 30 shows very

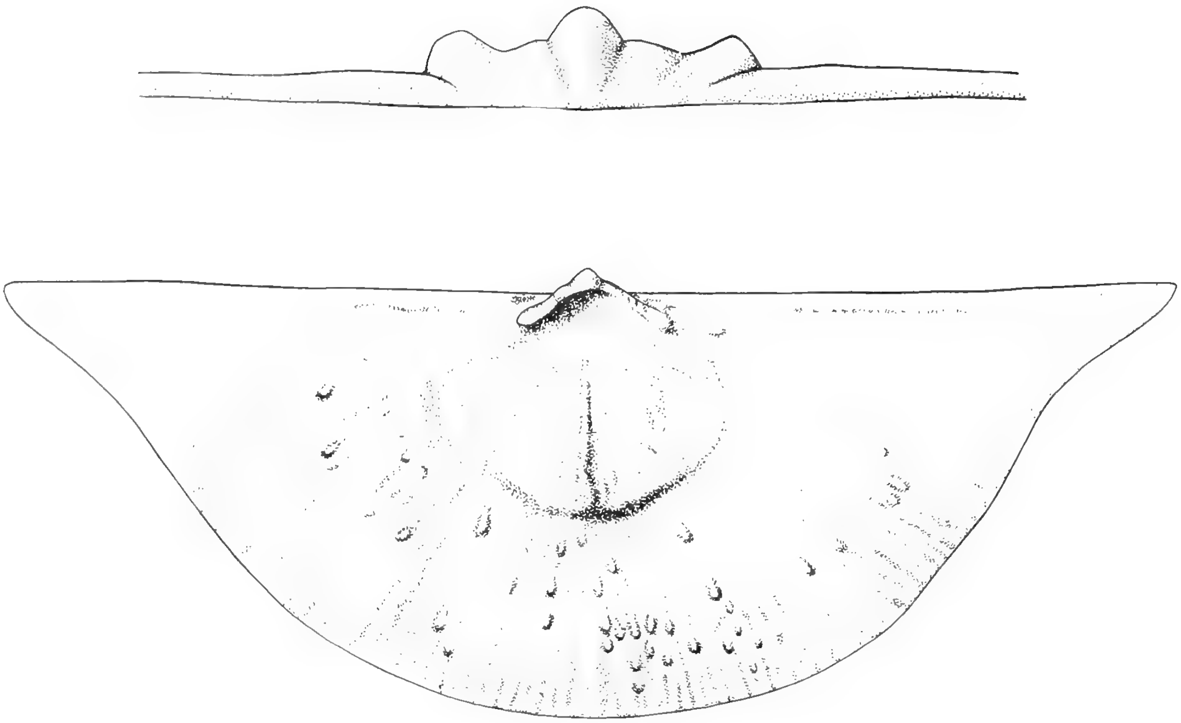


Fig. 94 *Aegiria* (*Aegiria*) *aquila aquila* (Barrande, 1848), from Zahoraný Formation (M. Caradoc), Palmovka, Praha-Libeň, Czechoslovakia; a, posterior view of cardinal process, × 25 and b, brachial valve interior, × 12 (based on BC 7212).

few papillae whilst the larger specimen in fig. 24 shows a great number. In addition, some species show many papillae in all their specimens, whilst in other species papillae can be uncommon. Young & Gibbons (1983) also discuss the problem and conclude that *Chonetoidea* and *Sericoidea* should be regarded as synonyms.

Only two specimens are known of *Sentolunia senta* (Havlíček, 1967: 53), one pedicle valve and one brachial valve. In the brachial valve the bema is more obvious and continuous than in the specimens of *Chonetoidea radiatula* from the same formation and locality (Havlíček 1967: pl. 5). We are not certain whether or not *Sentolunia* is correctly synonymized with *Chonetoidea*, but until more specimens become available we think it most likely that these two specimens are at the extreme limit of the range of variation of *Chonetoidea radiatula*.

SPECIES ASSIGNED

Sericoidea abdita Williams, *in* Whittington & Williams 1955: 418; pl. 39, figs 83–85 from Derfel Limestone (L. Caradoc), Pont Aberderfel, Gwynedd, Wales.

Sericoidea abdita complicata Lockley, 1980: 212, figs 54–59 from Nod Glas Formation (U. Caradoc), Rhiw March, Llanymawddwy, Powys, Wales.

Chonetoidea gamma Spjeldnaes, 1957: 106; pl. 2, figs 12–13 from Zone 4b (Caradoc–Ashgill), Blakstad, Asker, Norway.

Sericoidea homolensis Havlíček, 1967: 52; pl. 8, figs 1–5 from Bohdalec Formation (M. Caradoc), near Kačerov, Czechoslovakia.

Chonetoidea iduna Öpik 1933: 52; pl. 10, figs 6, 7; pl. 11, figs 1, 2 from Zone 4c (L. Ashgill), Frognö, Ringerike, Norway.

Sericoidea miaopoensis Chang, 1983: 479; pl. 1, figs 7, 14, 15 from Miaopo Formation (U. Llandeilo–L. Caradoc), Huanghuachang, Yichang County, Hubei, China.

Sericoidea minor Percival, 1979: 113, figs 5A', 9–16 from Malongulli Formation (U. Caradoc), Copper Mine Creek, Cheesemans Creek, New South Wales, Australia.

Orthis nina Davidson, 1883: 177; pl. 13, fig. 11 from Whitehouse Group (Caradoc–Ashgill), Whitehouse Bay, Girvan, Scotland.

Plectambonites papillosa Reed, 1905: 451; pl. 23, figs 13–15 from Slade and Redhill Mudstone (M. Ashgill), Haverfordwest, Dyfed, Wales (revised Cocks 1970: 193; pl. 17, figs 1–3).

Chonetes radiatulus Barrande, 1879: pl. 54, fig. 1 from Králův Dvůr Shales (L.–M. Ashgill), Králův Dvůr, Czechoslovakia (revised Havlíček 1967: 49; pl. 5, figs 7–14), a probable subjective senior synonym of *Sentolunia senta* Havlíček 1967: 53; pl. 5, fig. 6 from the same formation and locality; probably also a senior synonym of *Chonetoidea tenerrima* Havlíček 1952: 404; pl. 3, figs 2, 5 (revised Havlíček 1967: 50; pl. 5, figs 1–5) from the same formation at various localities. *C. radiatula* and *C. tenerrima* appear to be large and small individuals of the same population.

Leptaena sericea var. *restricta* Hadding, 1913: 62; pl. 5, figs 29–32 from Lower Chasmops Beds (L. Caradoc), Fågelsång, Scania, Sweden, a senior subjective synonym of *Plectambonites sericea* var. *craigensis* Reed, 1917: 883; pl. 15, figs 12–17 from Craighead Limestone (U. Caradoc), Craighead, Girvan, Scotland (revised Williams 1962: 187; pl. 18, figs 5–9).

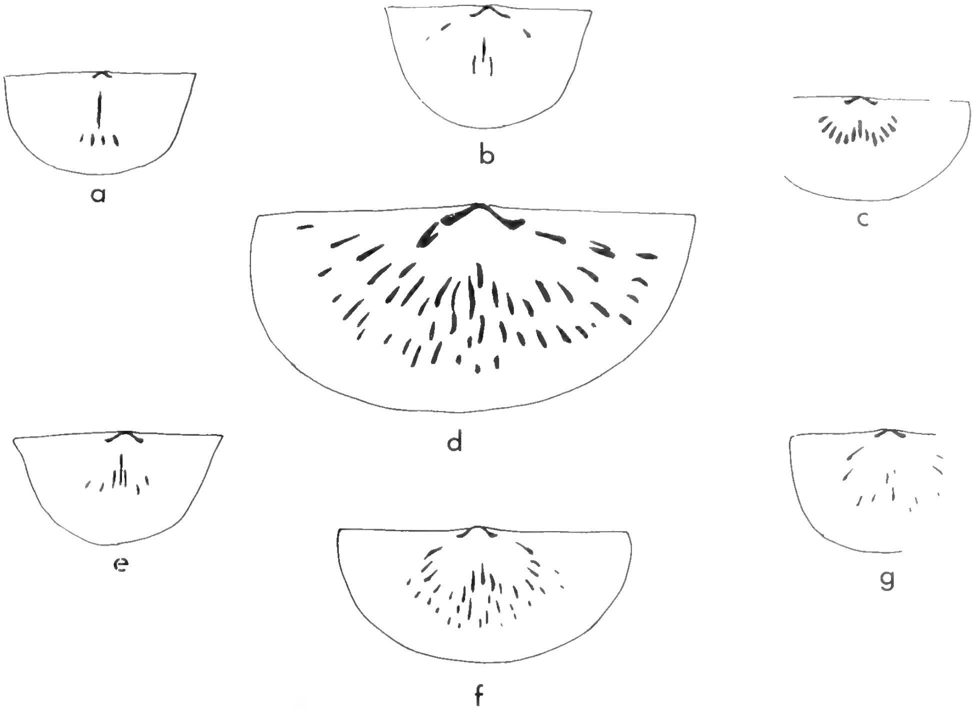


Fig. 95 Brachial valve interiors demonstrating all variants between *'Chonetoidea'* and *'Sericoidea'*. a, *'Sericoidea' minor* Percival, 1979, from Malongulli Formation (U. Caradoc), Copper Mine Creek, New South Wales, Australia (after Percival 1979: fig. 5.A12), × 5; b, *'Chonetoidea' tenerrima* Havlíček, 1952, from Králův Dvůr Shales (M. Ashgill), Vysebohý, Bohemia, Czechoslovakia (after Havlíček 1967: pl. 5, fig. 3), × 7; c, *'Chonetoidea' gamma* Spjeldnaes, 1957, from Zone 4bγ (Caradoc–Ashgill), Blakstad, Oslo, Norway (after Spjeldnaes 1957: pl. 2, fig. 12), × 4·5; d, *Chonetoidea papillosa* (Reed, 1905), from Slade and Redhill Mudstone Formation, Haverfordwest, Wales (after Cocks 1970: pl. 17, fig. 1), × 10; e, *'Chonetoidea' virginica* Cooper, 1956, from Edinburg Formation (L. Caradoc), Riverton, Virginia, USA (after Cooper 1956: pl. 215, fig. 33), × 5; f, g, *'Chonetoidea' radiatula* (Barrande, 1879), from Killey Bridge Formation (M. Ashgill), Pomeroy, Northern Ireland (after Mitchell 1977: pl. 18, figs 33, 30), × 7 and × 8.

Sericoidea sejuncta Percival, 1979: 113, figs 5A, 1–8 from Goonumbla Volcanics (U. Caradoc), Gunningbland, New South Wales, Australia.

Chonetoidea stoermeri Spjeldnaes, 1957: 108, fig. 24a from Zone 4aα (Llandeilo), Dalbo, Asker, Norway.

Chonetoidea virginica Cooper, 1956: 804; pl. 215, figs 30–33, from Edinburg Formation (L. Caradoc), Riverton, Virginia, USA.

SPECIES QUESTIONABLY ASSIGNED

Leptaena aequistriata Hadding, 1913: 62; pl. 5, figs 27, 28 from *Ogygiocaris* shales (Llanvirn–Llandeilo), Andersön, Scania, Sweden (no interiors illustrated).

Sericoidea hubeiensis Chang, 1983: 480; pl. 1, fig. 26 from U. Miaopo Formation (U. Llandeilo–L. Caradoc), Huanghuachang, Yichang County, Hubei, China.

Chonetoidea mohawkensis Howell, 1949: 7; pl. 2, figs 1–3 from Schenectady Formation (U. Caradoc), Rexford, New York, USA (no interiors illustrated).

Leptaena plicatella Ulrich, 1879: 15; pl. 7, figs 12–12c from Utica Shale with *Triarthrus becki* (M.–U. Caradoc), Cincinnati, Ohio, USA (no interiors known).

Sericoidea shanxiensis Fu, 1982: 118; pl. 34, figs 17–19 from Wufeng Formation (Ashgill), Yuanba, Nanzheng, Shaanxi Province, China (interiors poorly figured but brachial valve appears closer to *Kassinella* rather than *Sericoidea*).

Chonetoidea triangularis Reed, 1932*a*: 137; pl. 20, figs 8–11 from Hølandet Formation (Caradoc), Katuglåsen, Trondheim, Norway (no interiors known).

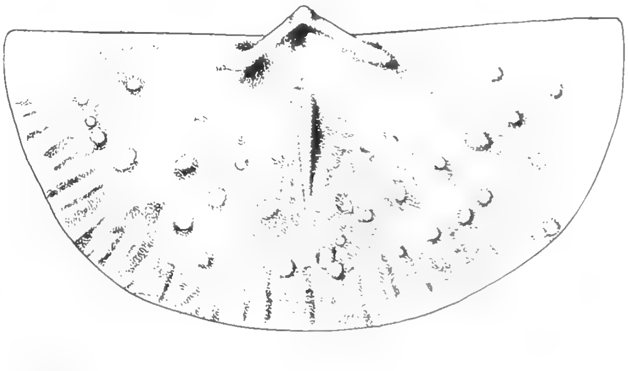


Fig. 96 *Jonesea grayi* (Davidson, 1849) gen. nov., interior of brachial valve, based on several specimens from the Ludlow of Shropshire, England, × 23.

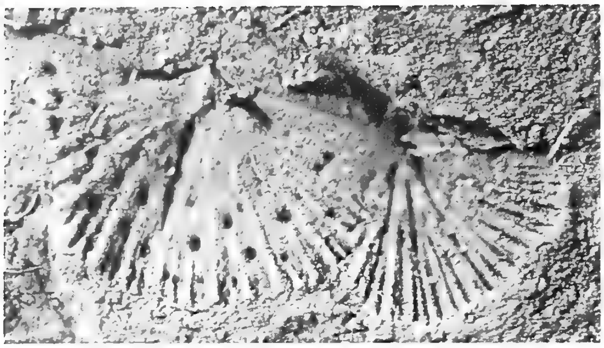
SPECIES REJECTED

Chonetoidea alpha Spjeldnaes, 1957: 107; pl. 2, figs 20–22 from Zone 4bα (U. Caradoc), Billingstad, Asker, Norway (assigned to *Aegiria*).

Chonetoidea (*Aegiria*) *nacta* Reed, 1952: 53; pl. 2, fig. 13 from Killey Bridge Formation (L. Ashgill), Pomeroy, Co. Tyrone, Northern Ireland (synonymized with *Sowerbyella thraivensis* Reed by Mitchell 1977: 81).

Chonetoidea garthensis Jones, 1928: 500; pl. 25, figs 25, 26 from Lower Llandovery Beds, N. of Garth, Dyfed, Wales (assigned to *Aegiria*).

Chonetoidea andersoni Johnson, Boucot & Murphy, 1976: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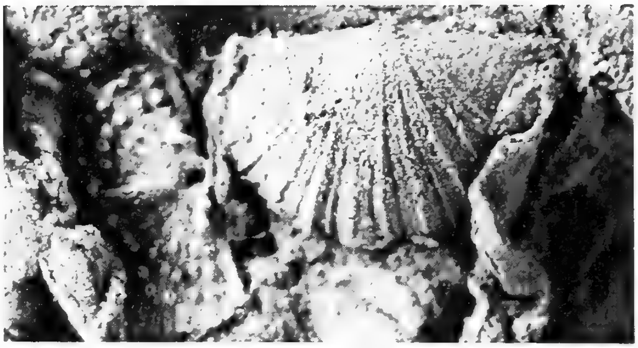
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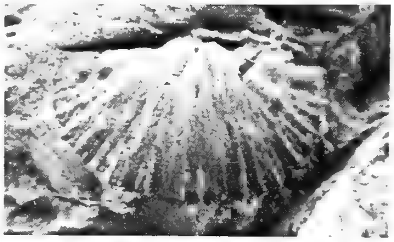
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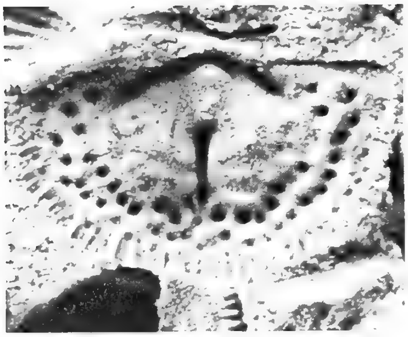
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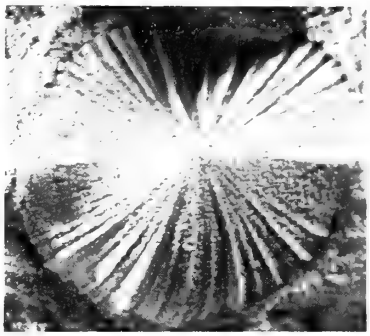
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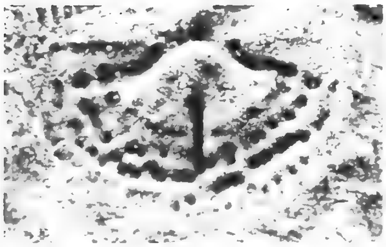
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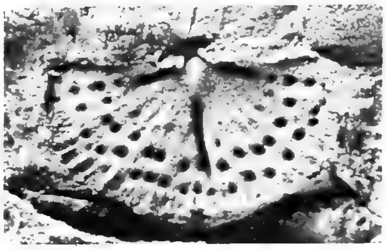
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Figs 97–106 *Jonesea grayi* (Davidson, 1849) gen. nov. Fig. 97, brachial valve interiors from Purple Shales (U. Llandovery), Onny River, Shropshire, England, OUM C12051–2, × 15; Fig. 98, latex cast of brachial valve interior and pedicle valve exterior from U. Rhydings Formation (M. Llandovery), Cefn Cerig Road, Llandovery, Dyfed, Wales, BB 32128, × 12; Fig. 99, exterior of conjoined valves from Purple Shales (U. Llandovery), Hughley, Shropshire, England, OUM C 13951, × 12; Fig. 100, natural internal mould of pedicle valve from Purple Shales (U. Llandovery), Domas, Shropshire, England, OUM C 13423, × 12; Fig. 101, natural internal mould of pedicle valve from 'Chonetoidea' Beds (M. Ludlow), Pont Shoni, Builth, Powys, Wales, BB 32430, × 9: Fig. 102, natural internal mould and latex cast of a brachial valve from U. Leintwardine Beds (M. Ludlow), Bengry Track, Ludlow, Shropshire, England, BC 10341, × 12; Fig. 103, latex cast of external moulds of conjoined valves from L. Bringewood Beds (U. Ludlow), Bengry track, Ludlow, Shropshire, BC 10343, × 12; Fig. 104, natural internal mould of brachial valve from U. Leintwardine Beds (M. Ludlow), Bengry track, Ludlow, Shropshire, BC 10340, × 12; Fig. 105, latex cast of internal mould of brachial valve from L. Bringewood Beds (U. Ludlow), Bengry track, Ludlow, Shropshire, BC 10375, × 12; Fig. 106, natural internal mould of brachial valve from L. Bringewood Beds (U. Ludlow), Bengry track, Ludlow, Shropshire, BC 10359, × 12.

58; pl. 20, figs 3–25 from Roberts Mountains Formation (Ludlow), Birch Creek, Roberts Mountains, Nevada, USA (to *Jonesea*).

Sericoidea postrestricta Kulkov, *in* Kulkov *et al.* 1985: 75; pl. 8, figs 1, 2 from Kizilchirinski Formation (M.–U. Llandovery), Chadan Section, Tuva, USSR (brachial valve interior different from *Chonetoidea* but true genus unknown).

JONESEA gen. nov.
Figs 96–106

TYPE SPECIES. *Leptaena grayi* Davidson, 1849. Named after O.T. Jones.

DIAGNOSIS. Like *Chonetoidea*, but with circular papillae rather than elongated. Sometimes septules with 2 prominent tubercles posterolaterally inside the pedicle valve.

REMARKS. Only *Kassinella* and *Trimurellina* within the Plectambonitacea also possess the pair of tubercles sometimes seen within the pedicle valve of *Jonesea* (e.g. Cocks 1970: pl. 17, fig. 13). The bema is usually absent, but is occasionally seen. The type species was previously assigned (e.g. Cocks 1970) to *Aegiria*, but the new genus differs from *Aegiria* in the virtual absence of a bema, as well as in possessing the prominent papillae and tubercles. It seems probable that systematic reassessment would much reduce the number of real species from the nominal list below.

SPECIES ASSIGNED

Chonetoidea andersoni Johnson, Boucot & Murphy, 1976: 58; pl. 20, figs 3–25 from Roberts Mountain Formation (Ludlow), Birch Creek, Roberts Mountains, Nevada, USA.

Aegiromena durbenensis Nikitin, *in* Nikitin *et al.* 1980: 52; pl. 13, figs 16–22 from Durben Formation (U. Ashgill), Durben, Chu-Ili Mountains, Kazakhstan, USSR.

Leptaena grayi Davidson, 1849: 271; figs 1, 1a from Much Wenlock Limestone (U. Wenlock), Dudley, West Midlands, England (revised Cocks 1970: 197; pl. 17, figs 8–14).

Aegiromena incerta Wan, 1982: 41; pl. 11, figs 19, 20 from Shihniulan Formation (U. Llandovery), Guanyinqiao, Oijiang County, Sichuan Province, SW China.

Chonetoidea luoheensis Su, 1980: 270; pl. 116, figs 5–10 from Luohe Formation (U. Ordovician), east side of Luohe River, Aihui County, Heilongjiang Province, NE China.

Aegiria mariaformis Lenz, 1677*a*: 67; pl. 8, figs 6–9, 12–21, from L. Road River Formation (Pridoli), Royal Creek, Yukon, Canada.

Aegiria cf. *mariaformis* Lenz, 1977*b*: 1536; pl. 5, figs 19, 22–28 from U. Whittaker Formation (Wenlock), Avalanche Lake, Mackenzie Mountains, Canada.

Aegiria mongoliensis Alekseeva, *in* Alekseeva & Erlanger 1983: 28; pl. 6, figs 5–10; pl. 12, figs 6–9 from Middle Silurian, River Yarmaty-Gol, NW Mongolia.

Orthis myrmido Barrande, 1879: pl. 64, fig. 1; pl. 127, fig. 7–1 from Liteň Formation (Wenlock), Dlouhá hora hill, near Beroun, Czechoslovakia (revised Havlíček 1967: 46; pl. 3, figs 15, 16).

