Bulletin British Museum (Natural History)

Geology Series

Papers on
Arenig trilobites, Devonian brachiopods, Triassic demosponges, Jurassic bivalve molluscs and a Carboniferous fern

Review of the brachiopod superfamily Plectambonitacea

VOLUME 45 NUMBER 1 29 JULY 1989

The *Bulletin of the British Museum (Natural History)*, instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

Papers in the *Bulletin* are primarily the results of research carried out on the unique and ever-growing collections of the Museum, both by the scientific staff and by specialists from elsewhere who make use of the Museum's resources. Many of the papers are works of reference that will remain indispensable for years to come.

A volume contains about 400 pages, made up by two numbers: published Spring and Autumn. Subscriptions may be placed for one or more of the series on an Annual basis. Individual numbers and back numbers can be purchased and a Bulletin catalogue, by series, is available. Orders and enquiries should be sent to:

Sales Department,
Natural History Museum Publications,
British Museum (Natural History),
Cromwell Road,
London SW7 5BD

Telephone: 01-938 9386
Telex: 929437 NH PUBS G
Fax: 01-938 8709

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Geol.)

ISBN 0 565 07025 8
ISSN 0007-1471

Geology Series
Vol 45 No 1 pp 1–164

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 29 July 1989

Bull. Brit. Mus. nat. Hist. (Geol.) **45** (1):1–20

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

A. J. BECKLY

British Petroleum Development Ltd., Britannic House, Moor Lane, London EC2Y 9BU

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*

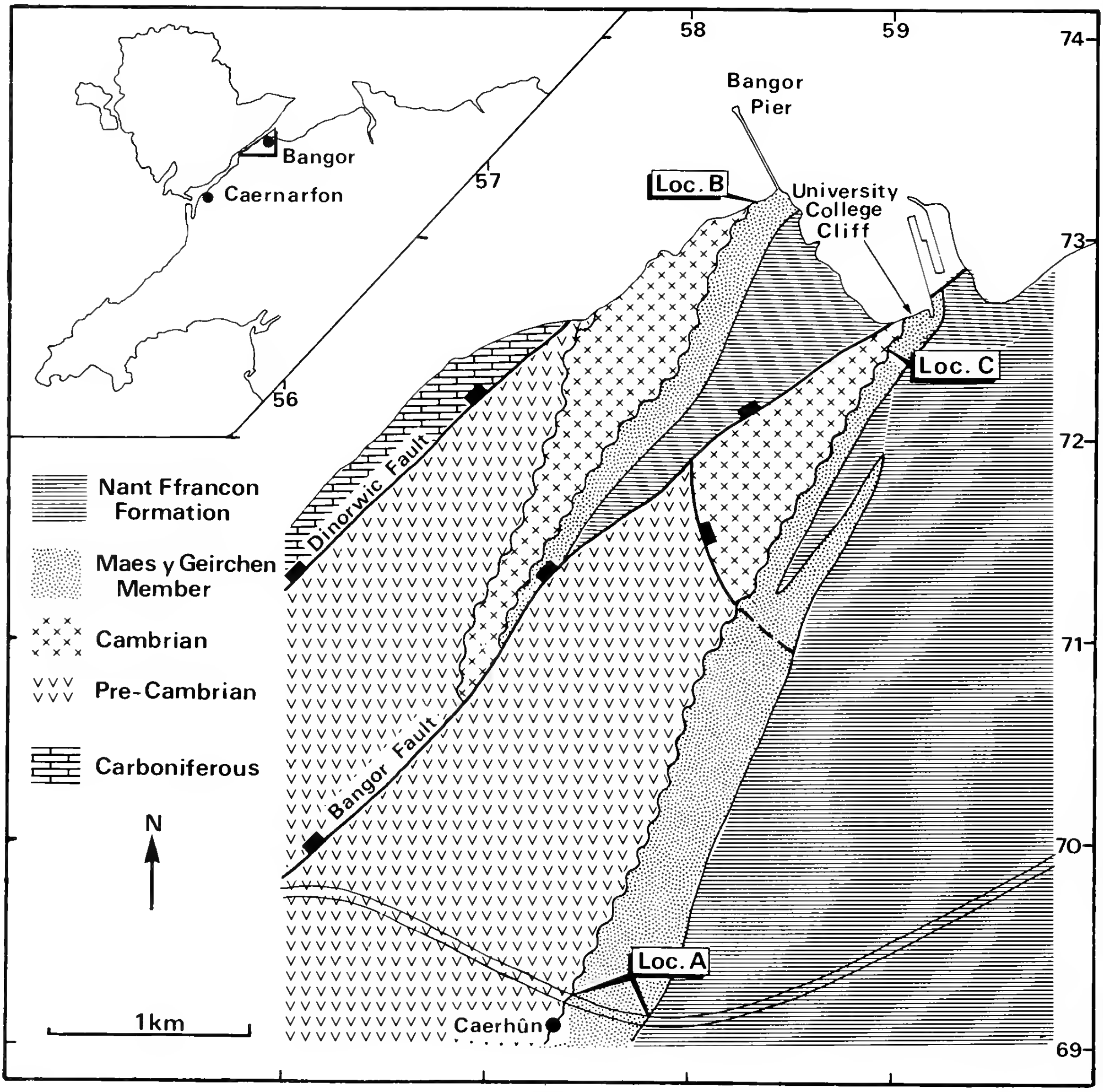


Fig. 1 Simplified geological map of the Bangor area. Loc. A, cutting on A5 near Caerhûn; Loc. B, foreshore section west of Bangor Pier; Loc. C, inland from Penrhyn Dock.