Aegiromena praeultima Mikuláš, 1983: 5; pl. 1, figs 1–9 from Podolí iron ore horizon, Králův Dvůr Formation (L.–M. Ashgill), Vlnitá ulice, Praha-Branik, Czechoslovakia.

Aegiria thomasi Talent, 1965: 24; pl. 6, figs 1, 3, 5–7 from Dargile Formation (Ludlow), Heathcote, Victoria, Australia.

Aegiromena ultima Marek & Havlíček, 1967: 281; pl. 3, figs 9–12 from Kosov Formation (U. Ashgill), Běchovice, Czechoslovakia.

Aegiromena yanheensis Rong & Yang, 1981: 171; pl. 2, figs 17–25 from Leijiatun Formation (U. Llandovery), Ganxi, Yanhe County, NE Guizhou Province, China.

Aegiria sp. of Fu. 1982: 119; pl. 34, fig. 20 from Zhouqu Group (Wenlock), Xiaolianggou, Miaogou, Zhouqu County, Gansu Province, N. China (very similar to *J. mariaformis*).

SPECIES QUESTIONABLY ASSIGNED

Plectodonta aknistensis Rybnikova, 1967: 188; pl. 19, figs 1, 2 from L. Ludlow borehole in Latvia, USSR (no interiors known but exteriors the same as *Jonesea*).

Plectambonites aequalis Teichert, 1928: 58; pl. 5, figs 18–20 from Tamsal Formation (L.–M. Llandovery), Kiltsi, Estonia, USSR (only brachial valve interior figured is not clear in detail, but the pedicle valve external figured shows *Jonesea*-like ornament).

Sowerbyella austrum Öpik, 1953: 14; pl. 3, figs 17, 18 from Wapentake Formation (U. Llandovery), Heathcote, Victoria, Australia (almost certainly assigned, but no brachial interior known.)

MEZOUNIA Havlíček, 1967

1967 *Mezounia* Havlíček: 31

TYPE SPECIES. *Strophomena bicuspis* Barrande, 1879.

DIAGNOSIS. Like *Aegiria* but with bema bilobed anteriorly.

REMARKS. This genus was previously assigned by Havlíček (1967) to the Leptestiinidae, but the cardinal process is undercut (Havlíček 1967: pl. 2, fig. 14) and thus *Mezounia* is placed here within the Aegiromeninae.

SPECIES ASSIGNED

Strophomena bicuspis Barrande, 1879: pl. 128, figs 1–5 from Liteň Formation (Wenlock), Loděnice, Czechoslovakia (revised Havlíček 1967: 31; pl. 2, figs 7–10, 13–15).

Family ***HESPEROMENIDAE*** Cooper, 1956

1956 Hesperomeninae Cooper: 744
1963 Anoptambonitidae Rõõmusoks: 231
1967 Anoptambonitidae Havlíček: 35
1979 Anoptambonitidae Percival: 94

DIAGNOSIS. Cardinal process undercut. No bema. No side septa. With platform.

REMARKS. Although *Hesperomena* is based on only one specimen, nevertheless Cooper (1956: pl. 185) was able to illustrate both the external and internal details of both valves and the genus does not differ enough from *Anoptambonites* to allow us to separate them into two different families. In the *Treatise* (Williams 1965: H373), *Hesperomena* is allocated to the Leptestiinae, but there is no doubt from Cooper's illustrations and descriptions that it possesses an undercut cardinal process, which immediately separates it from *Leptestia* and its allies. Therefore, we are forced to promote Cooper's subfamily. Hesperomeninae to familial rank, which is a senior synonym of the Anoptambonitidae.

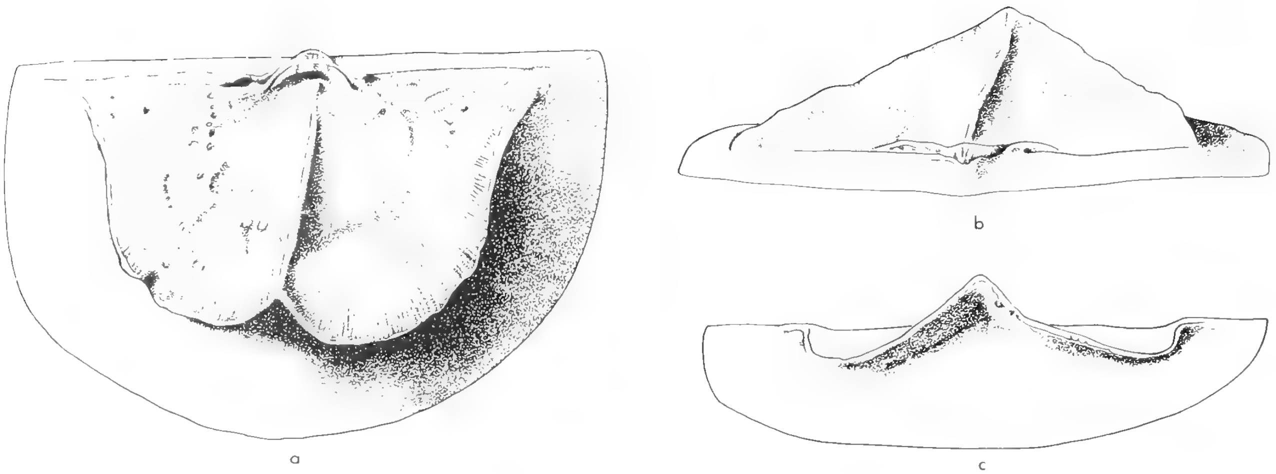


Fig. 107 *Anoptambonites grayae* (Davidson, 1883), downwards, posterior and anterior views of the brachial valve interior, from Craighead Limestone (U. Caradoc), Craighead, Girvan, Strathclyde, Scotland (based on BB 15869), × 2·5.

GENERA ASSIGNED. *Anoptambonites* Williams, 1962 (including *Chaganella* Nikitin, 1974); *Aulie* Nikitin & Popov, 1984; *Hesperomena* Cooper, 1956; *Kassinella* (*Kassinella*) Borrissiak, 1956 (including *Durranella* Percival, 1979); *Kassinella* (*Trimurellina*) Mitchell, 1977.

RANGE. U. Llanvirn (*Hesperomena leptellinoidea*) to M. Ashgill (*Kassinella moneta*).

ANOPTAMBONITES Williams, 1962
Figs 107–111

1962	*Anoptambonites* Williams: 170
1963	*Anoptambonites* Rõõmusoks: 233 *pars*
1965	*Anoptambonites* Williams: H376
1974	*Chaganella* Nikitin: 65

TYPE SPECIES. *Leptaena grayae* Davidson, 1883. The type species of *Chaganella* is *C. chaganensis* Nikitin, 1974.

DIAGNOSIS. Cardinal process striated posteriorly. With elevated platform. Small pedicle valve muscle scars restricted by bilobed muscle boundary ridges. No pedicle valve median septum. No posterolateral tubercles in ventral valve. With chilidium.

REMARKS. We can find no important points of difference in the morphologies of *Anoptambonites* and *Chaganella*, although Nikitin (1974) did not compare them, and thus we synonymize the two genera here.

SPECIES ASSIGNED

Chaganella chaganensis Nikitin, 1974: 66; pl. 6, figs 11–17 from L. Bestamak Formation (Llandeilo), Chagan River, Chinghiz Mountains, Kazakhastan, USSR.

Leptaena grayae Davidson, 1883: 171; pl. 12, figs 23–25 from Craighead Limestone (U. Caradoc), Craighead, Girvan, Scotland (revised Williams 1962: 171; pl. 16, figs 11–14, 17).

Anoptambonites grayae sibirica Severgina 1984*b*: 40; pl. 3, figs 6–11 from Chakirksi horizon (Ashgill), Gornoi Altai Mountains, USSR.

Anoptambonites orientalis Popov, 1980*b*: 149; pl. 2, figs 12–17 from Anderkenski horizon (U. Llandeilo–L. Caradoc), Anderken-Akchok, Chu-Ili Mountains, Kazakhstan, USSR.

Anoptambonites cf. *A. grayae* of Ross & Dutro 1966: 12; pl. 2, figs 1, 3, 5, 7, 9 from beds of Caradoc age, Hard Luck Creek, Alaska, USA.

Anoptambonites sp. of Mitchell 1977: 73; pl. 13, figs 21, 22, 24–29 from Killey Bridge Formation (L. Ashgill), Killey Bridge, Pomeroy, Northern Ireland.

SPECIES QUESTIONABLY ASSIGNED

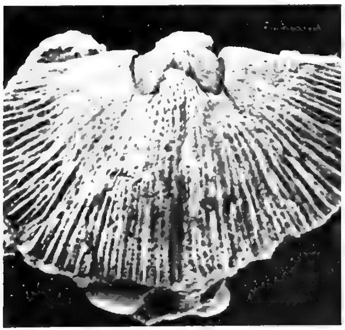
Anoptambonites aktasensis Nikitin & Popov, 1984: 147; pl. 18, figs 17–23 from Erkebinankski Horizon (Caradoc), Chinghiz Mountains, Kazakhstan, USSR (has pedicle valve platform and median septum in the brachial valve is much wider than in other *Anoptambonites*).

Fig. 108 *Anoptambonites* sp., natural internal mould of pedicle valve, the original of Williams 1962: pl. 16, fig. 10, from Balclatchie Conglomerate (L. Caradoc), Penwhapple Burn, Girvan, Strathclyde, Scotland, BB 25950, × 4.

Figs 109–111 *Anoptambonites grayae* (Davidson, 1883), topotypes from Craighead Limestone (U. Caradoc), Craighead, Girvan, Strathclyde, Scotland. Fig. 109, posterior and downward views of a pedicle valve interior, the original of Williams 1962: pl. 16, figs 11, BB 15868, × 3·5; Fig. 110, brachial valve interior, the original of Reed 1917: pl. 13, fig. 16, B 73410, × 3; Fig. 111, brachial valve interior, the original of Williams 1962: pl. 16, fig. 13, BB 15869, × 3·5.

Figs 112–114 *Kassinella* (*Kassinella*) sp. from China. Fig. 112, natural internal mould of brachial valve from L. Miapo Formation (Llandeilo), Huanghuachang, Yichang County, Hubei Province, BC 3307, × 14; Figs 113, 114, latex cast of brachial valve interior and natural internal mould of pedicle valve interior from Changwu Formation (M. Ashgill), hill to west of Jiangshan County, SW Zhejiang Province, NIGP 101836 and NIGP 101834, × 10.

Figs 115–117 *Kassinella* (*Kassinella*) *albida* (Reed, 1917), from Whitehouse Beds (Caradoc–Ashgill), Whitehouse Bay, Girvan, Strathclyde, Scotland. Fig. 115, natural internal moulds of conjoined valves, BB 92584, × 10; Fig. 116, natural internal mould of brachial valve, BB 92573, × 10; Fig. 117, natural internal mould of brachial valve, lectotype, selected Cocks 1978: 96, the original of Reed 1917: pl. 14, fig. 46, B 73542, × 10.



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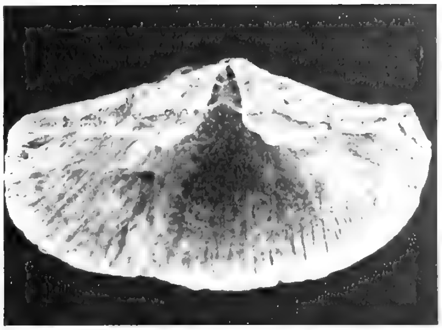

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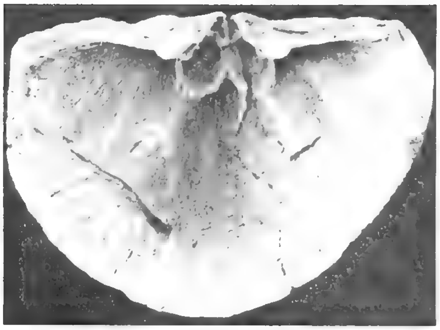

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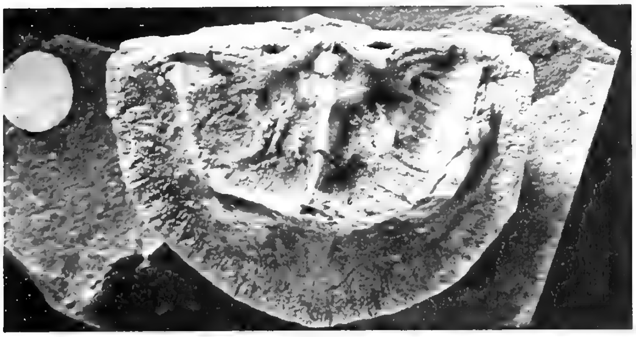

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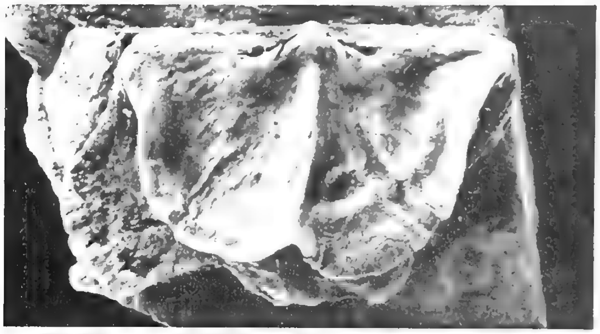

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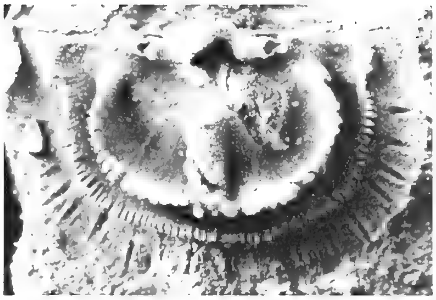

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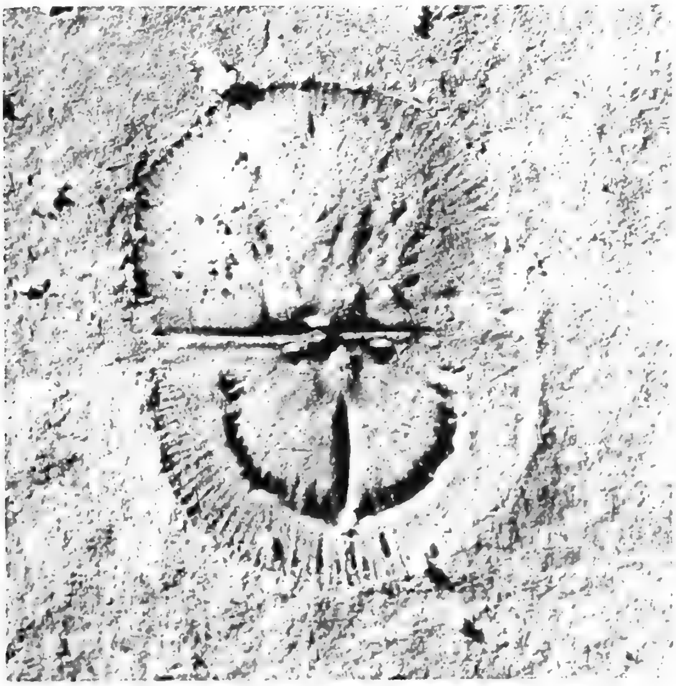

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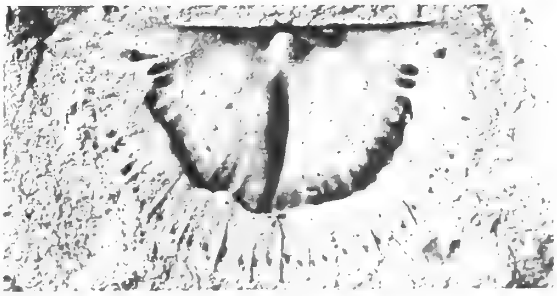

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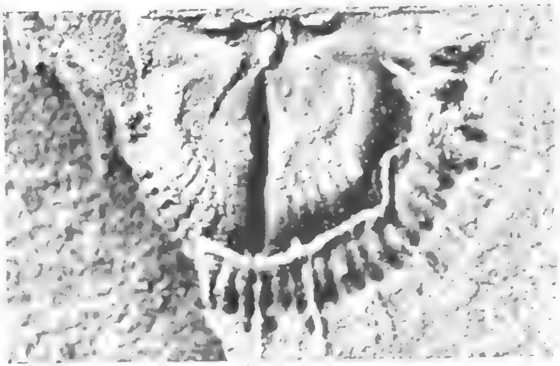


117

Rafinesquina carinata Holtedahl, 1916: 25; pl. 2, figs 4, 5 from 5a beds (M. Ashgill), Stavnaestangen, Ringerike, Norway. (No interiors figured by Holtedahl, but assigned to genus without illustrations by Rõõmusoks 1963: 233 and Havlíček 1967: 35).

SPECIES REJECTED

'Anoptambonites' incertus Xu, Rong & Lui, 1974: 153; pl. 66, figs 5, 6 from Chientsaokou Formation (L. Ashgill), Zunyi, N. Guizhou Province, China (allocated here to *Kassinella*).

Anoptambonites pirguensis Rõõmusoks, 1963: 233; pl. 1, figs 1–4 from Pirgu Formation (M. Ashgill), Pirgu River, Estonia, USSR (differs from *Anoptambonites* in brachial valve median septum being joined posteriorly to cardinal process and not reaching platform anteriorly: pedicle interior unknown: the true generic assignment requires re-investigation of a topotype population).

Strophomena quaesita Barrande, 1879: pl. 127, figs 2–3 from Králův Dvůr Shales (Ashgill), Kosov, Czechoslovakia (assigned to *Anoptambonites* by Havlíček 1967: 36; pl. 2, figs 17, 19, but subsequently made the type species of *Proboscisambon* Havlíček & Mergl, 1982 and reassigned to the Strophomenacea by Cocks & Rong 1988).

AULIE Nikitin & Popov, 1984

1984 *Aulie* Nikitin & Popov: 148

TYPE SPECIES. *Aulie convexa* Nikitin & Popov, 1984.

DIAGNOSIS. Like *Anoptambonites* but with brachial valve median septum extending a little anteriorly of platform and with pedicle valve muscle bounding ridges semicircular, not bilobed.

REMARKS. The length of the median septum in *Aulie* is variable anteriorly and if this feature was the only character distinguishing it from *Anoptambonites* then we would synonymize the two genera or consider them as two separate subgenera. However, the different shapes of the pedicle valve muscle field enables us still to treat them as separate.

SPECIES ASSIGNED

Aulie convexa Nikitin & Popov 1984: 149; pl. 17, figs 1–9 from Erkebidaiski horizon (U. Caradoc), Chinghiz Mountains, Kazakhstan, USSR.

HESPEROMENA Cooper, 1956

1956 *Hesperomena* Cooper: 744
1965 *Hesperomena* Williams: H373

TYPE SPECIES. *Hesperomena leptellinoidea* Cooper, 1956.

DIAGNOSIS. With weak platform. Large muscle scars in the pedicle valve.

REMARKS. *Hesperomena* differs from *Anoptambonites* in the lack of elevated platform and lack of bilobed muscle-bounding ridges in the pedicle valves. There are no posteriorly striated cardinal process or posterolateral tubercles in the pedicle valve.

SPECIES ASSIGNED

Hesperomena leptellinoidea Cooper 1956: 745; pl. 185, figs 1–10 from Antelope Valley Limestone, Pogonip Group (U. Llanvirn), Ikes Canyon, Roberts Mountains, Nevada, USA.

KASSINELLA (KASSINELLA) Borissiak, 1956

Figs 112–119

1956 *Kassinella* Borissiak: 50
1965 *Kassinella* Williams: H383
1979 *Durranella* Percival: 96
1979 *Kassinella* Percival: 101
1984 *Kassinella* Klenina: 86

TYPE SPECIES. *Kassinella globosa* Borissiak, 1956. Type species of *Durranella* is *D. septata* Percival, 1979.

DIAGNOSIS. Like *Aulie* but with peripheral rim developed and pedicle valve muscle-bounding ridges bilobed. Median septum well beyond platform, meeting, but not extending anteriorly of, the peripheral rim. No dental plates. Like *Trimurellina* but with brachial valve median septum not extending anteriorly of the platform. Peripheral rim variably developed. Posterolateral tubercles usually present in pedicle valve. Median septum always present in pedicle valve.

REMARKS. Percival (1979: 96) separated *Durranella* from *Kassinella* on the absence of posterolateral tubercles in the pedicle valve; however, these tubercles can be seen on the pedicle valve of both species of *Durranella* (e.g. Percival 1979: fig. 3A: 1, 2, 10, 11). In addition Percival said that the peripheral rim typical of *Kassinella* is only 'exceptionally and poorly' developed in *Durranella*, but the fact that it sometimes occurs does not enable us to separate the two genera. The peripheral rim is very variable in the type population of *Kassinella albida* (Reed), illustrated here (Figs 115–117) and is partly dependent on ontogeny. Even in the type species, *Kassinella globosa* (Borrissiak 1956: 50; pl. 12, figs 1c, 6) the peripheral rim is not developed.

SPECIES ASSIGNED

Plectambonites sericea var. *albida* Reed, 1917: 882; pl. 14, figs 42–46; pl. 15, figs 1–3 from Whitehouse Group (L. Ashgill), Whitehouse Bay, Girvan, Scotland.

Kassinella anisa Percival, 1979: 101, figs 5B: 1–3, 7A: 1–8 from Goonumbla Volcanics (U. Caradoc), Gunningbland, New South Wales, Australia.

Kassinella globosa Borissiak, 1956: 51; pl. 12, figs 1–7 from Ashgill Beds, Uly-Tay, Dzhezkazganski region, Kazakhstan, USSR.

'Anoptambonites' incertus Xu, Rong & Liu 1974: 153; pl. 66, figs 5, 6 from Chientsaokou Formation (L. Ashgill), Zunyi, N. Guizhou Province, China.

Strophomena moneta Barrande, 1879: pl. 57, fig. 6 from Králův Dvůr Formation (M. Ashgill), Kosov, Bohemia, Czechoslovakia (revised by Havlíček 1967: 35; pl. 2, figs 1–6 as *Anoptambonites moneta* including junior synonym *Orthis humillima* Barrande, 1879: pl. 69, fig. V-1 from the same horizontal locality).

Kassinella nana Klenina, 1984: 87; pl. 7, figs 2, 10; pl. 8, figs 20–27 from Taldiboiskaya Formation, bed tb_{iii} (Ashgill), River Taldiboi, Chinghiz Mountains, Kazakhstan, USSR.

Durranella rugosa Percival, 1979: 99, figs 3A: 10–20 from L. Malongulli Formation (L. Ashgill), Cliefden Caves, New South Wales, Australia.

Durranella septata Percival 1979: 97, figs 3A: 1–9 from Goomumbla Volcanics (U. Caradoc), Gunningbland, New South Wales, Australia.

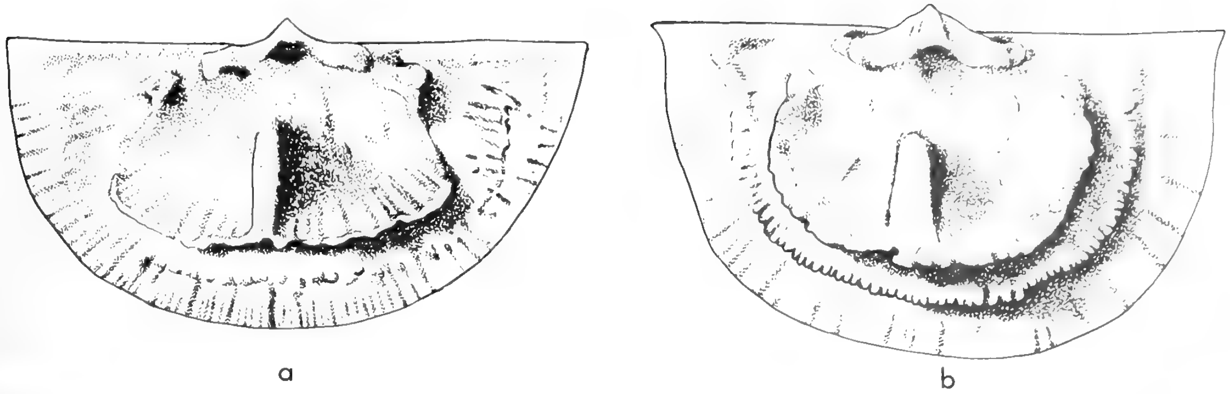


Fig. 118 *Kassinella* (*Kassinella*) sp. showing variation in the brachial valve interior from a population in the Changwu Formation (M. Ashgill), Jiangshan County, SW Zhejiang Province, China: a, after NIGP 101835, × 12; b, after NIGP 101836, × 12.

Chonetoidea simorini [Borissiak MS] Sokolskaya, 1960: pl. 27, figs 24, 25 from Middle Ordovician, N. Kazakhstan, USSR.

Anoptambonites sp. of Sheehan 1973: 62; pl. 2, figs 1, 2 from Jerrestad Mudstone (L. Ashgill), Fågelsång, Scania, Sweden.

SPECIES QUESTIONABLY ASSIGNED

Kassinella tschinghisensis Klenina, 1984: 87; pl. 8, figs 1–6 from Taldiboiskaya Formation, Bed tb_{iv} (Ashgill), River Taldiboi, Chinghiz Mountains, Kazakhstan, USSR (no interiors figured).

KASSINELLA (TRIMURELLINA) Mitchell, 1977
Figs 120–123

1977 *Trimurellina* Mitchell: 74

TYPE SPECIES. *Trimurellina superba* Mitchell, 1977.

DIAGNOSIS. Like *Kassinella* (*Kassinella*) but with brachial valve median septum extending anteriorly of the platform.

REMARKS. As stated in the remarks on *Kassinella* (*Kassinella*), the sub-peripheral rim is variably developed, but it is usually present in *K*. (*Trimurellina*) (except for the two specimens illustrated in Mitchell 1977: pl. 14, figs 3, 4). The brachial valve median septum is also variable in length, but only in *K*. (*Trimurellina*) does it regularly extend anteriorly beyond the platform, which is the basis for retaining a separate subgenus.

SPECIES ASSIGNED

Trimurellina superba Mitchell, 1977: 74; pl. 14, figs 1–16 from Killey Bridge Formation (L.–M. Ashgill), Killey Bridge, Pomeroy, Northern Ireland.

SPECIES QUESTIONABLY ASSIGNED

Trimurellina sp. of Williams & Wright 1981: 12, fig 4A from Wenallt Formation (Upper Ashgill), Wenallt, Garth, Powys, Wales.

Family **SOWERBYELLIDAE** Öpik, 1930

1930 Sowerbyellinae Öpik: 60
1938 Sowerbyellinae Ulrich & Cooper: 186
1953 Sowerbyellinae Williams: 8
1956 Sowerbyellidae Cooper: 774
1965 Sowerbyellidae Williams: H378 *pars*
1967 Sowerbyellidae Havlíček: 37 *pars*
1967 Dubioleptinidae Havlíček: 70
1970 Sowerbyellidae Cocks: 164

DIAGNOSIS. Undercut cardinal process. With side septa. With bema usually developed.

REMARKS. A bema is usually present in species assigned to this family, although it becomes better developed and thicker in gerontic individuals and is very often not seen in young specimens. In a few species it is not developed at all, for example in *Sowerbyella sinensis*, which on all other grounds

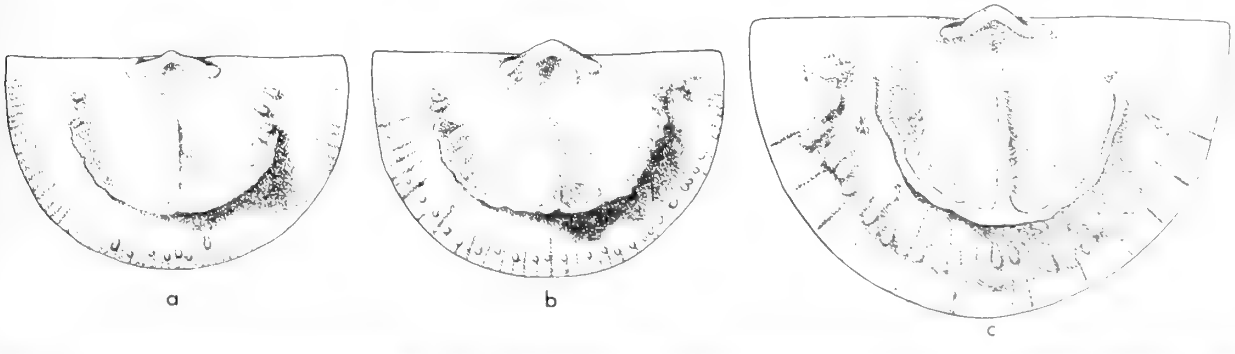
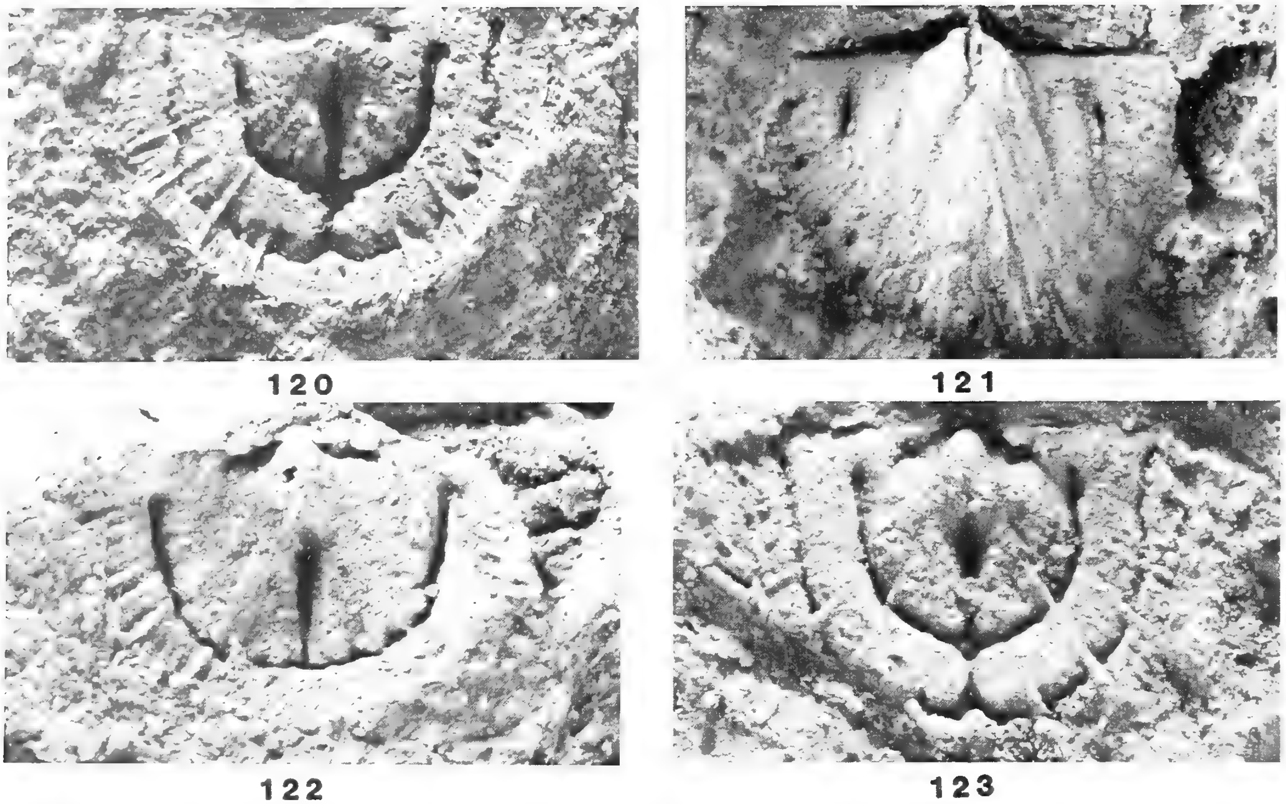


Fig. 119 *Kassinella* (*Kassinella*) *albida* (Reed, 1917), showing variation in the brachial valve interior in the topotype population from Whitehouse Beds (Caradoc–Ashgill), Whitehouse Bay, Girvan, Strathclyde, Scotland: a, after BB 92584; b, after BB 92573; c, after B 73542, the lectotype, all × 8.



Figs 120–123 *Kassinella* (*Trimurellina*) *superba* Mitchell, 1978, from Killey Bridge Formation (M. Ashgill), Pomeroy, Co. Tyrone, Northern Ireland. Fig. 120, natural internal mould of brachial valve, holotype, the original of Mitchell 1978: pl. 14, figs 5, 6, GSM GU 1109, × 18; Fig. 121, natural internal mould of pedicle valve, the original of Mitchell 1978: pl. 14, fig. 14, GSM GU 1113, × 20; Fig. 122, natural internal mould of brachial valve, the original of Mitchell 1978: pl. 14, fig. 3, GSM GU 1121, × 20; Fig. 123, natural internal mould of brachial valve, the original of Mitchell 1978: pl. 14, fig. 7, GSM GU 1124, × 20.

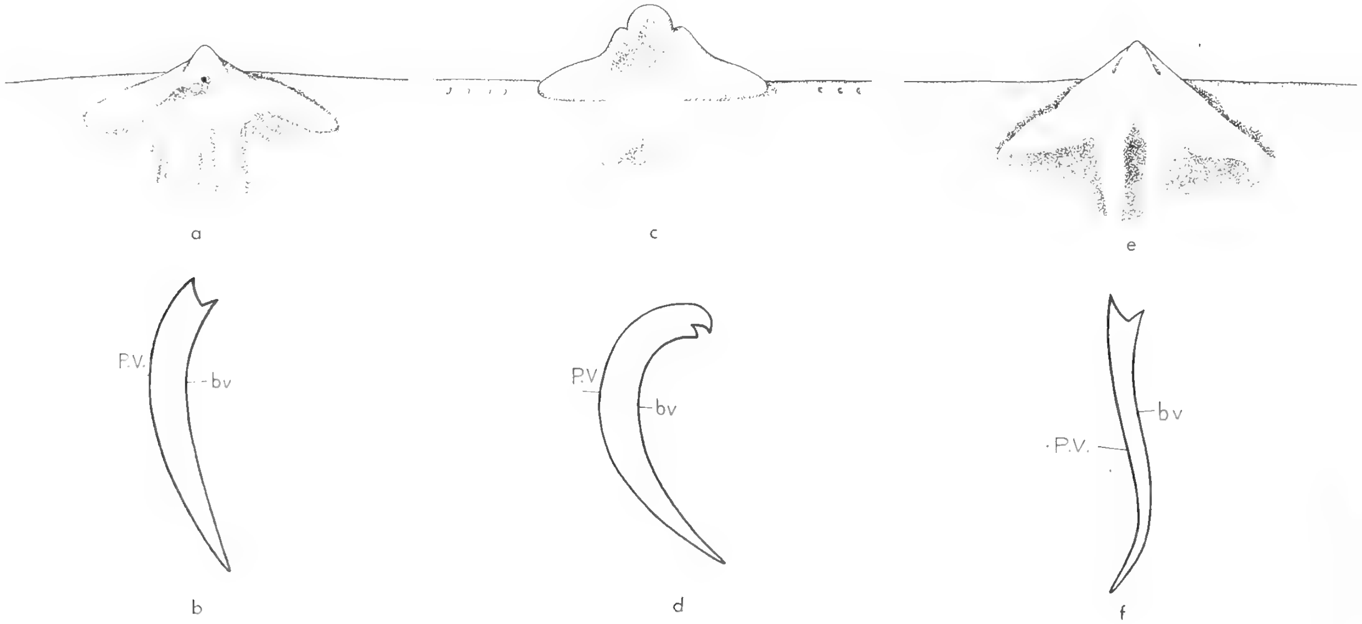


Fig. 124 Variation in the cardinal process and valve shape amongst various genera of Sowerbyellinae: a, b, *Sowerbyella eximia* Cooper, 1956, from Martinsburg Formation (L. Caradoc), Virginia, USA; c, d, *Eoplectodonta duvalii* (Davidson, 1847), from Slite Marl (Wenlock), Gotland, Sweden; e, f, *Gunningblandella resupinata* Percival, 1979, from Goonumbla Volcanics (U. Caradoc), New South Wales, Australia.

can be unequivocally assigned to *Sowerbyella*. In most of the species of *Sowerbyella* itself, including *S. sericea* the type species, the bema is well developed. The family is divided into three subfamilies on the division of the bema and whether or not the cardinal process is differentiated into a separate recognizable structure, or whether, as in the Craspedeliinae, it is totally fused and inseparable from the other central structures on the brachial valve hinge line.

SUBFAMILIES ASSIGNED. Sowerbyellinae Öpik, 1930; Craspedeliinae subfam. nov.; Ptychoglyptinae Cooper, 1956.

RANGE. Llanvirn to Eifelian.

Subfamily **SOWERBYELLINAE** Öpik, 1930

1965 Sowerbyellinae Williams: H378
1967 Sowerbyellinae Havlíček: 54
1970 Sowerbyellinae Cocks: 164

DIAGNOSIS. Bema divided. Cardinal process differentiated.

GENERA ASSIGNED. *Anisopleurella* Cooper, 1956; *Dubioleptina* Havlíček, 1967; *Eoplectodonta* (*Eoplectodonta*) Kozlowski, 1929, including *Ygera* Havlíček, 1961; *Eoplectodonta* (*Ygerodiscus*) Havlíček, 1967; *Eoplectodonta* (*Kozlowskites*) Havlíček, 1952; *Gunningblandella* Percival, 1979; *Plectodonta* (*Plectodonta*) Kozlowski, 1929; *Plectodonta* (*Plectodontella*) Havlíček, 1953; *Plectodonta* (*Dalejodiscus*) Havlíček, 1961; *Sowerbyella* (*Sowerbyella*) Jones, 1928, including *Viruella* Rõõmusoks, 1959; *Sowerbyella* (*Eochonetes*) Reed 1917, including *Thaerodonta* Wang, 1949; *Sowerbyella* (*Rugosowerbyella*) Mitchell, 1977.

RANGE. Llanvirn (*Sowerbyella antiqua*) to Eifelian (*Plectodonta comitans* and others).

ANISOPLEURELLA Cooper, 1956
Figs 125–127

1956 *Anisopleurella* Cooper: 804
1965 *Anisopleurella* Williams: H380
1970 *Anisopleurella* Cocks: 189

TYPE SPECIES. *Anisopleurella tricostellata* Cooper, 1956.

DIAGNOSIS. Prominent lateral side septa confined within suboval bema. No denticles on hinge line. Bema usually shorter than in *Eoplectodonta*. Median septum present in brachial valve. Like *Sowerbyella* but no prominent paired central side septa developed.

REMARKS. Cocks (1970: 190) drew attention to the presence of 'very faint crenulations' on the hinge line of some specimens of *A. gracilis*. Nevertheless, because of the very sporadic occurrence of these structures, we do not propose to recognize them generically; in particular we have not seen them on topotype specimens of *A. tricostellata* (Figs 125, 126), kindly presented in exchange by Dr G. A. Cooper.

SPECIES ASSIGNED

Plectambonites quinquecostata var. *balclatchiensis* Reed, 1917: 877; pl. 14, figs 4–9 from Balclatchie Mudstones (L. Caradoc), Balclatchie, Girvan, Scotland (revised Williams 1962: 185; pl. 17, figs 36, 37, 40, 41; pl. 18, figs 1–3), a senior synonym of P. *q. sublobata* Reed, 1917: 879; pl. 14, figs 10, 20–23 and of *Plectambonites praeteritus* Reed, 1945: 312; pl. 1, fig. 4, both from the same horizon and locality.

Sowerbyella gracilis Jones, 1928: 472; pl. 24, figs 21–25 from L. Haverford Mudstone Fm (U. Ashgill–L. Llandovery), Haverfordwest, Dyfed, Wales (revised Cocks 1970: 189; pl. 16, figs 1–9; Temple 1970: 38; pl. 8, figs 4–7, 10–13 and Temple 1987: 58; pl. 5, figs 9–15).

Anisopleurella inaequistriata Cooper, 1956: 805; pl. 193, figs 5–9 from M. Whitesburg Formation (Llandeilo), Bulls Gap, Tennessee, USA.

Eoplectodonta karina Spjeldnaes, 1957: 100; pl. 3, fig. 5 from 4bα Beds (M. Caradoc), south end of Nakholmen, Oslo, Norway.

Sowerbyella multiseptata Williams, *in* Whittington & Williams 1955: 416, figs 74–78 from the Derfel Limestone (L. Caradoc), Derfel, Gwynedd, Wales.

Anisopleurella novemcostata Nikitin, *in* Nikitin *et al.* 1980: 50; pl. 13, figs 13–15 from Durben Formation (U. Ashgill), Durben Well, Chu-Ili Mountains, Kazakhstan, USSR.

Anisopleurella ovalifera Havlíček, 1967: 55; pl. 6, figs 8, 9 from the Králův Dvůr Shales (Ashgill), Praha-Spořilov, Czechoslovakia.

Anisopleurella tricostellata Cooper, 1956: 806; pl. 193, figs 1–4; pl. 195, figs 1–5 from Pratt Ferry Formation (Llandeilo), Pratt Ferry, Alabama, USA.

SPECIES QUESTIONABLY ASSIGNED

Anisopleurella anceps Mitchell 1977: 86; pl. 17, figs 9–19 from Killey Bridge Formation (Ashgill), Killey Bridge, Pomeroy, Northern Ireland (if the specimens figured by Mitchell 1977: pl. 17, figs 14, 17, 18 possess denticles, then the species should be transferred to *Eoplectodonta*).

DUBIOLEPTINA Havlíček, 1967

1967 *Dubioleptina* Havlíček: 70

TYPE SPECIES. *Strophomena expulsa* Barrande, 1879.

DIAGNOSIS. Like *Sowerbyella* but with no socket plates. Hinge line not denticulate.

REMARKS. Although only two brachial valve internals are known, they clearly lack the socket plates of *Eoplectodonta*, which separates *Dubioleptina* from that genus. However, we do not agree with the familial difference which Havlíček feels warranted because the arrangement of the valves is generally reminiscent of *Eoplectodonta*, and in the shales in which *Dubioleptina* is found the socket plates may not have been preserved.

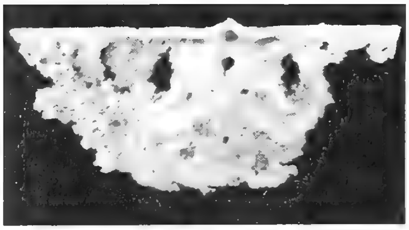
SPECIES ASSIGNED

Strophomena expulsa Barrande, 1879: pl. 53, fig. 4 from U. Liteň Formation (Wenlock), Lodeniče, Czechoslovakia (revised Havlíček 1967: 71; pl. 2, figs 11, 12; pl. 9, figs 11, 14–19; pl. 51, figs 2, 6), and its junior synonym *Strophomena plicatilis* Barrande, 1879: pl. 48, fig. 2 from the same horizon and locality.