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

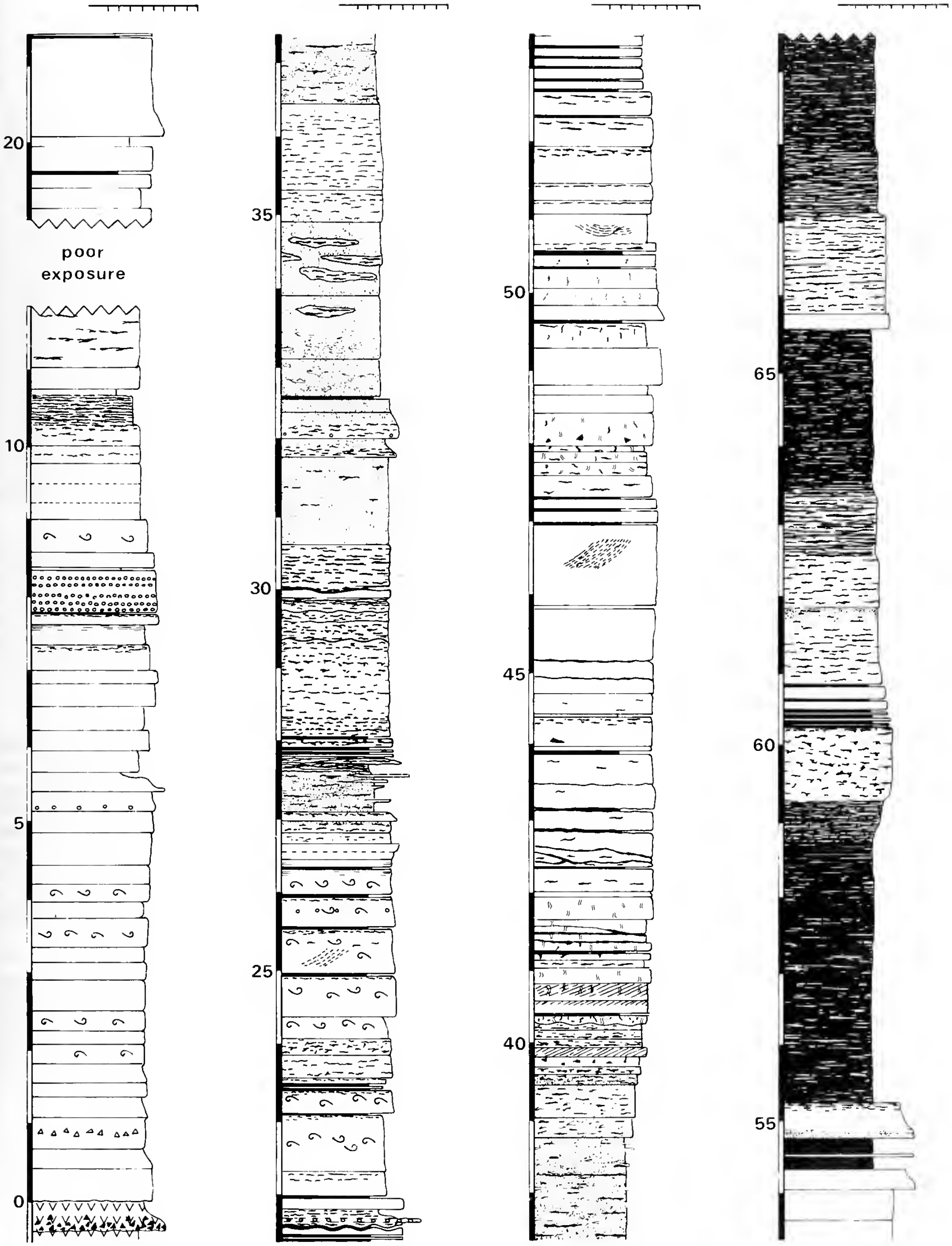


Fig. 2 Sedimentary log of the Maes y Geirchen Sandstone Member in cutting on A5 near