EOPLECTODONTA (EOPLECTODONTA) Kozlowski, 1929
Figs 128–137

1929 *Plectodonta* (*Eoplectodonta*) Kozlowski: 112
1956 *Eoplectodonta* Cooper: 807


125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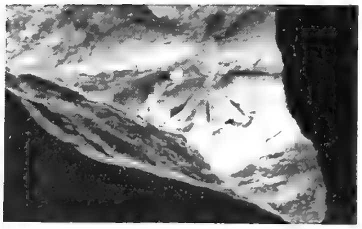
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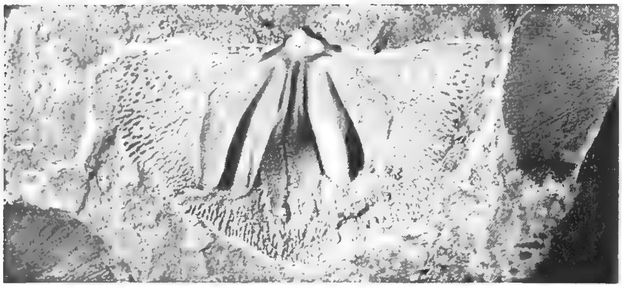
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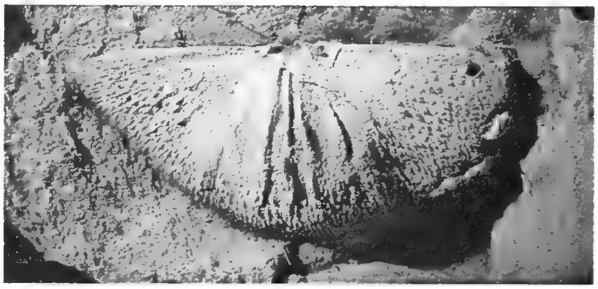
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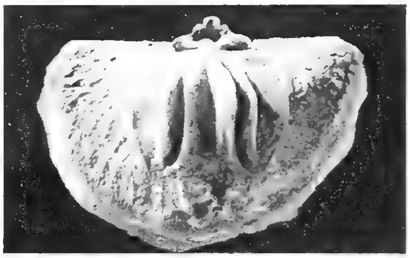
130a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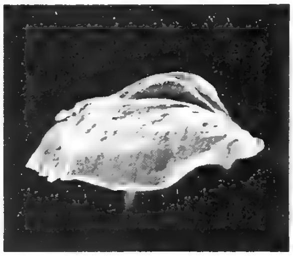
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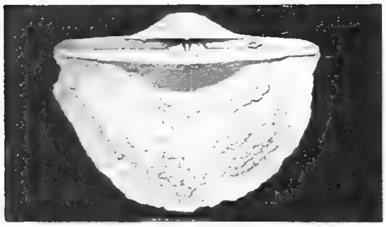
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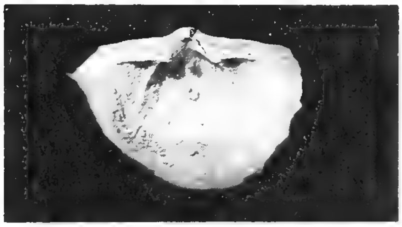
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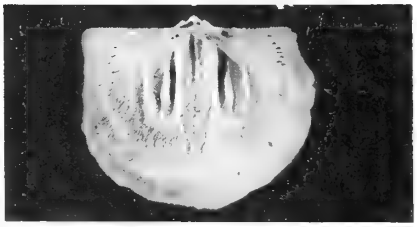
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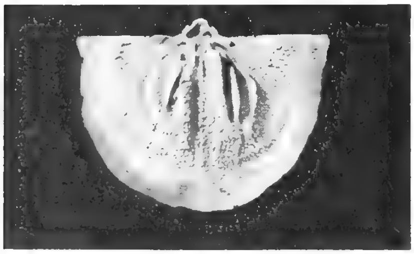
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Figs 125, 126 *Anisopleurella tricostellata* Cooper, 1956, from Pratt Ferry Formation (Llandeilo), SE of Pratt Ferry, Blocton, Alabama, USA. Fig. 125, exterior view of silicified pedicle valve, BB 32855, × 7; Fig. 126, interior of silicified brachial valve, BB 32856, × 7.

Figs. 127 *Anisopleurella* sp., internal mould of brachial valve from the L. Miaopo Formation (Llandeilo), Huanghuachang, Yichang County, Hubei Province, China, BC 3305, × 6.

Fig. 128, 129 *Eoplectodonta duplicata* (J. de C. Sowerby, 1839), from U. Haverford Mudstone Formation (L. Llandovery), lane opposite Gasworks, Haverfordwest, Dyfed, Wales; Fig. 128, internal mould of brachial valve, BB 31670, × 3; Fig. 129, latex cast of internal mould of brachial valve, BB 31693, × 3.

Fig. 130 *Eoplectodonta duvalii* (Davidson, 1847), a brachial valve from Slite Marl (Wenlock), 1·6 km south of church at Västergarn, Gotland, Sweden, the original of Cocks 1970: pl. 12, figs 14, 15, BB 31837; a, viewed posteriorly, × 4; b, c, viewed downwards and laterally, × 3.

Figs 131–136 *Eoplectodonta transversalis* (Wahlenberg, 1818), from L. Visby Marl (U. Llandovery). Figs 131–3 and 136 from beach 1 km west of Lundbjars, Figs 134–5 from beach north of Nyhamn, all north of Visby, Gotland, Sweden. Fig. 131, brachial view of conjoined valves, BB 34810, × 3; Fig. 132, slightly inclined view of pedicle valve interior, the original of Cocks 1970: pl. 12, fig. 12, BB 32423, × 3; Figs 133–6, all interiors of brachial valves, showing variations in the bema and even an incipient platform in Fig. 136; Fig. 133, BB 34826; Fig. 134, BB 34846; Fig. 135, BB 34847; Fig. 136, BB 34827; all × 3.

1961 *Ygera* Havlíček: 449
1965 *Eoplectodonta* Williams: H380 *pars* (*non Thaerodonta*)
1967 *Ygera* Havlíček: 58
1970 *Eoplectodonta* Cocks: 166

TYPE SPECIES. *Sowerbyella precursor* Jones, 1928, a junior subjective synonym of *Leptaena duplicata* J. de C. Sowerby, 1839. The type species of *Ygera* is *Y. ygerens* Havlíček, 1961.

DIAGNOSIS. Like *Sowerbyella* but with denticulate hinge line in pedicle valve and corresponding fossettes in the brachial valve hinge line.

REMARKS. Havlíček (1967: 58) differentiated *Eoplectodonta* with a median septum in the brachial valve from *Ygera* which lacked a septum, and also the 'ill-defined lobes of visceral field' (= bema) in *Ygera*. In fact, many populations of *Eoplectodonta* have specimens which lack a median septum, even in *E. duplicata* the type species, and similarly the bema is very variably developed and can even be entirely absent, particularly in small and young specimens. Thus we follow Cocks (1970) in not recognizing *Ygera* as a distinct genus. Hurst (1975) has described the ontogenetic development of the brachial valve septa and possible evolution of the lophophore in *Eoplectodonta transversalis*.

SPECIES ASSIGNED

Plectambonites trabeata var. *acuminata* Holtedahl, 1916: 79; pl. 14, figs 6–7 from 4bα Beds (M. Caradoc), Royal Palace, Oslo, Norway (revised Spjeldnaes, 1957: 96; pl. 3, figs 6–12).

Eoplectodonta acuminata Rozman, 1981 (*non* Holtedahl, 1916): 135; pl. 33, figs 1–11 from Bairimski Beds (Caradoc), south part of Mongolian Altai, W. Mongolia (certainly *Eoplectodonta* but different ornament from true *E. acuminata*).

Sowerbyella alternata Butts, 1942: 109; pl. 95, figs 22, 23 from Chambersburg Limestone (Caradoc), Strasburg, Shenandoah County, Virginia, U.S.A. (revised Cooper 1956: 808; pl. 184, figs 1–3; pl. 207, figs 2–25; pl. 208, figs 1–18; pl. 269, figs 23, 24).

Strophomena bidecorata Barrande, 1879: pl. 53, fig. 3 from Liteň Formation (Wenlock), hills between Loděnice and Bubovice, Czechoslovakia (revised Havlíček 1967: 61; pl. 7, figs 1–6).

Eoplectodonta budgei Sheehan, 1976: 726; pl. 4, figs 12–17 from Roberts Mountains Formation (U. Wenlock), Silver Island Mountains, Utah, USA.

Eoplectodonta california Boucot, Johnson & Zhang, 1988: 110; pl. 3, figs 6–13 from Hidden Valley Dolomite (M. Wenlock), 2 km NW of Pyramid Peak, Funeral Mountains, California, USA.

Plectambonites sericea conspicua Reed, 1917: 882; pl. 15, figs 4–11 from Craighead Limestone (U. Caradoc), Craighead, Girvan, Scotland (revised Williams, 1962: 182; pl. 17, figs 32, 38, 39).

Plectodonta thraivensis var. *divergens* Reed, 1944: 216; pl. 3, figs 3, 3a from Craighead Limestone (U. Caradoc), Craighead, Girvan, Strathclyde (a junior synonym of *Eoplectodonta conspicua* – see Williams 1962: 182; Cocks 1978: 100).

Leptaena duplicata J. de C. Sowerby, 1839: 636; pl. 22, fig. 2 from Goleugoed Formation (L. Llandovery), Cefn Rhyddan, Llandovery, Wales, senior synonym of *Plectambonites transversalis* var. *mullochensis* Reed, 1917: 887; pl. 15, figs 41, 42; pl. 16, figs 1, 2 from Mulloch Hill Formation (L. Llandovery), Mulloch Hill, Girvan, Scotland; *Plectambonites transversalis* var. *tricostata* Reed, 1917: 889; pl. 16, figs 8–13 from Woodland Formation (L. Llandovery), Woodland Point, Girvan, Scotland; *Sowerbyella precursor* Jones, 1928: 437; pl. 23, figs 3–5 from U. Haverford Mudstone Formation (L. Llandovery), Haverfordwest, Dyfed, Wales; and *Sowerbyella superstes* Jones, 1928: 441; pl. 23, figs 10–12 from Gasworks Sandstone (L.–M. Llandovery), Haverfordwest, Dyfed, Wales (all revised Cocks 1970: 169; pl. 5, figs 1–12; pl. 6, figs 1–13; pl. 7, figs 1–11; pl. 8, figs 1–11 and Temple 1987: 60; pl. 6, figs 1–17).

Leptaena duvalii Davidson, 1847: 58; pl. 12, figs 20, 21 from Coalbrookdale Formation (U. Wenlock), Walsall, West Midlands, England, a senior synonym of *Sowerbyella transversalis* var. *lata* Jones, 1928: 450; pl. 24, fig. 2 from Buildwas Formation (L. Wenlock), Buildwas, Shropshire, England (all revised Cocks, 1970: 182; pl. 12, figs 14–16; pl. 13, figs 3, 7, 10)

Plectodonta exceptionis Rybnikova 1967: 189; pl. 19, figs 8–12 from M. Llandovery borehole in Latvia, USSR.

Plectodonta lenis Williams, *in* Whittington & Williams 1955: 417; pl. 39, figs 79–81 from Derfel Limestone (L. Caradoc), Trawsnant, Gwynedd, Wales.

Eoplectodonta oscitanda Cocks, 1982: 769; pl. 81, figs 7, 9 from Langåra Limestone-Shale Formation (M.–U. Ashgill), Ringeriksveien, Sandvika, Norway.

Plectambonites schmidti var. *precedens* Holtedahl, 1916: 81; pl. 15, figs 10–11 from 4b Beds (M.–U. Caradoc), Bratterud, Ringerike, Norway (revised Spjeldnaes 1957: 101; pl. 4, fig. 9; pl. 6, fig. 7).

Leptaena sericea var. *rhombica* M^cCoy, *in* Sedgwick & M^cCoy 1852: 239 (figured Jones 1928: pl. 22, fig. 1) from Crag Hill Beds (L. Ashgill), Horton-in-Ribblesdale, Cumbria, England (also revised Cocks 1982: 769; pl. 81, figs 5, 6).

Plectambonites sericea semirugata Reed, 1917: 884; pl. 15, figs 18–26 from L. Ardwell Mudstones (M. Caradoc), Ardmillan Braes, Girvan, Scotland (revised Williams 1962: 181; pl. 17, figs 24–27) and subspecies *plicata* Williams, 1962: 182; pl. 17, figs 28–31, 33–35 from Kiln Mudstones (U. Caradoc), Craighead, Girvan, Scotland.

Leptaena transversalis var. *sowerbyana* Barrande, 1848: 225; pl. 21, figs 19–20 from Liteň Formation (Wenlock), hills between Loděnice and Bubovice, Czechoslovakia (revised Havlíček 1967: 59; pl. 7, figs 12–24 as *Ygera sowerbyana*.

Anomites transversalis Wahlenberg, 1818: 64 from L. Visby Beds (U. Llandovery), Lundbjars, Gotland, Sweden (revised Cocks, 1970: 177; pl. 12, figs 1–13).

Plectambonites transversalis var. *penkillensis* Reed, 1917: 888; pl. 16, figs 3–7 from Wood Burn Formation (U. Llandovery), Bargany Pond Burn, Girvan, Scotland, senior synonym of *Sowerbyella millinensis* Jones, 1928: 444; pl. 23, figs 13–16 and subspecies *parabola* Jones, 1928: 446; pl. 23, figs 18–20 and *canastonensis* Jones, 1928: 447; pl. 23, figs 17, 21, 22 all from Millin Mudstone (U. Llandovery), near Haverfordwest, Dyfed, Wales (all revised Cocks, 1970: 172; pl. 9, figs 1–15; pl. 10, figs 1–12; pl. 11, figs 1–16).

Ygera ygerens Havlíček 1961: 450; pl. 1, figs 7–12 from U. Liteň Beds (Wenlock), Svaty Jan Hliník, Czechoslovakia

Eoplectodonta sp. 1 of Cooper 1956: 813; pl. 192, figs 25–28 from Edinburg Formation (L. Caradoc), Wadesville, Winchester, Virginia, USA.

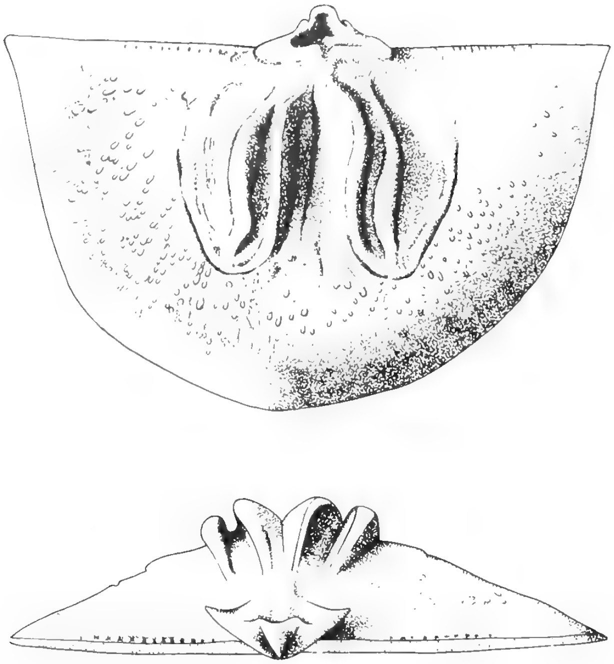


Fig. 137 *Eoplectodonta duvalii* (Davidson, 1847), from Slite Marl (Wenlock), Gotland, Sweden, posterior and downward views of a brachial valve interior (based on BB 31837), × 5.

SPECIES QUESTIONABLY ASSIGNED

Leptaena transversalis var. *alabamensis* Foerste, 1890: 293; pl. 5, fig. 9 from Clinton Group (U. Llandovery), Collinsville, Alabama, USA (no interiors figured).

Plectambonites delicatula Butts, 1926: 116; pl. 26, figs 20–21 from Little Oak Limestone (U. Llandeilo–L. Caradoc), Pelham, Alabama, USA (no interiors figured).

Sowerbyella elegans Poulsen, 1943: 15; pl. 2, fig. 4 from Offley Island Formation (Wenlock–Ludlow), Cape Bryan, north Greenland (no brachial interior illustrated).

Strophomena elegantula Hall, 1843: 72; fig. 17.1 from Clinton Group (U. Llandovery), Rochester, New York, USA (no interiors figured).

Leptaena transversalis var. *elegantula* Foerste, 1890: 293; pl. 6, fig. 6 from Clinton Group (U. Llandovery), Hanover, Indiana, USA (no interiors figured).

Eoplectodonta foerstei Cooper, 1956: 811; pl. 209, figs 1–3 from Wells Formation (L. Caradoc), SW of Cumberland City, Tennessee, USA (no interiors figured).

Eoplectodonta (*Eoplectodonta*) *semirugata paucicostellata* Rozman, 1978: 92; pl. 15, figs 1–6 from Obikalon Beds (U. Caradoc), Shakhriomon, Tian-Shan, USSR (denticles not preserved).

Leptaena transversalis var. *prolongata* Foerste, 1890: 293; pl. 5, fig. 13 from Clinton Group (U. Llandovery), Wildwood Station, Georgia, USA (no interiors figured).

Eoplectodonta ? pumila Lopushinskaya 1976: 36; pl. 3, figs 3–8 from *Dalmanella neocrassa* Beds (U. Llandovery), River Sukhaya Tunguska, N. Siberia USSR (no interiors known).

Plectambonites tenera Shaler, 1865: 65, not illustrated, but said by Twenhofel (1928: 192) to be a synonym of *E. transversalis* and come from Gun River and Jupiter Formations (M.–U. Llandovery), Anticosti Island, Quebec, Canada (no interiors known).

Eoplectodonta transversalis sibirica Lopushinskaya, 1976: 37; pl. 3, figs 1–2 from *Dalmanella neocrassa* Beds (U. Llandovery), River Sukhaya, N. Siberia, USSR (no interiors known).

SPECIES REJECTED

Eoplectodonta? dubia Cooper 1956: 810; pl. 207, fig. 1; pl. 209, figs 8–13 from Botetourt Formation (L. Caradoc), Brownsburg, Virginia, USA (no hinge denticles, transferred to *Sowerbyella*).

Eoplectodonta karina Spjeldnaes, 1957: 100; pl. 3, fig. 5 from 4bα Beds, southern end of Nakholmen, Oslo, Norway (to *Anisopleurella*).

Plectodonta (*Eoplectodonta*) *killeyensis* Reed, 1952: 51; pl. 2, figs 8, 9 from Killey Bridge Formation (L. Ashgill), Pomeroy, Co. Tyrone, Northern Ireland (revised Mitchell 1977: 81 as a junior synonym of *Sowerbyella thraivensis* Reed).

EOPLECTODONTA (KOZLOWSKITES) Havlíček, 1952

1952 *Kozlowskites* Havlíček: 406
1965 *Eoplectodonta* (*Kozlowskites*) Williams: H381
1967 *Kozlowskites* Havlíček: 56

TYPE SPECIES. *Strophomena nuntia* Barrande, 1879.

DIAGNOSIS. Like *Eoplectodonta* but ventral muscle scars not united centrally. Pedicle valve pallial markings simple and subparallel.

REMARKS. We agree with Havlíček (1967: 56) that the denticles in Kozlowskites can occupy only a very short distance of the central parts of the hinge line. We follow Williams (1965: H381) in regarding *Kozlowskites* as a subgenus of *Eoplectodonta*.

SPECIES ASSIGNED

Spirifer? *ichnusae* Vinassa, 1927: 491; pl. 4, fig. 35 from Portixeddu Formation (U. Caradoc), Portixeddu, Sardinia, Italy (revised Havlíček *et al.* 1987: 307; pl. 8, figs 23, 24; pl. 9, figs 1, 2).

Strophomena nuntia Barrande, 1879: pl. 49, fig. 3 from Králův Dvůr Formation (M. Ashgill), Králův Dvůr, Bohemia, Czechoslovakia (revised Havlíček 1967: 56; pl. 6, figs 10–18).

Eoplectodonta (*Kozlowskites*) *ragnari* Sheehan, 1973: 63; pl. 2, figs 3–8 from Jerrestad Mudstone (L. Ashgill), Fågelsång, Scania, Sweden.

Kozlowskites yichangensis Chang, 1983: 479; pl. 1, figs 16–23 from Miaopo Formation (L. Caradoc), Huanghuachang, Yichang County, Hubei, China.

EOPLECTODONTA (YGERODISCUS) Havlíček 1967

1967 *Ygerodiscus* Havlíček: 62
1970 *Ygerodiscus* Cocks: 184
1970 *Eoplectodonta* Temple: 43 *pars*
1974 *Ygerodiscus* Bassett: 90

TYPE SPECIES. *Leptaena transversalis* var. *undulata* Salter, 1848.

DIAGNOSIS. Like *Eoplectodonta* (*Eoplectodonta*) but with distinctive shell undulations.

REMARKS. Since Havlíček established this genus there has been discussion on the proper systematic weighting to be given to the distinctive undulations, for example Temple (1970: 43) considered that those in the type species which he was revising merited no more than subspecific recognition. However, we follow Cocks (1970: 184) in treating *Eoplectodonta* and *Ygerodiscus* as distinct because of the presence of the two forms in the same bedding plane at Meifod without intermediates, but consider the differences to be of subgeneric rather than generic rank.

SPECIES ASSIGNED

Leptaena segmentum var. *cornuta* Davidson, 1883: 166; pl. 12, figs 1–3 from Coalbrookdale Formation (Wenlock), Coalbrookdale, Shropshire, England (revised Cocks 1970: 188; pl. 13, figs 11, 12; pl. 14, figs 1, 2 and Bassett 1974: 90; pl. 22, figs 7–10).

Ygerodiscus novemcostatus Havlíček, 1967: 62; pl. 9, figs 21, 22 from U. Liteň Formation (Wenlock), Lištice, Beroun, Czechoslovakia.

Plectodonta propinqua Rybnikova, 1967: 191; pl. 19, figs 3–7 from L. Llandovery rocks in boreholes, Latvia, USSR.

Plectambonites striatacostatus Twenhofel, 1928: 191; pl. 16, figs 16, 17 from L. Jupiter Formation (U. Llandovery), Jupiter River, Anticosti Island, Canada.

Leptaena transversalis var. *undulata* Salter, *in* Phillips & Salter 1848: 372; from V_2C Beds (L. Llandovery), Mathyrafal, Meifod, Wales, a senior synonym of *Sowerbyella undulata* var. *maccoyi* Jones, 1928: 457; pl. 24, fig. 7 from the same horizon and locality, *Sowerbyella plicata* Jones, 1928: 459; pl. 24, figs 10, 11 from Rosemarket Beds (M. Llandovery), Bullford, Dyfed, Wales, and *Sowerbyella compressa* Jones, 1928: 460; pl. 24, figs 12, 13 from the same horizon and locality (all revised Cocks 1970: 185; pl. 14, figs 3–12; pl. 15, figs 1–12).

SPECIES QUESTIONABLY ASSIGNED

Plectambonites tennesseensis Foerste, 1903: 708 from Waldron Formation (Wenlock), Clifton, Tennessee, USA (no interiors or exteriors figured).

GUNNINGBLANDELLA Percival, 1979

1979 *Gunningblandella* Percival: 111

TYPE SPECIES. *Gunningblandella resupinata* Percival, 1979.

DIAGNOSIS. Like *Sowerbyella* but resupinate in shell profile. Hinge line not denticulate.

REMARKS. This is the only resupinate genus within the Sowerbyellidae and is so far definitely known only from the type species in the Caradoc of Australia.

SPECIES ASSIGNED

Gunningblandella resupinata Percival, 1979: 111, fig. 9:1–25, from Goonumbla Volcanics (U. Caradoc), Gunningbland, New South Wales, Australia.

SPECIES QUESTIONABLY ASSIGNED

Stropheodonta katuglåsensis Reed, 1932*a*: 136; pl. 21, figs 1–6, ?fig. 13 from Hølandet Formation (Caradoc), Katuglåsen, Trondheim, Norway (one shell is certainly resupinate, but whether or not all the shells figured by Reed belong to one species, and whether or not the 'minute denticulations' described but not figured by Reed are real, all remain doubtful).

PLECTODONTA (PLECTODONTA) Kozlowski, 1929

Figs 153–157

1929 *Plectodonta* Kozlowski: 112
1954 *Plectodonta* Nikiforova: 79
1965 *Plectodonta* Williams: H381 *pars*

TYPE SPECIES. *Plectodonta mariae* Kozlowski, 1929.

DIAGNOSIS. Hinge line denticulate. Bema weak or absent. Platform absent. Like *Eoplectodonta* except with strong deltidium, less incurved, more quadrate and less alate valve extremities, and with coarse papillae on the brachial valve interior.

REMARKS. The distinctive deltidium has been illustrated by Kozlowski (1929: fig. 36A), Cocks (1970: fig. 3) and Nikiforova *et al.* (1985: pl. 3, fig. 6b). Although the form and presence of coarse papillae inside the brachial valve is not usually regarded by us as a good generic character within the Plectambonitacea, nevertheless their universal presence within the *Plectodonta* group is noteworthy.

SPECIES ASSIGNED

Chonetes bipartita Chapman, 1913: 104; pl. 10, figs 8–10 from Yering Siltstones (Pridoli–Lochkov), Ruddock's Quarry, near Lilydale, Victoria, Australia.

Stropheodonta davidi Mitchell, 1923: 470; pl. 41, figs 19–21 from Upper Trilobite Bed of Hume Series (Pridoli–Lockhov), Bowning railway station, New South Wales, Australia, and *Stropheodonta striato-costata* Mitchell, 1923: 472; pl. 42, figs 29, 30 and *Stropheodonta striato-punctata* Mitchell, 1923: 472; pl. 42, fig. 31, both from the same horizon and locality and regarded as synonyms of *davidi* by Brown (1949: 199). Savage (1974:27) regards them all as junior synonyms of *Plectodonta bipartita* (Chapman).

Plectambonites minor var. *digitata* Wolburg, 1933: 53; pl. 2, fig. 6 from Robecke Shale (M. Devonian), Winkhausen, Girkhausen, Germany (as revised by Solle 1938: 268, fig. 5).

Plectodonta mariae Kozlowski, 1929: 114; pl. 3, figs 30–32 from Mitkov Beds, Borshchov Horizon (Lochkov), Podolia, Ukraine, USSR (formerly Poland).

Strophomena mimica Barrande, 1879; pl. 107, fig. 9 from Lochkov Limestones (Lochkov), Lochkov, Czechoslovakia (revised Havlíček 1967: 64; pl. 8, figs 6, 7, 10).

Plectodonta pacifica Hamada, 1969: 4; pl. 1, figs 5–7; pl. 2, fig. 3 from beds of L.–M. Devonian age, Kampong Pahil, south of Kroh, Perak, Malaysia.

Plectodonta petila Amsden, 1958: 93; pl. 13, figs 8–17 from Haragan Formation (L. Devonian), White Mound, Murray County, Oklahoma, USA.

Sowerbyella ? *plebia* Talent, 1965: 23; pl. 5, figs 6, 7 from McIvor Formation (Pridoli?), Redcastle, Victoria, Australia.

Plectodonta sanglangensis Xian, 1978: 262; pl. 97, figs 2–3 from Nabiao Formation (Eifelian), Sanglang, Luodian County, S. Guizhou Province, China.

Plectodonta thuringica Schmidt, 1939: 80; pl. 3, figs 1, 2 from Ludlow–Pridoli beds, Ebersdorf-Katzenwich, Thuringia, Germany.

SPECIES QUESTIONABLY ASSIGNED

Plectodonta minor var. *alatiformis* Schmidt, 1939: 83; pl. 4, fig. 8 from Tentaculitenkalk (L. Devonian), Schleizer Stadtwald, Thuringia, Germany.

Plectodonta biplexa Xu, 1979: 370; pl. 2, figs 14–16 from

Tangxiang Formation (Eifelian), Luofu of Nandan, Guanxi Province, China (no interiors illustrated).

Plectodonta burtonae Hamada, 1969: 5; pl. 1, figs 8, 9 from beds of L.–M. Devonian age, Kampong Pahil, south of Kroh, Perak, Malaysia (no brachial interiors figures; might be chonetacean).

Sowerbyella (*Plectodonta*) *hopfi* Volk, 1939: 388; fig. 1 from Lower Middle Devonian Beds, Pfeiffersberg, Steinach, Thuringia, Germany (poorly preserved specimens, but Jahnke (1971: 51) considers the species to be a junior synonym of *Plectodonta* (*Dalejodiscus*) *minor*).

Plectodonta loilemensis Reed, 1936: 113; pl. 4, figs 16–20 from Loilem Formation (Ludlow?), Loilem, Southern Shan States, Burma (no brachial interiors figured).

SPECIES REJECTED

Plectodonta aknistensis Rybnikova 1967: 188; pl. 19, figs 1, 2 from L. Ludlow borehole in Latvia, USSR (assigned here to *Jonesea*).

Plectodonta thraivensis var. *divergens* Reed, 1944: 216; pl. 3, figs 3, 3a from Craighead Limestone (U. Caradoc), Craighead, Girvan, Strathclyde, Scotland (transferred to *Eoplectodonta* (*Eoplectodonta*)).

Plectodonta exceptionis Rybnikova, 1967: 189; pl. 19, figs 8–12 from M. Llandovery borehole in Latvia, USSR (assigned here to *Eoplectodonta* (*Eoplectodonta*)).

Plectodonta propinqua Rybnikova, 1967: 191; pl. 19, figs 3–7 from L. Llandovery borehole in Latvia, USSR (assigned here to *Eoplectodonta* (*Ygerodiscus*)).

Plectodonta shiqianensis Xian, 1978: 262; pl. 96, fig. 16 from Xiushan Formation (U. Llandovery), Raochaguan, Shiqian County, NE Guizhou, China (to *Mesopholidostrophia*).

Plectodonta sp. of Harper 1973: 51; pl. 16, figs 1, 2 from French River Formation (L. Wenlock), Cobequid Mountains, Nova Scotia, Canada (certainly *Eoplectodonta*).

PLECTODONTA (DALEJODISCUS) Havlíček, 1961

1961	*Dalejodiscus* Havlíček: 449
1965	*Plectodonta* Williams: H381 *pars*
1967	*Dalejodiscus* Havlíček: 65
1971	*Plectodonta* (*Dalejodiscus*) Jahnke: 51

TYPE SPECIES. *Strophomena comitans* Barrande, 1879.

DIAGNOSIS. Like *Plectodonta* (*Plectodonta*), but with elevated and radially striated bema.

REMARKS. Havlíček's (1967) illustrations of the two Bohemian species clearly show the internal characteristics of the brachial valve and can be compared with the interior of *Plectodonta mariae*, e.g. the specimen figured by Williams (1965: fig. 243). Solle's illustrations of *P. wolburgi* provide the link between *Plectodonta* and *Dalejodiscus*, where it can be seen that, although the bema is slightly elevated anteriorly and also has a few striations, nevertheless the general morphology is close to that of *Plectodonta mariae*.

SPECIES ASSIGNED

Strophomena comitans Barrande, 1879: pl. 56, figs 4–6, 21–23, 30–32, 42, 43, 46–48 from Daleje shales (Eifelian), Praha-Hlubocepy, Czechoslovakia (revised Havlíček 1967: 67; pl. 7, figs 8–11).

Leptaena minor Roemer, 1850: 12; pl. 3, fig 1 from Wissenbach Shale (Eifelian), Ziegenberger Teich, NE Buntenbock, Germany (revised Jahnke 1971: 51; pl. 2, figs 1–3; Jahnke also considered *P. comitans*, *P. wolburgi* and *P. hopfi* to be junior synonyms of *P. minor*).

Plectodonta subcomitans Havlíček 1956: 554; pl. 8, figs 14–18 from Dvorce-Prokop limestones (Pragian), Praha-Branik, Czechoslovakia (revised Havlíček 1967: 65; pl. 8, figs 8, 9, 11–16, but not *D. subcomitans* of Havlíček 1977; pl. 1, fig. 6, from Zlichovian, Stary Rozmital, Czechoslovakia, here assigned to *Plectodonta* (*Plectodonta*)).

Sowerbyella (*Plectodonta*) *wolburgi* Solle, 1938: 271, figs 6–10 from Lower Devonian of Hilgenfeld, Kellerwald, Germany.

SPECIES QUESTIONABLY ASSIGNED

Dalejodiscus? sp. of Gratsianova 1967: 34; pl. 2, fig. 1 from Yarkushinski Beds (L. Devonian), Gornoi Altai, Central USSR (no interiors known).

PLECTODONTA (PLECTODONTELLA) Havlíček, 1953

1953	*Plectodontella* Havlíček: 8
1965	*Plectodontella* Williams: H381 *pars* (*non Ygera*)
1967	*Plectodontella* Havlíček: 69

TYPE SPECIES. *Plectodontella redunca* Havlíček, 1953.

DIAGNOSIS. Like *Plectodonta* (*Plectodonta*) but with strong raised bema. Weak platform present.

SPECIES ASSIGNED

Plectodontella redunca Havlíček, 1953: 9; pl. 1, fig. 4 from Třebotov Limestones (L. Eifelian), Holyně, Prague, Czechoslovakia (revised Havlíček 1967: 69; pl. 9, figs 5, 8, 9, 12).

SOWERBYELLA (SOWERBYELLA) Jones, 1928

Figs 138–148

1928	*Sowerbyella* Jones: 384
1930	*Sowerbyella* Öpik: 144 *pars*
1959	*Sowerbyella* (*Viruella*) Rõõmusoks: 14
1965	*Sowerbyella* Williams: H378
1981	*Sowerbyella* (*Sowerbyella*) Rozman: 133
1984	*Sowerbyella* Klenina: 77

TYPE SPECIES. *Leptaena sericea* J. de C. Sowerby, 1839. The type species of *Viruella* is *Sowerbyella liliifera* Öpik, 1930.

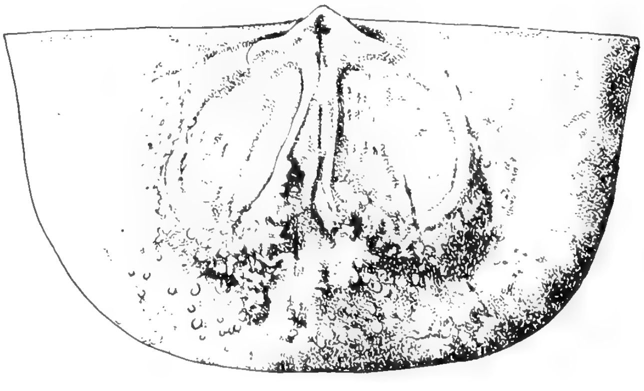


Fig. 138 *Sowerbyella* (*Sowerbyella*) *sericea* (J. de C. Sowerby, 1839), from Horderley Sandstone (L. Caradoc), Shropshire, England, brachial valve interior (based on BC 6051–3), × 6.

DIAGNOSIS. Bema variable, sometimes absent. No denticles on hinge line. Median septum in brachial valve variably developed, usually absent. Like *Anisopleurella* but with prominent pair of central side septa, which sometimes form the edge of the bema and are sometimes developed above it.

REMARKS. Rõõmusoks (1959) separated a subgenus *Viruella* based on ornamentation (like *Eoplectodonta*), the presence of a median septum in the brachial valve, and a raised muscle platform in the brachial valve. However, those three characters show great variation, and in fact all are present in the type species of *Sowerbyella*, *S. sericea*, apart from the ornamental difference, which we regard as of specific, not generic importance. We illustrate topotype specimens of both nominal genera.

SPECIES ASSIGNED

Sowerbyella (*Viruella*) *acculica* Misius, 1986: 154; pl. 14, figs 14–32 from Tabilgat Formation (U. Llandeilo), River Tabilgat, Moldo-Too, N. Khirgizia, USSR.

Sowerbyella aequicostellata Cooper, 1956: 774; pl. 199, figs 9–17 from Edinburg Formation (L. Caradoc), Strasburg Junction, Virginia, USA.

Sowerbyella (*Sowerbyella*) *akdombakensis* Klenina, *in* Klenina *et al.* 1984: 82; pl. 7, figs 12, 15, 17, 19, 20, 22; pl. 9, figs 2, 3 from Akdombak Formation (M. Ashgill), Akdombak Hill, Chinghiz Mountains, Kazakhstan, USSR.

Sowerbyella angulata Cooper, 1956: 776; pl. 206, figs 1–7 from Hermitage Formation (L. Caradoc), Birmingham, Alabama, USA.

Sowerbyella antiqua Jones, 1928: 419; pl. 21, figs 7–11 from Llandeilo beds, Llandeilo, Dyfed, Wales (revised Lockley & Williams 1981: 58; figs 196–212), including its junior synonym *Sowerbyella antiqua llandeiloensis* Williams, 1949: 234; pl. 11, figs 12–14 from L. Llandeilo beds, Dynevor, Llandeilo, Dyfed, Wales.

Sowerbyella sericea askerensis Spjeldnaes, 1957: 92; pl. 6, fig. 5 from 4bδ Beds (M. Caradoc), Hvalstad, Asker, Norway.

Sowerbyella (*Viruella*) *bystrovi* Nikanorova 1976: 117; figs 1b–k from Tallinn Horizon (Llandeilo–L. Caradoc), Tolbykhin, River Yaroslavlyar, Moscow syneclise, USSR.

Sowerbyella cava Cooper, 1956: 777; pl. 203, figs 21–43 from Martinsburg Formation (L. Caradoc), Green Mount Church, Virginia, USA.

Sowerbyella compacta Cooper 1956: 778; pl. 196, figs 51–59; pl. 197, figs 11–24; pl. 200, figs 1–6; pl. 202, figs 1–8 from Benbolt Formation (L. Caradoc), Rye Cove, Clinchport, Virginia, USA.

Plectambonites curdsvillensis Foerste, 1912: 122; pl. 10, figs 15a, b from Curdsville Formation (M. Caradoc), Glenn Creek Station, Woodford County, Kentucky, USA (revised Cooper 1956: 780; pl. 201, figs 1–13, Howe 1979: 1; pl. 1, figs 6–16, and Rice 1987: 156; pl. 3, fig 1).

Eoplectodonta? *dubia* Cooper, 1956: 810; pl. 207, fig. 1; pl. 209, figs 8–13 from Botetourt Formation (L. Caradoc), Brownsburg, Virginia, USA.

Sowerbyella elusa Williams, 1962: 181; pl. 17, figs 20–23, from Craighead Limestone (U. Caradoc), Craighead, Girvan, Scotland.

Sowerbyella eximia Cooper, 1956: 781; pl. 204, figs 13–33; pl. 205, figs 7, 8 from Martinsburg Formation (L. Caradoc), Green Mount Church, Virginia, USA.

Sowerbyella fallax Jones, 1928: 493 (illustrated Reed 1917: pl. 13, fig. 14) from Craighead Limestone (U. Caradoc), Craighead, Girvan, Scotland.

Sowerbyella (*Soweryella*) *forumi* Rõõmusoks, 1959: 30; pl. 5, figs 1–9 from Keila Horizon (M.–U. Caradoc), Rakvere, Estonia, USSR.

Sowerbyella fupingensis Fu, 1982: 118; pl. 35, figs 4–6 from Beiguoshan Formation (U. Caradoc–L. Ashgill), Hongshui, Fuping County, Shaanxi Province, China.

Sowerbyella grierensis Howe, 1979: 3; pl. 1, figs 1–5 from Grier Limestone Member of Lexington Formation (M. Caradoc), Grier, Kentucky, USA.

Sowerbyella sericea hadelandica Spjeldnaes, 1957: 93; pl. 4, figs 1, 7 from Lower Cyclocrinus Beds (Caradoc), between Jonsrud and Stensrud, Hadeland, Norway.

Sowerbyella hainanensis Xu & Su, 1979: 106 from Middle Ordovician beds, Yaxian, Hainan Island, China.

Sowerbyella indistincta Cooper, 1956: 782; pl. 202, figs 24–26 from Bromide Formation (U. Llandeilo), NE of Springer, Carter County, Oklahoma, USA.

Sowerbyella (*Viruella*) *insueta* Klenina, *in* Klenina *et al.* 1984: 84; pl. 8, figs 8–10 from Taldiboiskaya Formation (L. Ashgill), Taldiboy River, Chinghiz Mountains, Kazakhstan, USSR.

Sowerbyella intricata Nikiforova, 1978: 108; pl. 19, figs 12–20 from Archalyk Beds (Ashgill), Shakhriomon, Tian Shan, USSR.

Plectodonta (*Eoplectodonta*) *killeyensis* Reed, 1952: 51; pl. 2, figs 8, 9 from Killey bridge Formation (L. Ashgill), Pomeroy, Co. Tyrone, Northern Ireland (revised Mitchell 1977: 81 and put in the synonymy of *Sowerbyella thraivensis* Reed).

Sowerbyella lanxiensis Liang, *in* Liu *et al.* 1983: 276; pl. 99, figs 1–3 from Changwu Formation (M. Ashgill), Zhuganshan, Lanxi County, Zhejiang Province, SE China.

Sowerbyella lebanonensis Bassler, 1935: 406 from Lebanon Formation (L.–M. Caradoc), Shelbyville, Bedford County, Tennessee, USA (revised Cooper 1956: 782; pl. 201, figs 14–25).

Sowerbyella (*Sowerbyella*) *lepta* Percival, 1979: 108, figs 3B.4–7, 8 from Goonumbla Volcanics (L. Caradoc), Gunningbland, New South Wales, Australia.

Sowerbyella liliifera Öpik, 1930: 148; pl. 8, fig. 112; pl. 9, fig. 119; pl. 21, figs 262–4 from Kukruse Formation, (L. Caradoc), Kohtla, Estonia, USSR and subspecies *milis* Öpik 1930: 151; pl. 9, figs 115, 120 from same horizon and locality, and the subspecies *tegula* Öpik, 1930: 151; pl. 8, fig. 113; pl. 9, fig. 117 and *triangulum* Öpik 1930: 153; pl. 9, fig. 118, both from Idavere Formation (L. Caradoc), Kohtla, Estonia, USSR (all revised Rõõmusoks, 1959: 18; pl. 2, figs 1–13).

Sowerbyella limata Öpik, 1930: 163; pl. 9, fig. 128 from Kukruse Formation (L. Caradoc), Kohtla, Estonia, USSR.

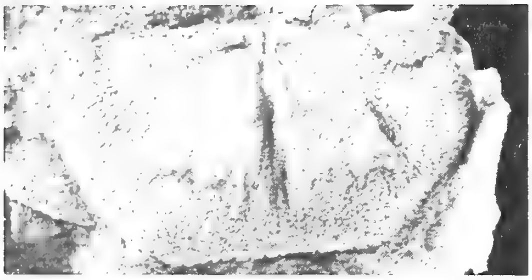
Sowerbyella (*Viruella*) *minima* Rõõmusoks, 1959: 22; pl. 3, figs 1–6 from Kukruse Horizon (L. Caradoc), Lasnamagi, Estonia, USSR.

Leptaena minnesotensis Sardeson, 1892: 329; pl. 4, figs 24, 25 from Decorah Shale (M. Caradoc), Minnesota, USA (revised Rice 1987: 157; pl. 3, fig. 2).

Sowerbyella monilifera Cooper, 1956: 785; pl. 199, figs 1–8; pl. 206, figs 16–28 from Decorah Formation (L.–M. Caradoc), Ellsworth, Wisconsin, USA.

Sowerbyella multipartita Williams, *in* Cocks 1978: 98, nom. nov. pro *S. multiseptata* Williams, 1974: 132; pl. 23, figs 14–19; pl. 24, figs 1, 3 from Spy Wood Grit (L. Caradoc), 1 km NNE of Rorrington, Shropshire, England.