Caerhûn. Key given with Fig. 5, p. 7.

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.

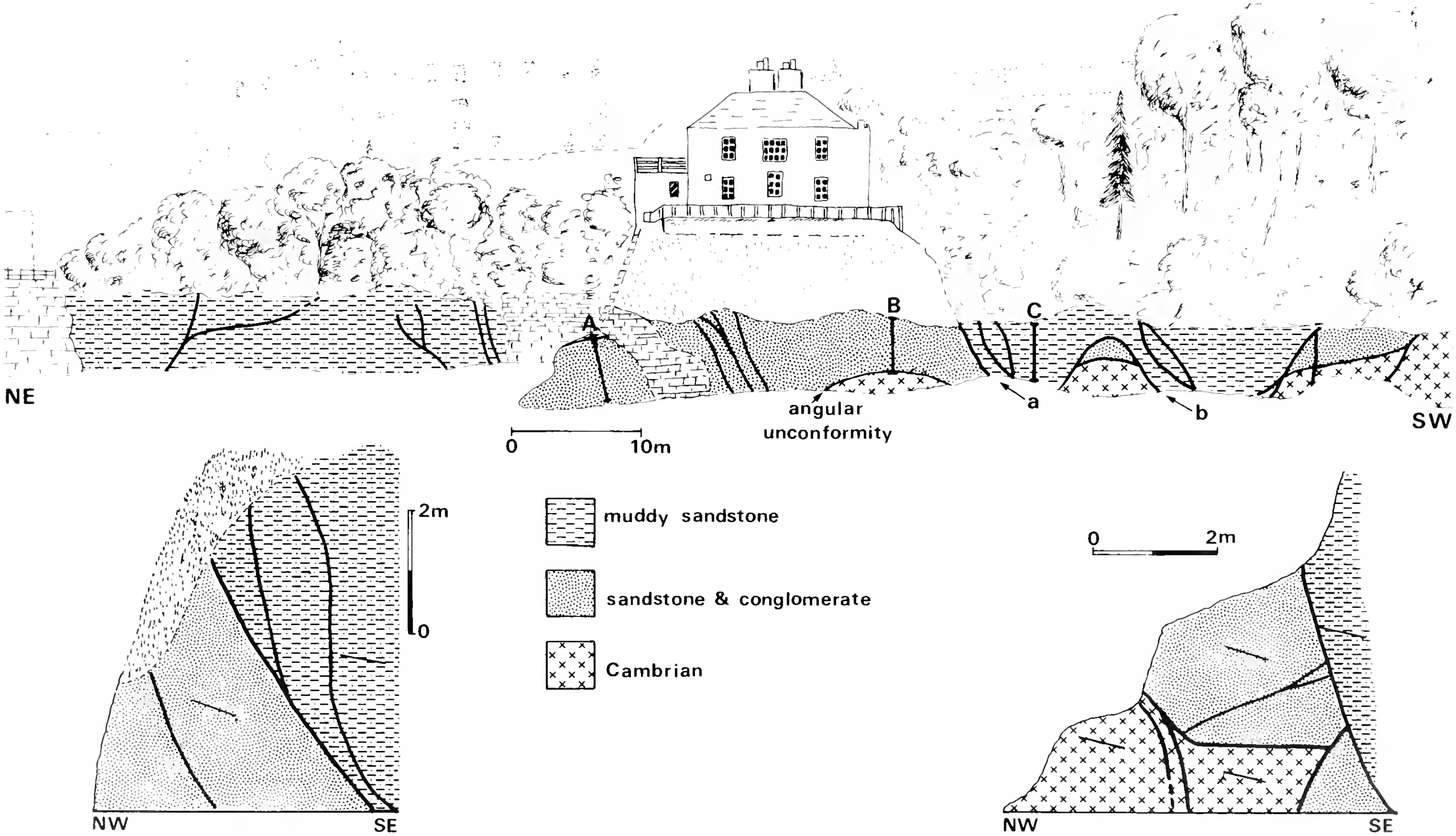


Fig. 3 Sketch of cliff section west of Bangor Pier.