Sowerbyella musculosa Williams, 1963: 433; pl. 11, figs 18–27 from Allt Ddu Group (L. Caradoc), Bala, Gwynedd, Wales.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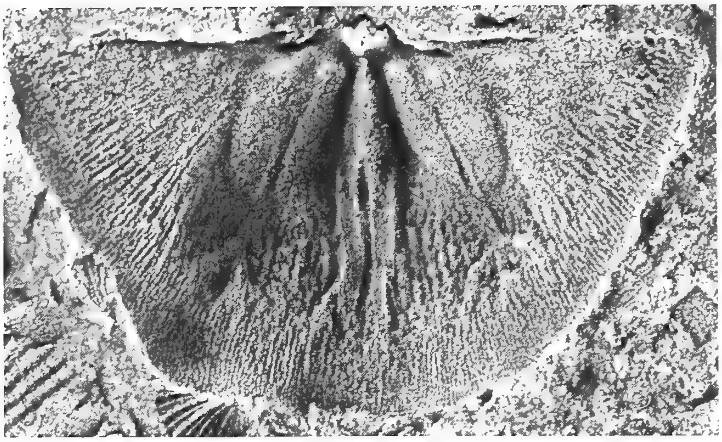
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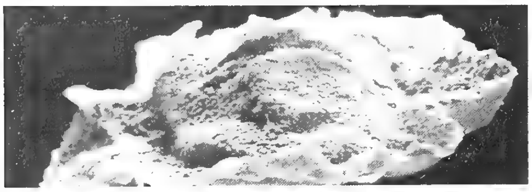
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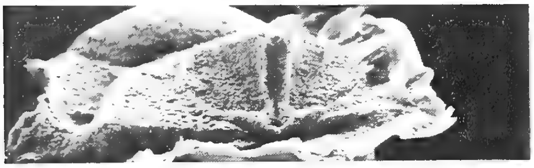
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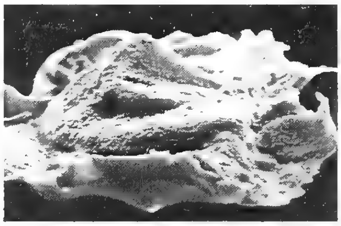
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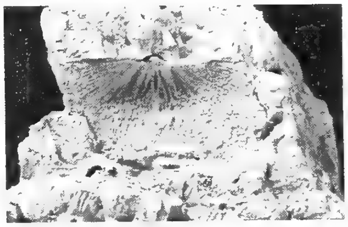
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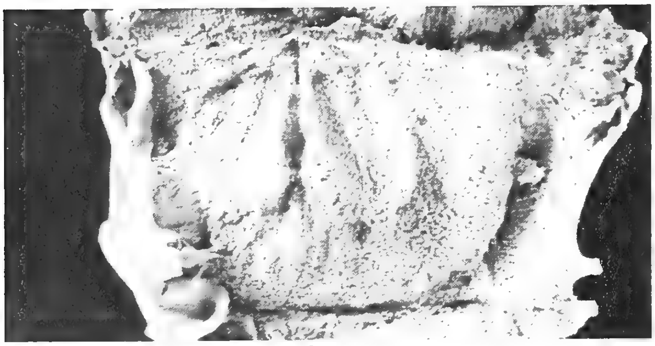
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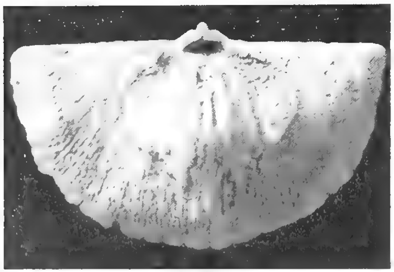
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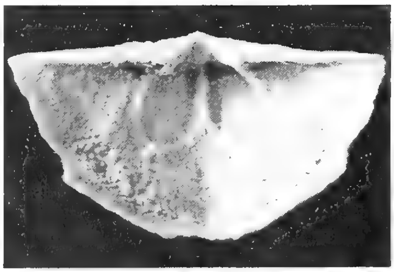
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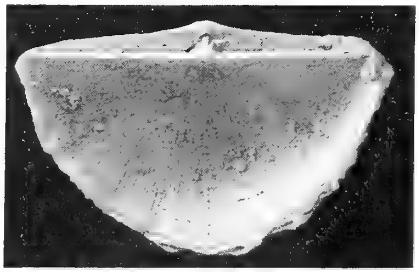
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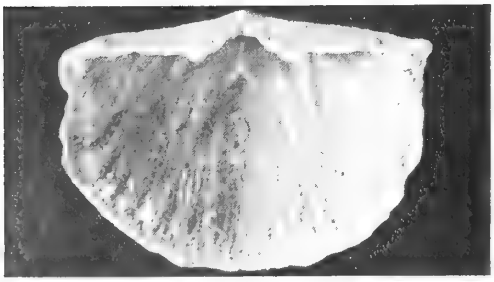
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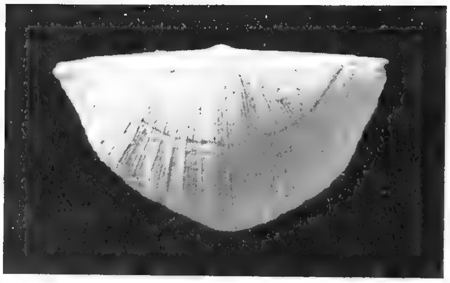
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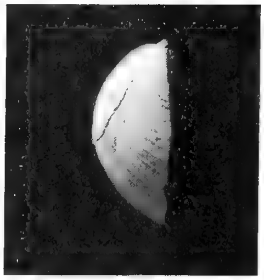
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Chonetoidea (*Aegiria*) *nacta* Reed, 1952: 53; pl. 2, fig, 13 from Killey Bridge Formation (L. Ashgill), Pomeroy, Co. Tyrone, Northern Ireland (revised Mitchell 1977: 81 and put in the synonymy of *Sowerbyella thraivensis*).

Sowerbyella nasuta Cooper, 1956: 787; pl. 199, figs 18–34; pl. 215, figs 1–4 from Chatham Hill Formation (L. Caradoc), Walker Mountain, Chatham Hill, Virginia, USA.

Sowerbyella (*Sowerbyella*) *nativa* Klenina, *in* Klenina *et al.* 1984: 78; pl. 6, figs 4–6, 8, 9; pl. 7, fig. 11 from Abaevskaya Formation (Llanvirn–Llandeilo), SE Ordatas Hill, NE Pre-Chinghiz, Kazakhstan, USSR.

Sowerbyella (*Sowerbyella*) *oepiki* Rõõmusoks, 1959: 32; pl. 6, figs 1–9 from Keila Horizon (M.–U. Caradoc), Lekhtmetsa-Saky, Estonia, USSR.

Viruella orientalis Su, 1980: 272; pl. 115, figs 5–9 from Guanniaohe Formation (M. Ordovician), Less Hinggan, Heilongjiang Province, NE China.

Sowerbyella papiliunculus Borissiak, 1972: 183; pl. 49, figs 4–7 from *Amsassia* Beds (U. Caradoc), Kulunbulak River, Tarbagatau Mountains, E. Kazakhstan, USSR.

Sowerbyella parva Cooper, 1956: 789; pl. 202, figs 9–15 from Ward Cove Formation (L. Caradoc), N. of Rye Cove, Clinchport, Tennessee, USA.

Sowerbyella perplexa Cooper, 1956: 790; pl. 196, figs 30–44 from Chatham Hill Formation (L. Caradoc), Sharon Springs, Burkes Garden, Virginia, USA.

Plectambonites punctostriatus Mather, 1917: 38; pl. 1, figs 15–17 from Rockland Formation (M. Caradoc), Wolfe Island, Lake Ontario, Canada (revised Cooper 1956: 792; pl. 205, figs 9–25; pl. 206, figs 14, 15 and put into the synonymy of *Sowerbyella curdsvillensis* by Rice 1987: 156).

Sowerbyella (*Sowerbyella*) *raegaverensis* Rõõmusoks, 1959: 36; pl. 8, figs 1–8 from Rakvere Horizon (L. Ashgill), Ragavere, Estonia, USSR.

Sowerbyella ringsakerensis Spjeldnaes, 1957: 94; pl. 6, figs 1–4 from Coelosphaeridium Beds (M. Caradoc), between Tørud and Bratberg, Ringsaker, Norway.

Plectambonites rugosa Meek, 1873: 72; pl. 5, figs 3f–h from L. Edenian Strata (U. Caradoc), Ohio River, Cincinnati, Ohio, USA (revised Howe 1972: 444; pl. 1, figs 4–7 and Howe, 1979: 3; pl. 1, figs 17–20).

Sowerbyella rukavishnikovae Popov, 1980*b*: 151; pl. 2, figs 1–4 from Anderkenskaya Horizon (U. Llandeilo–L. Caradoc), Anderken-Ashkov river, Chu-Ili Mountains, Kazakhstan, USSR.

Sowerbyella semiluna Öpik, 1930: 155; pl. 9, figs 123–6 from Idavere Formation (L. Caradoc), Kohtla, Estonia, USSR.

Leptaena sericea J. de C. Sowerby, 1839: 636; pl. 19, fig. 1 from Horderley Sandstone (L. Caradoc), Whittingslow, Shropshire, England (revised Williams 1963: 430; pl. 11, figs 1–9) and subspecies *brynensis* Whittington, 1938: 253; pl. 11, figs 6–9 from L. Caradoc beds, Powys, Wales and *permixta* Williams, 1963: 434; pl. 11, figs 10–17 from Nant-Hir Group (L. Caradoc), Bala, Gwynedd.

Sowerbyella sericea jugata Ruedemann, 1912: 92; pl. 4, fig. 7 from Snake Hill Shale (U. Caradoc), Snake Hill, Mohawk Valley, New York, USA.

Sowerbyella sericea tchernyshevi Rozman, 1977: 92; pl. 6, figs 1–3 from *P. linearis* Zone (U. Caradoc), River Bairimgol, NW Mongolia.

Sowerbyella sladensis Jones, 1928: 421; pl. 21, figs 14–17 from Slade and Redhill Mudstone Formation (M. Ashgill), Llan Mill, Dyfed, Wales, and subspecies *simulans* Jones, 1928: 423; pl. 21, figs 18–20 from same formation at Narberth, Dyfed, Wales (comments in Cocks 1978: 98).

Sowerbyella socialis Cooper, 1956: 794; pl. 198, figs 23–44; pl. 205, figs 1–6 from Wardell Formation (L. Caradoc), Rye Cove, Clinchport, Tennessee, USA (and subspecies *crassa* Cooper, 1956: 796; pl. 200, figs 7–14, from same horizon and locality).

Sowerbyella soudleyensis Jones, 1928: 417; pl. 21, figs 5, 6 from Horderley Sandstone (L. Caradoc), Whittingslow, Shropshire, England (revised Williams 1963: 432; pl. 12, figs 1–8).

Plectambonites subcarinatus Ulrich, *in* Butts 1926: 126; pl. 31, figs 9–15 from Chickamauga Limestone (L.–M. Caradoc), Cedar Mountain, Argo, Alabama, USA (revised Cooper 1956: 797; pl. 200, figs 15–18).

Sowerbyella (*Sowerbyella*) *tamdysvensis* Misius, 1986: 150; pl. 15, fig 1–18; pl. 16, figs 1–6 from Ichkebash Formation (M. Caradoc), Djebagl Mountain, N. Khirgizia, USSR.

Sowerbyella (*Sowerbyella*) *tenera* Rõõmusoks, 1959: 34; pl. 7, figs 1–11 from Oandu Horizon (U. Caradoc), Rakvere, Estonia, USSR.

Plectambonites sericea var. *thraivensis* Reed, 1917: 885; pl. 15, figs 27–32 from Upper Drummuck Group (M. Ashgill), Thraive Glen, Girvan, Scotland (revised Mitchell 1977: 81; pl. 16, figs 9–22).

Sowerbyella (*Sowerbyella*) *trivia* Rõõmusoks, 1959: 27; pl. 4, figs 5–12 from Keila Horizon (M.–U. Caradoc), Kaikula, Estonia, USSR.

Sowerbyella (*Viruella*) *uhakuana* Rõõmusoks, 1959: 16; pl. 1, figs 3–12 from Uhaku Horizon (U. Llandeilo), Kivili River, Estonia, USSR.

Sowerbyella variabilis Cooper, 1956: 798; pl. 197, figs 35–43; pl. 202, figs 27–40 from Bromide Formation (U. Llandeilo), Hickory Creek, Criner Hills, Oklahoma, USA.

Sowerbyella varicostellata Cooper, 1956: 799; pl. 196, figs 1–8 from M. Arline Formation (U. Llandeilo), Friendsville, Concord, Tennessee, USA.

Sowerbyella verecunda Nikitin & Popov, 1983: 239; pl. 3, figs 7, 8, 10, 12, 16, 17 from Andriushenkaya Formation (M. Ordovician), Ishim River, Central Kazakhstan, USSR.

Figs 139–141 *Sowerbyella* (*Sowerbyella*) *sericea* (J. de C. Sowerby), from Horderley Sandstone Formation (L. Caradoc). Figs 139, 141 from quarry by New House, Onny Valley, Shropshire, England, Fig. 140 from Cheney Longville Lane, Onny Valley, Shropshire; Fig. 139, downwards and oblique lateral views of latex cast of a brachial valve interior, BC 6052, × 5 and × 4; Fig. 140, natural internal mould of brachial valve, BC 7303, × 5; Fig. 141, posterior, oblique lateral and downwards views of latex cast of a brachial valve, BC 6051, a, b, × 4, c, × 5.

Fig. 142 *Sowerbyella* (*Sowerbyella*) sp., natural internal mould of a brachial valve from Lower Miapo Formation (Llandeilo), Huanghuachang, Yichang County, Hubei Province, China, BC 3307, × 2·5.

Fig. 143 *Sowerbyella* (*Sowerbyella*) *fallax* Jones, 1928, holotype by monotypy, a brachial valve, the original of Reed 1917: pl. 13, fig. 14, from Craighead Limestone (U. Caradoc), Craighead Quarry, Girvan, Strathclyde, Scotland, B 73436, × 3.

Figs 144–148 *Sowerbyella* (*Sowerbyella*) *liliifera* Öpik, 1930, topotypes from Kukruse Formation (L. Caradoc), Kohtla-Jarve, Estonia, USSR Fig. 144, brachial valve interior, BB 5149, × 5; Fig. 145, pedicle valve interior, BB 5150, × 5; Fig. 146, conjoined valves, BB 5147, × 5. Fig. 147, interior of pedicle valve, BB 5151, × 5; Fig. 148, downward and lateral views of conjoined valves, BB 5148, × 3

Sowerbyella vulgata Cooper, 1956: 801; pl. 198, figs 1–22; pl. 202, figs 16–23; pl. 206, figs 8–12 from Bromide Formation (U. Llandeilo), S. of Sulphur, Murray County, Oklahoma, USA.

SPECIES QUESTIONABLY ASSIGNED

Plectambonites aequistriatus Willard, 1928: 276; pl. 3, figs 8, 9 from Ottosee Formation (L. Caradoc), Liberty Hill, Tennessee, USA (revised Cooper 1956: 775; pl. 197, figs 25–34, but no interiors figured).

Plectambonites angulatus Phleger, 1933: 18; pl. 1, fig. 1 from Barrel Spring Formation (Llandeilo–L. Caradoc), E. of Barrel Spring, Inyo Mountains, California, USA (no brachial interior figured).

Sowerbyella (*Sowerbyella*) *asperecostellata* Rozman, 1964: 155; pl. 11, figs 6–9 from Nalchan Formation (U. Ordovician), Kalychan River, Selenniyakh Mountains, NE USSR (no brachial interiors figured).

Sowerbyella cava orientale Oradovskaya, *in* Balashov *et al.* 1968: 49; pl. 47, figs 10–13 from L. Kharkindzhin Formation (Caradoc), River Inania, Omulev Mountains, NE USSR (no brachial interiors known).

Plectambonites centricarinatus Ruedemann, 1912: 92; pl. 4, fig. 7 from Indian Ladder Beds (Caradoc), Indian Ladder, Albany, New York, USA (no interiors figured).

Plectambonites crassus Willard, 1928: 278; pl. 3, fig. 10 from Holston Formation (L. Caradoc), McNutt Quarry, Sharon Springs, Virginia, USA (no interiors figured).

Leptaena? *detrita* Salter, *in* Salter & Blanford 1865: 30; pl. 3, fig. 6 from Llandeilo? beds, Kalajowar, Niti, India (no interiors known).

Sowerbyella eha Öpik, 1930: 158; pl. 9, fig. 122 from Kukruse Formaton (L. Caradoc), Kohtla, Estonia, USSR (no brachial interiors figured).

Leptaena geometrica Kutorga, 1846: 104; pl. 4, fig. 3 from middle Ordovician beds, Pulkowa, near Leningrad, USSR (no interiors figured).

Sowerbyella gigantea Cooper, *in* Schuchert & Cooper 1930: 271; pl. 1, figs 19–20 from beds of Ashgill age, Percé, Québec, Canada (no information on denticles – might be *Eoplectodonta*).

Plectambonites? *kristianiae* Holtedahl, 1916: 76; pl. 16, fig. 2 from 3cβ Beds (L. Llanvirn), Oslo City Centre, Norway (no interiors figured).

Sowerbyella medioplicata Cooper, 1956: 784; pl. 204, figs 1–5 from Upper Lincolnshire Formation (L.–M. Caradoc), Tumbling Run, Strasburg, Virginia, USA (no interiors figured).

Sowerbyella merriami Cooper, 1956: 785; pl. 269, figs 18–22 from shale below Eureka Quartzite (U. Llanvirn), Blair Ranch, Antelope Mountains, Nevada, USA (no interiors figured).

Sowerbyella? *minuta* Wilson, 1946: 50; pl. 3, fig. 23 from Cobourg Formation (U. Caradoc), Notre Dame Cemetery, Eastville, Ontaria, Canada (no interiors figured).

Sowerbyella minuta Kulkov, 1967: 67; pl. 11, figs 7–9 from L. Chagyrskaya Formation (U. Llandovery), River Yarovski, Gornoi Altai, USSR (no brachial interior figured – n.b. this is an objective homonym of *S.*? *minuta* Wilson, 1946).

Plectambonites negritus Willard, 1928: 278; pl. 3, fig. 13 from Lenoir Formation (U. Llandeilo), Catawba Valley, N. of Salem, Virginia, USA (no interiors figured).

Sowerbyella (*Viruella*) *orechovensis* Nikanorova, 1976: 115; figs 1a–b from Tallinn Horizon (Llandeilo–L. Caradoc), Buiskayar, Orekovo, Moscow syneclise, USSR (no brachial interior figured).

Sowerbyella (*Viruella*?) *orviku* Rõõmusoks, 1959: 15; pl. 1, figs 1, 2 from Uhaku Horizon (U. Llandeilo), Viyarke-Pakri, Estonia, USSR (no interiors figured).

Sowerbyella patula Öpik, 1930: 154; pl. 9, fig. 116 from Kukruse Formation (L. Caradoc), Kohtla, Estonia, USSR (no brachial interior figured).

Sowerbyella (*Sowerbyella*) *plana* Rõõmusoks, 1959: 26; pl. 4, figs 1–4 from Idavere Horizon (M. Caradoc), Aluvere, Estonia, USSR (no interiors figured).

Sowerbyella (*Sowerbyella*) *plana* Klenina, 1984: 80; pl. 7, figs 9, 13, 14, 16, 18 [name objectively preoccupied by *S. plana* Rõõmusoks] from Abaevskaya Formation (Llanvirn–Llandeilo), SE Ordatas Hill, NE Pre-Chinghiz Mountains, Kazakhstan, USSR (no interiors known).

Sowerbyella plicatifera Cooper, 1956: 791; pl. 203, figs 1–15 from Bromide Formation (U. Llandeilo), Decker's section, Nebo, Oklahoma, USA (no interiors figured).

Leptaena praecosis Sardeson, 1892: 329; pl. 4, figs 26–28 from Maquoketa Formation (Ashgill), Fillmore County, Minnesota, USA (no interiors known).

Plectambonites quinquecostata var. *depressa* Reed, 1917: 878; pl. 14, figs 18, 19 from Shalloch Formation (L. Ashgill), Shalloch Mill, Girvan, Scotland (no interiors figured).

Sowerbyella quinquecostata estona Öpik, 1930: 164; pl. 9, fig. 130 from Kukruse Formation (L. Caradoc), Kohtla, Estonia, USSR (no interiors figured).

Leptaena repanda Salter, *in* Salter & Blanford 1865: 29; pl. 3, fig. 3 from lower Ordovician beds, Damchen, Niti, NW India, and probable junior synonyms *Leptaena himalensis* and *L. himalensis* var. *textilis* Salter, *in* Salter & Blanford 1865: 28; pl. 3, figs 4, 5 from similar beds at Chorhoti Pass, Niti (no interiors known, but revised Reed 1912).

Sowerbyella? *rotunda* Rozman, 1964: 157; pl. 12, figs 1–5 from Nalchan Formation (U. Ordovician), Kalychan River, Selenniyakh Mountains, NE USSR (no brachial interiors figured).

Leptaena schmidti [Törnquist MS] Lindström, *in* Angelin & Lindström 1880: 29; pl. 14, figs 25, 26 from late Ordovician Beds, Boda, Sweden (no interiors figured).

Sowerbyella rugosa triradiata Butts, 1942: 113; pl. 96, fig. 9 from Oranda Formation (L. Caradoc), W. of Strasburg, Virginia, USA (no interiors figured).

Sowerbyella silicica Cooper, 1956: 793; pl. 196, figs 20–26 from Arline Formation (U. Llandeilo), Porterfield Quarry, Virginia, USA and subspecies *nana* Cooper, 1956: 794; pl. 196, figs 15–19, from same horizon and locality (no interiors figured).

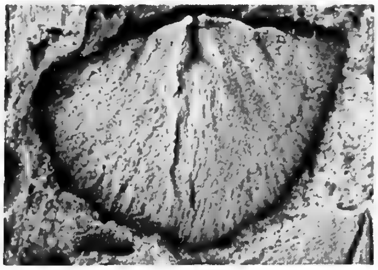
Sowerbyella subovalis Wilson, 1932: 393; pl. 4, figs 10, 11 from L. Coburg formation (U. Caradoc), Cornwall, Ontario, Canada (no interiors figured).

Orthis tennuissimestriata M^c^Coy, 1846: 35; pl. 3, fig. 20 from beds of Caradoc age, Slieve Roe, Co. Wicklow, Ireland (no interiors figured).

Chonetes? *thebavensis* Reed, 1906: 57; pl. 5, fig. 16 from Naungkangyi Beds (? L. Caradoc), Lebyaungbyan, Northern Shan States, Burma (no interiors known).

Leptaena trabeata Lindström, *in* Angelin & Lindström 1880: 30; pl. 17, figs 1–4 from Upper Ordovician Beds (?Fjäcka Shales), Västergötland, Sweden (no interiors figured).

Sowerbyella undosa Öpik, 1930: 159; pl. 21, figs 265–6 from Idavere Formation (L. Caradoc), Kohtla, Estonia, USSR (no interiors figured).



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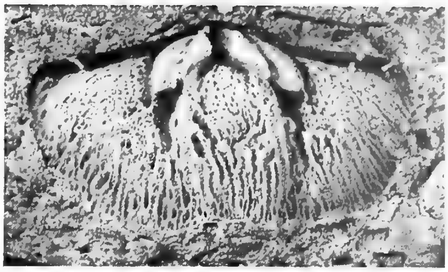

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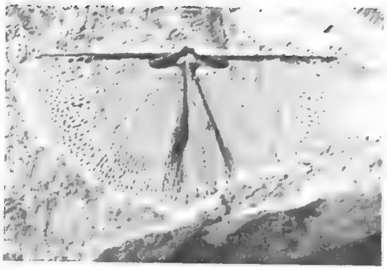

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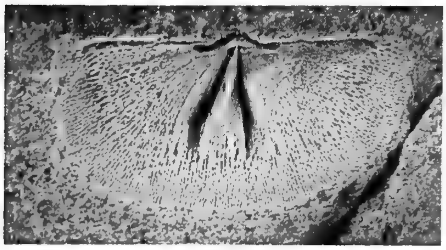

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151b

Figs 149–152 *Sowerbyella* (*Eochonetes*) *advena* Reed, 1917, from Starfish Bed, South Threave Formation (Ashgill: U. Rawtheyan), 650 m ENE of South Threave Farmhouse, Girvan, Strathclyde, Scotland. Fig. 149, natural internal mould of pedicle valve on the same slab as the lectotype, BC 10817, × 5; Fig. 150, natural internal mould of pedicle valve, lectotype selected Cocks 1978: 100, the original of Reed 1917: pl. 21, fig. 6, B 73920, × 3; Fig. 151a, downward view of natural internal mould of brachial valve and 151b, tilted obliquely to give an anterior view of the distinctive '*Thaerodonta*' hinge line, BC 10291, × 3 and × 5; Fig. 152, interior of natural mould of brachial valve, the original of Reed 1917: pl. 21, fig. 11, B 73919, × 3.

Sowerbyella wilsoni Reed, 1936: 41; pl. 4, figs 4–8 from Naungkangyi Formation (?L. Caradoc), Taung-bu, Southern Shan States, Burma (no brachial interior figured).

SPECIES REJECTED

Leptaena aspera James, 1874: 151 (citing as types the specimens figured by Meek 1873: pl. 5, figs 3f, 3g under *Leptaena sericea*) from the Cincinnati Group (L.–M. Caradoc), Ohio River, Cincinnati, Ohio (the illustrated specimens show a bilobed cardinal process, and the species appears to be an early davidsoniacean).

Sowerbyella ? *austrum* Öpik, 1953: 14; pl. 3, figs 17, 18 from Wapentake Formation (U. Llandovery), Heathcote, Victoria, Australia (to *Jonesea* gen. nov.)

Sowerbyella transversalis brevis Northrop, 1939: 176; pl. 15, figs 11–14 from Clemville Formation (L. Wenlock), Clemville, Gaspé, Québec, Canada (no interiors known, but shape almost certainly indicates *Leangella*).

Sowerbyella fasciola Yin, 1937: 288; pl. 1, fig. 10 from beds of probable Caradoc age, Shihtien, W. Yunnan Province, China (only brachial valve external known, but it looks like a strophomenacean).

Sowerbyella ? *plebia* Talent, 1965: 23; pl. 5, figs 6, 7 from McIvor Formation (Pridoli?), Redcastle, Victoria, Australia (to *Plectodonta* (*Plectodonta*)).

SOWERBYELLA (EOCHONETES) Reed, 1917

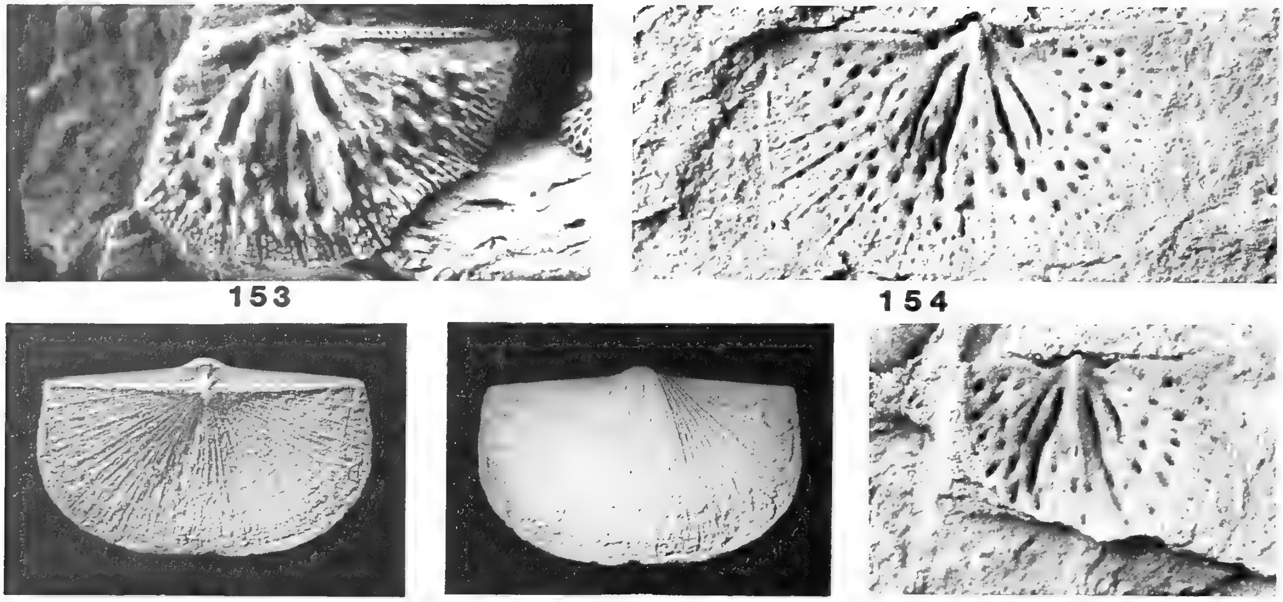
Figs 149–152

1917	*Chonetes* (*Eochonetes*) Reed: 916
1928	*Sowerbyella* Jones: 474 *pars*
1949	*Thaerodonta* Wang: 19
1965	*Thaerodonta* Howe: 648
1965	*Eoplectodonta* Williams: H380 *pars*
1965	*Eochonetes* Williams: H380
1967	*Thaerodonta* Havlíček: 58
1972	*Thaerodonta* Howe: 441
1974	*Thaerodonta* Amsden: 61
1974	*Eochonetes* Amsden: 61
1977	*Eoplectodonta* Mitchell: 89 *pars*
1981	*Thaerodonta* Rõõmusoks: 61

TYPE SPECIES. *Chonetes* (*Eochonetes*) *advena* Reed, 1917. Type species of *Thaerodonta* is *Thaerodonta aspera* Wang, 1949.

DIAGNOSIS. Like *Sowerbyella* (*Sowerbyella*) but with denticles on the brachial valve hinge line and opposing small sockets on the pedicle valve hinge line. Canals in pedicle valve hinge line variably developed, usually absent.

DISCUSSION. Close examination of topotype *Eochonetes advena* reveals the presence of denticles on the brachial valve hinge line (particularly laterally) and corresponding fossettes on the pedicle valve hinge line (Fig. 151). As discussed below, this is the only point of difference between *Thaerodonta* and *Sowerbyella*, and thus *Eochonetes* is placed here as a subgenus of *Sowerbyella*. Various plectambonitaceans, e.g. *Chonetoidea radiatula*, have perforated hinge lines in the same way as *Eochonetes* and we follow Jones (1928) in not considering this feature of generic or subgeneric importance, particularly since over half of the specimens in *Eochonetes* populations lack these canals. Since the original erection of *Thaerodonta* by Wang (1949) many authors have discussed the true generic characters and how the genus may best be separated from *Eoplectodonta*, *Sowerbyella*, *Viruella* and other closely related genera (e.g. Spjeldnaes 1957, Howe 1965, Williams 1965, Havlíček 1967, Cocks 1970, Macomber 1970, Howe 1972, Amsden 1974, Mitchell 1977, and Rõõmusoks 1981). Of all these papers, by far the best is Howe (1972) since he not only figures the hinge lines of the various genera very



Figs 153–156 *Plectodonta mariae* Kozlowski, 1929, from Taina Formation, Borshchov Group (Lochkovian), Figs 153, 155 from river bank at Krzywcze, Figs 154, 156 from Rukhotin Valley in Rukhotin Village, both Podolia, Ukraine, USSR. Fig. 153, brachial valve interior, B 81372, × 6; Fig. 154, natural internal mould of brachial valve, BB 65810, × 11; Fig. 155, dorsal and ventral views of a pair of conjoined valves, B 81371, × 4·5; Fig. 156, natural internal mould of brachial valve, BB 65811, × 11.

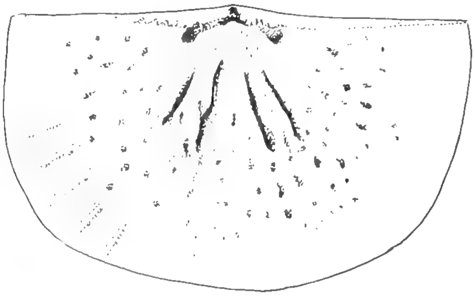


Fig. 157 *Plectodonta mariae* Kozlowski, 1929, internal mould of brachial valve, from Taina Formation (Lochkovian), Rukhotin, Podolia, Ukraine, USSR (based on BB 65810), × 12.

well, but also discusses their various characters. We follow Wang and Howe in accepting the nature of the denticles on the hinge line as the fundamental difference between *Thaerodonta* and *Eoplectodonta* – in the former the protuberances are all on the brachial valve and the pits all on the pedicle valve, whilst in *Eoplectodonta* the denticles are on the pedicle valve and the pits on the brachial valve. In some species and specimens of *Thaerodonta* the denticles are confined to the lateral parts of the hinge line, in contrast to *Eoplectodonta* in which some species only have denticles in the centre, near the teeth. However, again following Howe (1972), apart from the presence of denticles we can find no consistent differences between *Thaerodonta* and *Sowerbyella* and thus we treat *Thaerodonta* as a subgenus of *Sowerbyella* here. However, in a few species attributed to *Sowerbyella* by Howe, such as '*S.*' *rugosa*, because of the partial denticulation we prefer to refer them to *Eochonetes*. Various authors have found differences between *Sowerbyella* and *Thaerodonta* in their side septa; however, there is so much variation in *Sowerbyella* that we cannot use these features to separate the two subgenera. Some authors, e.g. Wang (1949) and Howe (1972), have argued that there are strongly developed accessory teeth and delthyrial thickening in *Thaerodonta* which distinguish it from *Eochonetes*, but we can find no substantial differences between them. Therefore *Eochonetes* is now established as a senior synonym of *Thaerodonta*.

SPECIES ASSIGNED

Chonetes (*Eochonetes*) *advena* Reed, 1917: 915; pl. 21, figs 6–11 from Drummuck Group (M. Ashgill), Thraive Glen, Girvan, Scotland.

Thaerodonta aspera Wang, 1949: 20; pl. 11, figs 1–5 from Elgin Member of Maquoketa Formation (L. Ashgill), Orleans, Iowa, USA.

Eochonetes canaliferus Havlíček, 1971: 69; pl. 20, figs 12, 13 from U. Ktaoua Formation (Ashgill), Jbel Mimount, Maïdere, Morocco.

Eochonetes celticus Mitchell, 1977: 88; pl. 17, figs 20–25 from Junction Beds (Caradoc–Ashgill), Pomeroy, Co. Tyrone, Northern Ireland.

Thaerodonta convexa Rõõmusoks, 1981: 67; pl. 2, figs 1–5 from Kõrgessaare Formation (L. Ashgill), Paopa, Estonia, USSR.

Thaerodonta dignata Wang, 1949: 22; pl. 11, figs 1–6 from L. Maquoketa shale (L. Ashgill), Clermont, Iowa, USA.

Thaerodonta johnsonella Amsden, 1974: 60; pl. 23, figs 3a–e; pl. 24, figs 1a–u from Leemon Formation (U. Ashgill), Blue Shawnee Creek, Cape Girardeau County, Missouri, USA.

Thaerodonta magna Howe, 1965: 651; pl. 82, figs 1–7 from Aleman Limestone (L. Ashgill), Hueco Mountains, Texas, USA.

Thaerodonta moelsi Rõõmusoks, 1981: 66; pl. 1, figs 6–11 from Kõrgessaare Formation, (L. Ashgill), Kõrgessaare, Estonia, USSR.

- *Thaerodonta mucronata* Howe, 1965: 648; pl. 81, figs 18–29 from Aleman Limestone (L. Ashgill), Trans-Pecos, Texas, USA (and subspecies *scabra* Howe, 1965: 648; pl. 82, figs 9–11, also from the Aleman Limestone)
- *Plectambonites rugosus noquettensis* Hussey, 1926: 160; pl. 7, fig. 6 from Ogontz Member of Stonington Formation (Caradoc–Ashgill), east of Church, Michigan, USA.
- *Thaerodonta nubila* Rõõmusoks, 1981: 68; pl. 2, figs 6–10 from Adila Formation (U. Ashgill), Kaapsalyski Cliff, Estonia, USSR.
- *Leptaena recedens* Sardeson, 1892: 330; pl. 4, figs 29–32 from Cincinnati Group (L. Ashgill), Spring Valley, Fillmore County, Minnesota, USA (revised Wang 1949: 20; pl. 11, figs 1–3 and Howe 1988: 214; figs 2.9–2.12, 2.14–2.17, 10, 11).
- *Plectambonites rugosa-clarksvillensis* Foerste, 1912: 127; pl. 1, figs 7a–c; pl. 10, figs 7a–d from the Richmond Group (L. Ashgill), Oxford, Ohio, USA (revised Howe 1972: 445; pl. 1, figs 1–3 and Howe 1979: 4; pl. 2, figs 14–17 and placed in synonymy of *Thaerodonta recedens* by Howe 1988: 214).
- *Thaerodonta saunjaensis* Rõõmusoks, 1981: 65; pl. 1, figs 1–5 from Saunja Member of Voore Formation (L. Ashgill), Miaremetsa, Estonia, USSR.
- *Leptaena saxea* Sardeson 1892: 330; pl. 4, figs 33–35 from Cincinnati Group (L. Ashgill), Bristol, Fillmore County, Minnesota, USA (revised Wang 1949: 21; pl. 11, figs 1–5).

SPECIES QUESTIONABLY ASSIGNED

- *Plectambonites glabra* Shaler, 1865: 64 from Ellis Bay Formation (M.–U. Ashgill), Anticosti Island, Quebec, Canada (revised by Twenhofel (1928: 190) as *P. sericeus* var. *glaber*, but unfigured; probably a *Sowerbyella* but true subgenus unknown).

SOWERBYELLA (RUGOSOWERBYELLA) Mitchell, 1977

1977 *Sowerbyella* (*Rugosowerbyella*) Mitchell: 83

TYPE SPECIES. *Plectambonites subcorrugatella* Reed, 1917, a subjective senior synonym of *Ptychoglyptus ambiguus* Reed, 1952.

DIAGNOSIS. Like *Sowerbyella* (*Sowerbyella*) but with concentric rugae truncated and offset by accentuated costae.

REMARKS. Mitchell's figures (1977: pl. 16, figs 31, 32) again call attention to the fact that a median septum is sometimes present and sometimes absent within a single population of *Sowerbyella*, and this feature cannot be used as a generic character. Of the two specimens of *S. (R.) insueta* figured by Klenina (1984: pl. 8) only the holotype (fig. 19) has concentric rugae over the whole valve: the other specimen (fig. 18) has strong posterolateral rugae but these are not developed in the central part of the valve.

SPECIES ASSIGNED

- *Plectambonites subcorrugatella* Reed, 1917: 886; pl. 15, figs 33, 34 from Whitehouse Group (L. Ashgill), Shalloch Mill, Girvan, Scotland, a senior synonym of *Ptychoglyptus shallochensis* Reed, 1935: 7; pl. 1, fig. 5 from the same horizon and locality, *Ptychoglyptus ambiguus* Reed 1952: 56; pl. 2, figs 15, 16 from the Killey Bridge Formation (L. Ashgill), Killey Bridge, Pomeroy, Co. Tyrone, Northern Ireland and *Sowerbyella foveata* Reed, 1952: 52; pl. 2, fig. 11 from the same horizon and locality (all revised Mitchell 1977: 83; pl. 16, figs 23–27).

SPECIES QUESTIONABLY ASSIGNED

- *Sowerbyella bellarugosa* Ulrich & Cooper, 1938: 186; pl. 38, figs 1–3 from Antelope Valley Formation (U. Llanvirn), Ikes Canyon, Nevada, USA (certainly rugose and a *Sowerbyella*; uncertainly assigned to this subgenus).
- *Sowerbyella* (*Viruella*) *praestans* Klenina, *in* Klenina *et al.* 1984: 83; pl. 8, figs 18, 19 from Babanskaya Formation (Caradoc), SW Pre-Chinghiz Mountains, Kazakhstan, USSR (certainly rugose and a *Sowerbyella*; uncertainly assigned to this subgenus).
- *Sowerbyella* ? *rosettana* Henningsmoen, 1948: 396; pl. 24, figs 9–12 from Red Tretaspis Mudstone (L. Ashgill), Jonstorp, Västergötland, Sweden (certainly rugose and a *Sowerbyella*; no interiors illustrated).

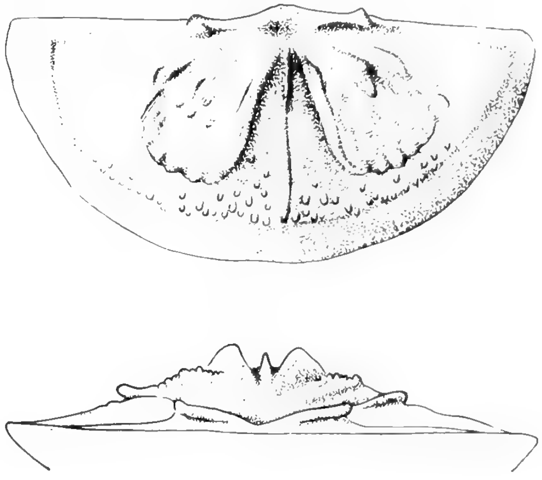


Fig. 158 *Cooperea siphonata* (Cooper, 1956), interior views of the brachial valve, from Pratt Ferry Formation (Llandeilo), Pratt Ferry, Alabama, USA (based on BC 10305), × 15.

Subfamily **CRASPEDELIINAE** subfam. nov.

DIAGNOSIS. Bema divided. Cardinal process undifferentiated (i.e. present but fused and indivisible laterally from its surrounding structures, see Fig. 158).

GENERA ASSIGNED. *Craspedelia* Cooper, 1956; *Cooperea* gen. nov.

RANGE. Llandeilo (*Craspedelia marginata*) to M. Caradoc (*Craspedelia gabata*).

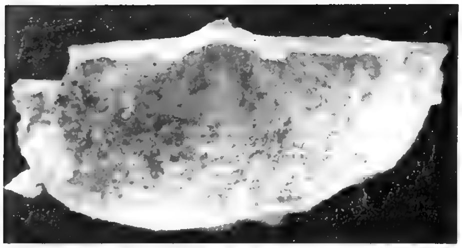
REMARKS. This new subfamily differs from the other two within the family in having an undifferentiated cardinal process, which we feel warrants separation at subfamilial level. It differs from the Ptychoglyptinae in its divided bema.

CRASPEDELIA Cooper, 1956
Figs 164, 165

1956 *Craspedelia* Cooper: 772
1965 *Craspedelia* Williams: H383

TYPE SPECIES. *Craspedelia marginata* Cooper, 1956.

DIAGNOSIS. As for subfamily. Geniculate with additional anterior deflection and with a fold and sulcus. No ornament known.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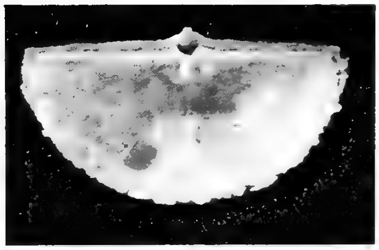
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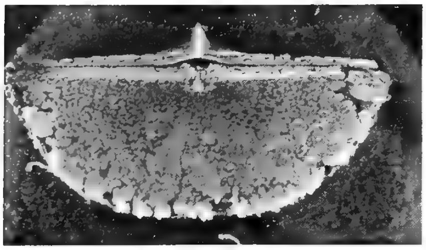
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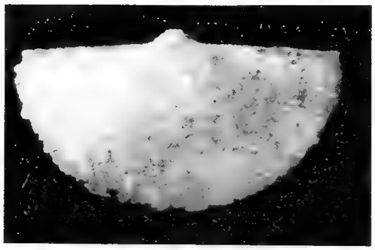
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164a


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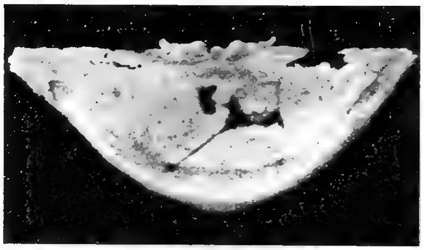
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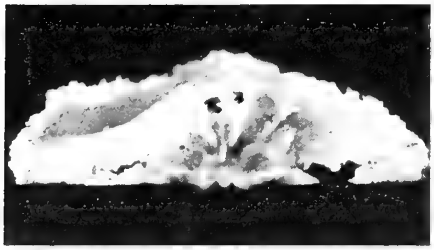
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165c


166a


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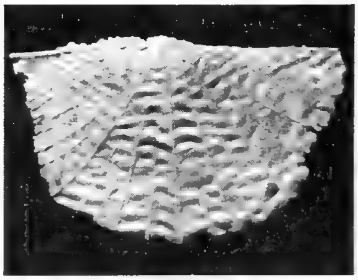

166b


168

Figs 159–163 *Cooperea siphonata* (Cooper, 1956) gen. nov., from Pratt Ferry Formation (Llandeilo), SE of Pratt Ferry, Blocton, Alabama, USA. Fig. 159, interior of pedicle valve, BC 10303, × 10; Fig. 160, interior of brachial valve, BC 10305, × 10; Fig. 161, dorsal and ventral views of a pair of conjoined valves, BC 10302, × 10; Fig. 162, pair of conjoined valves, holotype, the original of Cooper 1956: pl. 210, figs 17, 18, 21, 22, USNM 117470a, × 10; Fig. 163, interior of brachial valve, the original of Cooper 1956: pl. 210, figs 23, 24, USNM 117470e, × 10.

Figs 164, 165 *Craspedelia marginata* Cooper, 1956, from Pratt Ferry Formation (Llandeilo), SE of Pratt Ferry, Blocton, Alabama, USA. Fig. 164, external and internal views of a pedicle valve, BC 7300, × 8; Fig. 165, external, posterior and internal views of a brachial valve, BC 7301, × 8.

Figs 166–168 *Ptychoglyptus virginiensis* Willard, 1928, from Pratt Ferry Formation (Llandeilo), SE of Pratt Ferry, Blocton, Alabama, USA. Fig. 166, dorsal and ventral views of a pair of conjoined valves, BC 10317, × 3; Fig. 167, brachial valve interior, BC 10316, × 3·5; Fig. 168, brachial valve interior, BC 10318, × 7.

REMARKS. *Craspedelia* has previously been assigned to the Bimuriidae, but that family has a simple cardinal process whilst the cardinal process of *Craspedelia* is undoubtedly undercut. The geniculation is very distinctive, buckling both ways and paralleled in the Plectambonitacea only by *Reinversella*.

SPECIES ASSIGNED

Craspedelia gabata Williams, 1962: 179; pl. 17, figs 11, 12, 16, 17 from lower Ardwell Greywackes (M. Caradoc), Pinmore, Girvan, Scotland.

Craspedelia marginata Cooper, 1956: 773; pl. 213, figs 1–20 from Pratt Ferry Formation (Llandeilo), Pratt Ferry, Alabama, USA.

Craspedelia tata Popov, 1980*a*: 55; pl. 17, figs 6–9 from Erkebidaikski Horizon (M. Ordovician), Tselinogradsk, N. Kazakhstan, USSR.

SPECIES QUESTIONABLY ASSIGNED

Craspedelia sp. of Nikitin & Popov 1984: 151; pl. 18, figs 3, 4 from Sargaldakskaya Formation (U. Caradoc), Sargaldak River, Chinghiz Mountains, Kazakhstan, USSR (no interiors known).

COOPEREA gen. nov.
Figs 158–163

TYPE SPECIES. *Bimuria siphonata* Cooper, 1956. Named after Dr G.A. Cooper.

DIAGNOSIS. Like *Craspedelia* but with no geniculation.

REMARKS. The species assigned to *Bimuria* by Cooper (1956) can be divided into two groups, the first, including the type species *B. superba*, has a simple cardinal process, but the second group, consisting of *B. siphonata* and *B. immatura*, has an undercut cardinal process and so can be put into a different family, the Sowerbyellidae. The new genus is close to *Craspedelia* in morphology, but in very many specimens lacks any sign of geniculation or other deviation from normal plectambonitacean convexity. *C. siphonata* is common in the Pratt Ferry Formation; Dr G. A. Cooper very kindly allowed one of us (L.R.M.C.) to pick over briefly some duplicate residues and there are now over 80 valves in the British Museum (Natural History) registered (including BC 7289–99). In none of the brachial valves available to us or to Cooper (1956: 770) is a cardinal process preserved; this may however be owing to the lack of silicification of the very thin sheet-like cardinal process which we think may have been present between the robust socket plates.

SPECIES ASSIGNED

Bimuria immatura Cooper, 1956: 776; pl. 211, figs 1–13 from Effna–Rich Valley Formation (L. Caradoc), Porterfield Quarry, Virginia, USA.

Bimuria siphonata Cooper, 1956: 770; pl. 210, figs 17–24 from Pratt Ferry Formation (Llandeilo), Pratt Ferry, Alabama, USA.

Subfamily **PTYCHOGLYPTINAE** Cooper, 1956

1956 Ptychoglyptinae Cooper: 815
1965 Ptychoglyptinae Williams: H381

DIAGNOSIS. Weak bema not divided. Cardinal process differentiated.

REMARKS. The very distinctive ornament of *Ptychoglyptus* can only be regarded as a generic character, nevertheless the genus stands on its own in view of the unique combination of possessing an undivided bema, side septa and undercut cardinal process. Cooper (1956: 815) erected the subfamily on the 'poorly developed septa in the brachial valve' as opposed to the Sowerbyellinae, but they are present in some *Ptychoglyptus* and we prefer to separate the subfamily on the undivided bema.

GENUS INCLUDED. *Ptychoglyptus* Willard, 1928.

RANGE. L.–U. Caradoc.

PTYCHOGLYPTUS Willard, 1928
Figs 166–168

1928 *Ptychoglyptus* Willard: 283
1956 *Ptychoglyptus* Cooper: 815
1965 *Ptychoglyptus* Williams: H381

TYPE SPECIES. *Ptychoglyptus virginiensis* Willard, 1928.

DIAGNOSIS. Ornament of small rugae interrupted by costellae.

REMARKS. The bema and side septa are not developed in most members of the population; nevertheless, when they are seen in gerontic specimens the bema can be seen to be undivided.

SPECIES ASSIGNED

Ptychoglyptus virginiensis var. *irregularis* Reed, 1941: 274; pl. 5, fig. 8 from Balclatchie Beds (L. Caradoc), Balclatchie, Girvan, Scotland.

Ptychoglyptus virginesis [sic] *mendocina* Levy & Nullo, 1975: 27; pl. 1, figs 1–5 from L. Caradoc beds, Ponon-Trehué, Mendoza, Argentina.

Ptychoglyptus valdari Spjeldnaes, 1957: 58; pl. 1, figs 1–3 from Zone 4bα (M. Caradoc), Slependen, Oslo, Norway.

Ptychoglyptus virginiensis Willard, 1928: 283; pl. 2, fig. 12 from Effna Formation (L. Caradoc), McNutt Quarry, Bland, Virginia, USA.

SPECIES QUESTIONABLY ASSIGNED

Ptychoglyptus bellarugosus Cooper, *in* Schuchert & Cooper 1930: 269; pl. 1, fig. 5 from U. Ashgill Beds, Priest's Road, Percé, Québec, Canada (no interiors known).

Ptychoglyptus geniculatus Oradovskaya, *in* Balashov *et al.* 1968: 50; pl. 47, figs 1–5 from Kharkindzhin Formation (Caradoc), Inaniya River, Omulev Mountains, NE USSR (no interiors illustrated).

Ptychoglyptus ? kindlei Cooper, 1956: 816; pl. 172, figs 7–12 from boulder in Mystic Conglomerate (Llandeilo–Caradoc), Stanbridge, Québec, Canada (no interiors known).

Ptychoglyptus ? matura Cooper, 1956: 817; pl. 174, figs 5, 6 from Pratt Ferry Formation (Llandeilo), Pratt Ferry, Alabama (no interiors known).

Ptychoglyptus pauciradiatus Reed, 1932*a*: 122; pl. 18, figs 1, 2 from Hovin Sandstone (Caradoc), Grimsåsen, Trondheim, Norway (no interiors illustrated).

Rafinesquina ? ringerikiensis Holtedahl, 1916: 30; pl. 3, fig. 7 from Zone 4b (M.–U. Caradoc), Bratterud, Ringerike, Norway (no interiors known).

Ptychoglyptus shanensis Reed, 1932*b*: 195; pl. 3, fig. 15 from Pindaya Formation (Caradoc?), Yeosin, Southern Shan States, Burma (no interiors known).

Ptychoglyptus ulrichi Endo, 1932: 46; pl. 35, figs 1–6 from

Middle Ordovician beds, Huang-pa-yi, Shaanxi Province, China (no interiors known).

Ptychoglyptus 'ex gr. *virginiensis*' of Rozman 1981: 138; pl. 31, figs 1–3 from *Christiania subquadrata* beds (Llandeilo), Agach-Ula, W. Mongolia (no interiors known).

Ptychoglyptus sp. of Klenina 1984: 86; pl. 8, fig. 17 from Sargaldakskaya Formation (U. Caradoc), NE Prechinghiz Hills, Kazakhstan, USSR (no interiors known).

Ptychoglyptus sp. of Nikitin & Popov 1984: 150; pl. 18, figs 1, 2 from Sargaldakskaya Formation (U. Caradoc), Sargaldak River, Chinghiz Mountains, Kazakhstan, USSR (no interiors known).

SPECIES REJECTED

Ptychoglyptus ambiguus Reed, 1952: 56; pl. 2, figs 15, 16 from Killey Bridge Formation (L. Ashgill), Killey Bridge, Pomeroy, Northern Ireland (junior synonym of *Rugosowerbyella subcorrugatella*).

Ptychoglyptus shallochensis Reed, 1935: 7; pl. 1, fig. 5 from Whitehouse Group (L. Ashgill), Shalloch Mill, Girvan, Scotland (junior synonym of *Rugosowerbyella subcorrugatella*).

Ptychoglyptus ulrichi Endo, *sensu* Fu 1982: 118; pl. 36, fig. 1 from Xiliangsi Formation (Arenig–Llanvirn), Liangshan, Nanzheng County, S. Shaanxi, China (wrong ornament for *Ptychoglyptus*, no interior known, superfamily uncertain).

PLECTAMBONITACEAN GENERA UNASSIGNED TO FAMILIES

It is probable that *Goniotrema*, *Leptoptilum*, *Nabiaoia*, *Paucicostella*, *Pseudoanisopeurella* and *Ukoa* are all plectambonitaceans, but they cannot yet be assigned to any family with confidence, largely because the published material is inadequate.

GONIOTREMA Ulrich & Cooper, 1936

1936	*Goniotrema* Ulrich & Cooper: 626
1938	*Goniotrema* Ulrich & Cooper: 193
1956	*Goniotrema* Cooper: 711
1965	*Goniotrema* Williams: H373

TYPE SPECIES. *Goniotrema perplexum* Ulrich & Cooper, 1936.

DISCUSSION. Only a single specimen of the genus has ever been found, although both valves are present and they are now disarticulated. The cardinal process is not undercut but may not be completely preserved (Cooper 1956: 711) and the correct systematic position of the genus remains unknown. There is no bema and no side septa, although a weak platform is developed, and the genus may perhaps be a leptellinid.

SPECIES ASSIGNED

Goniotrema perplexum Ulrich & Cooper, 1936: 626 (illustrated Ulrich & Cooper 1938: pl. 40, figs 23–28) from U. Pogonip Group (Llanvirn), Ikes Canyon, Nevada, USA.

LEPTOPTILUM Öpik, 1930

1930	*Leptestia* (*Leptoptilum*) Öpik: 130
1960	*Leptoptilum* Sokolskaya: 208
1965	*Leptestia* Williams: H373 *pars*

TYPE SPECIES. *Leptestia* (*Leptoptilum*) *bekkeri* Öpik, 1930.

DISCUSSION. Öpik (1930: pl. 7, fig. 81) only figured a broken fragment of pedicle valve interior and another broken pedicle valve exterior upon which no generically diagnostic characters can be seen. Until the type species is properly revised from topotype specimens the genus should remain of doubtful validity. Öpik distinguished his new subgenus on the basis of distinctive transverse sculpture, but this cannot be seen clearly in his illustration.

SPECIES ASSIGNED

Leptestia (*Leptoptilum*) *bekkeri* Öpik, 1930: 131; pl. 7, fig. 81 from Kukruse Formation (L. Caradoc), Kohtla, Estonia, USSR.

SPECIES QUESTIONABLY ASSIGNED

Plectambonites transversum Pander, 1830 from U. Arenig–Llandeilo, south of Leningrad, USSR (assigned to *Leptoptilum* by Sokolskaya 1960: pl. 27, fig. 16, but no interior figured).

NABIAOIA Xu, 1979

1979	*Nabiaoia* Xu: 370

TYPE SPECIES. *Nabiaoia pusilla* Xu, 1979.

DISCUSSION. Only two brachial valves and no pedicle valve are known of this genus. They are small (width 4·2 mm and length 2·3 mm) and the structures do not appear well developed in the interiors. Although it is possible that these Lower Devonian specimens are plectambonitaceans, they might in fact be chonetaceans or even pholidostrophiids.

SPECIES ASSIGNED

Nabiaoia pusilla Xu, 1979: 371; pl. 2, figs 18–20 from Tangxiang Formation (Eifelian), Luofu of Nandan, Guangxi Province, China.

PAUCICOSTELLA Cooper, 1956

1956	*Paucicostella* Cooper: 711
1965	*Paucicostella* Williams: H373

TYPE SPECIES. *Paucicostella canadensis* Cooper, 1956.

DISCUSSION. Although Cooper (1956: 711) described the interior of this genus in generalized terms (as seen by wetting the exteriors), only the exteriors are figured, and until internal views are available the familial assignment and true status of this genus must remain doubtful.

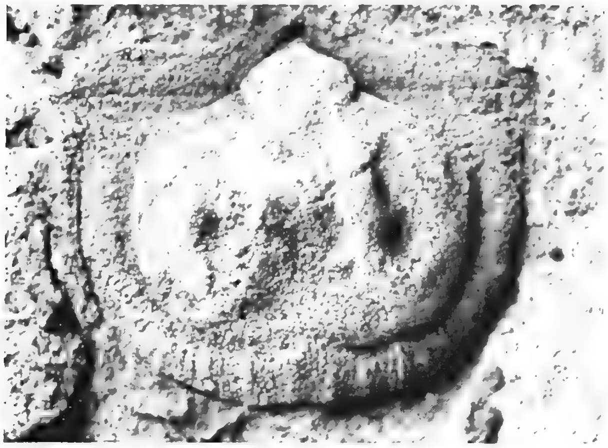
SPECIES ASSIGNED

Paucicostella canadensis Cooper, 1956: 712; pl. 172, figs 1–6; pl. 173, fig. 24 from boulder in Mystic Conglomerate (Arenig–Llanvirn), Mystic, Québec, Canada.

PSEUDOANISOPEURELLA Xu, 1978

1978	*Pseudoanisopeurella* Xu, *in* Wang & Yan: 222

TYPE SPECIES. *Pseudoanisopeurella aletheta* Xu, 1978.



169a

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169b

171a

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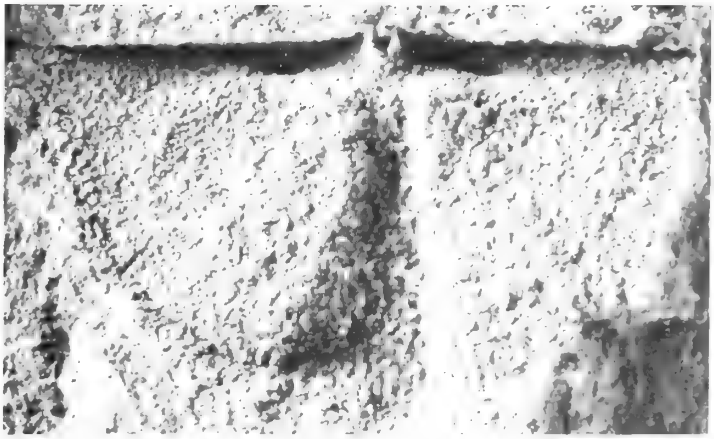
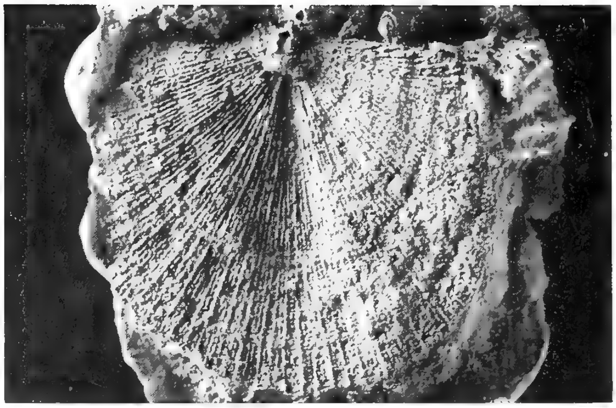


171b

Figs 169–172 *Kozhuchinella mariinica* Severgina, 1967, from Algan Formation (Tremadoc), River Poperechnaya, Kuznetz Alatau, Altai Mountains, USSR. Fig. 169, natural internal mould and latex cast of pedicle valve, the original of Severgina 1967: pl. 5, fig. 6, VSEGEI 422/1323, × 9; Fig. 170, natural internal mould of pedicle valve, holotype, the original of Severgina 1967: pl. 5, figs 4, 4A, VSEGEI 420/1323, × 7·5; Fig. 171, latex cast and natural internal mould of a brachial valve, the original of Severgina 1967: pl. 5, fig. 5, VSEGEI 423/1323, × 10; Fig. 172, latex cast of external mould of a pedicle valve, the original of Severgina 1967: pl. 5, fig. 7, VSEGEI 421/1323, × 7.

173a



173b

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173c

Figs 173, 174 *Murjukiana ilovata* Severgina, 1967, from Ilovatski Horizon (L.–M. Ordovician), Suresov, Kuznetz Alatau, Altai Mountains, USSR. Fig. 173, latex casts of interior and exterior and natural internal mould of interior of a brachial valve, the original of Severgina 1967: pl. 5, figs 12, 13, VSEGEI 430–1/1323, × 3; Fig. 174, natural internal mould of a pedicle valve, holotype, the original of Severgina 1967: pl. 5, fig. 11, VSEGEI 428/1323, × 4.

DISCUSSION. Only the exterior of a pedicle valve is figured by Wang & Yan (1978: pl. 54, fig. 20) and no internals are known; the genus can be considered a *nomen dubium*.

SPECIES ASSIGNED

Pseudoanisopeurella aletheta Xu, *in* Wang & Yen 1978: 222; pl. 54, fig. 20 from U. Miaopo Formation (L. Caradoc), Fenxiang, Yichang County, W. Hubei Province, China.

UKOA Öpik, 1932

1932 *Ukoa* Öpik: 33
1965 *Ukoa* Williams: H372

TYPE SPECIES. *Ukoa ornata* Öpik, 1932.

DISCUSSION. Although Williams (1965: H272) states the shell is impunctate, the close-up view of a part of the ornament and adjacent shell figured by Öpik (1932: pl. 8, fig. 35) suggests to us that the type species possesses pseudopunctae and is properly classified within the Strophomenida. The type species is resupinate and weakly geniculate and may be related to *Inversella* and *Ahtiella*, but the interior is unknown and thus the genus cannot be accurately classified in this paper.

SPECIES ASSIGNED

Ukoa ornata Öpik, 1932: 33; pl. 4, figs 26–28; pl. 8, fig. 35 from Aseri Formation (Llanvirn), Tsitri, Estonia, USSR.

GENERA REJECTED FROM THE PLECTAMBONITACEA

The following genera have all been attributed to the Plectambonitacea by their original authors, but we do not consider them as forming part of the superfamily.

EOCRAMATIA Williams, 1974

1974 *Eocramatia* Williams: 128

TYPE SPECIES. *Eocramatia dissimulata* Williams, 1974.

DISCUSSION. The only known specimens of *Eocramatia* are of internal and external moulds, and, although we agree with Williams (1974: 128) that no traces of pseudopunctae are seen, a final decision on this point must await the discovery of calcite shells. The cardinal process is undoubtedly bilobed and extending posteriorly from the hinge line, and with a pseudodeltidium and other features of the interarea so similar to *Gacella* and *Fardenia*, we place this genus within the Davidsoniacea.

SPECIES ASSIGNED

Eocramatia dissimulata Williams, 1974: 129; pl. 21, figs 9, 12, 14, 15; pl. 22, figs 1–3, 5, 6 from Hope Shales (L. Llanvirn), Brithdir, Shelve District, Shropshire, England.

KOZHUCHINELLA Severgina, 1967
Figs 169–172

1967 *Kozhuchinella* Severgina: 131
1984*b* *Kozhuchinella* Severgina: 48

TYPE SPECIES. *Kozhuchinella mariinica* Severgina, 1967.

DISCUSSION. The cardinal process is 'rudimental' (Severgina 1967). No shell material is preserved and thus its plectambonitacean affinities are not proven. The general form of the hinge, muscle fields and pallial markings indicate to us that placement within the Billingsellacea appears to be more appropriate. The original specimens are re-illustrated here.

SPECIES ASSIGNED

Kozhuchinella mariinica Severgina, 1967: 132; pl. 5, figs 4–7 from Algainski Horizon (Tremadoc), Poperechnaya River, Kusnetz-Altai, USSR.

MURJUKIANA Severgina, 1967
Figs 173, 174

1967 *Murjukiana* Severgina: 134

TYPE SPECIES. *Murjukiana ilovata* Severgina, 1967.

DISCUSSION. We are fortunate in being able to revise this genus from Severgina's original specimens, which consist of a brachial valve (both internal and external moulds) and a pedicle valve internal mould, all reillustrated here. In addition there are two incomplete pedicle valve internal moulds on the same slab as the brachial valve. There are no traces of pseudopunctae on any of the valve surfaces (although of course there is no original shell material remaining) and the genus does not come close to any known plectambonitacean in morphology. The general form and shape of the valves, with a normally convex pedicle valve and a more or less flat brachial valve, coupled with well-defined interareas on both valves, indicate to us that the genus is probably an orthacean. The precise details of the cardinal process are slightly obscure, but it appears to consist of a simple small knob which is connected anteriorly to a shallow myophragm which extends approximately half the valve length. Although the delthyrium seems open, there appear to be some small chilidial plates. Its precise relationships to other contemporary orthaceans remain uncertain, but its affinities might lie within the Hesperonomiidae or Orthidae.

SPECIES ASSIGNED

Murjukiana ilovata Severgina, 1967: 135; pl. 5, figs 11–13 from Ilovatski Formation (Llanvirn), Kuznetz Alatau, Altai-Sayan, USSR.

OTTADALENITES Harper, 1981

1981 *Ottadalenites* Harper, *in* Bruton & Harper: 165

TYPE SPECIES. *Ottadalenites incertus* Harper, 1981.

DISCUSSION. Only internal and external moulds of this monospecific genus are known and thus there is no proof of pseudopunctate shell structure. The cardinalia and above all the style of ornamentation seem to be very similar to those of contemporary orthids, and we find no reason for assigning this genus to the Plectambonitacea. It is also poorly preserved and based on few specimens, and may best be treated as a *nomen dubium*.

SPECIES ASSIGNED

Ottadalenites incertus Harper, *in* Bruton & Harper 1981: 165; pl. 3, figs 1–6 from Otta Conglomerate (L. Llanvirn), Otta, Norway.

UJUKITES Andreeva, 1985

1985 *Ujukites* Andreeva: 41

TYPE SPECIES. *Ujukites altaicus* Andreeva, 1985.

DISCUSSION. Although interiors of this genus are figured, they do not show the cardinal process, and this is not mentioned in the text. The general internal and external form of the type species suggest that it may be better classified within the Strophomenacea rather than the Leptestiinae where the author placed it.

SPECIES ASSIGNED

Ujukites altaicus Andreeva, 1985: 41; pl. 4, figs 7–12, 15 from Stretinski? Formation (M. Ordovician), River Tuloi, Altai Mountains, USSR.

SPECIES QUESTIONABLY ASSIGNED

Ujukites tarlykensis Andreeva, 1985: 41; pl. 4, figs 13, 14, 16–19 from Tarliski Formation (M. Ordovician), River Uiuk, Tuva, USSR.

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[1] This title means 'Geological Bureau of Hubei Province' – no authors were named in it.

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