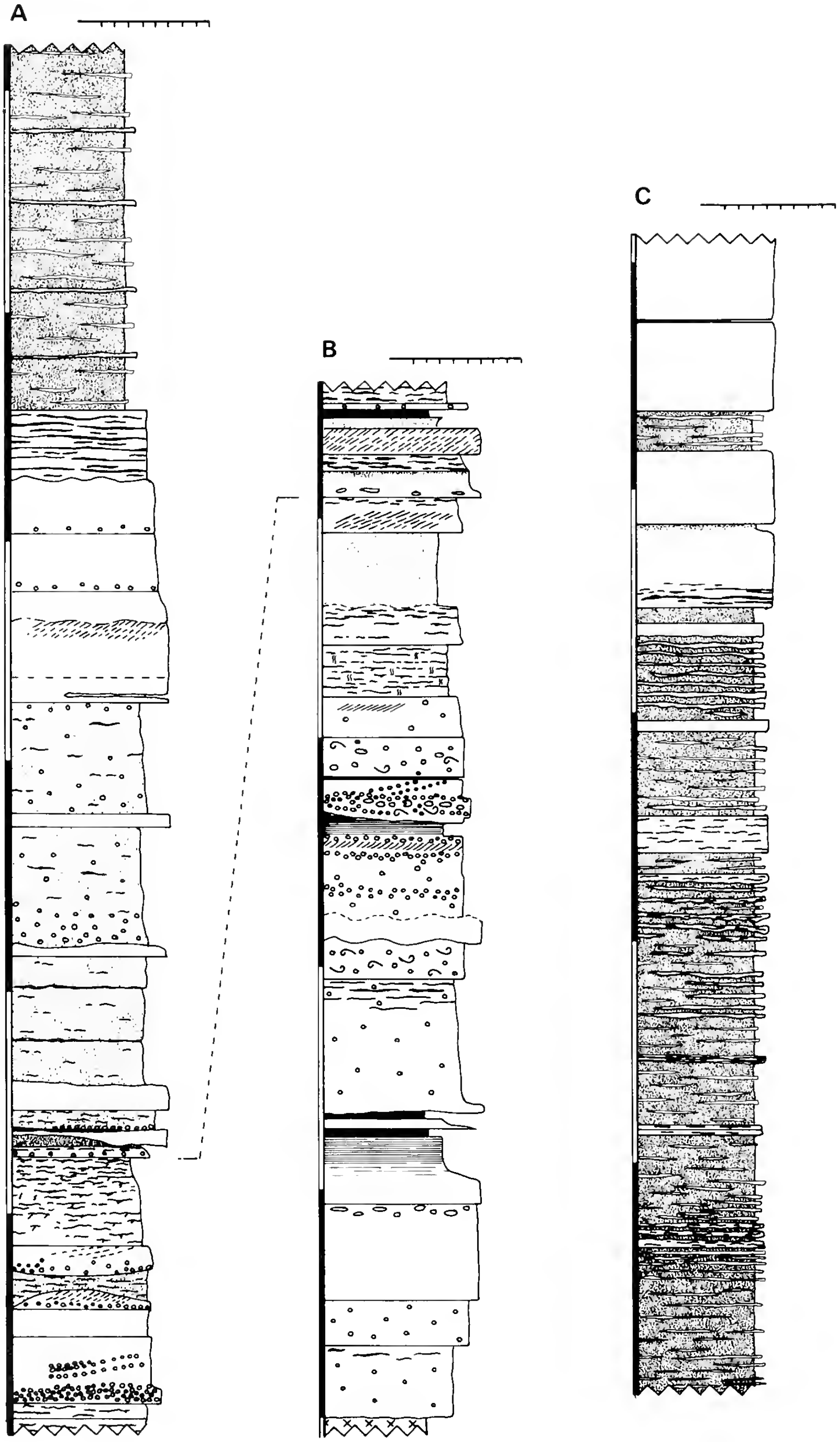


Fig. 4 Sedimentary logs of the Maes y Geirchen Sandstone Member west of Bangor Pier. Positions of sections are shown in Fig. 3. Possible correlation between sections A and B is indicated. Key given with Fig. 5, opposite.

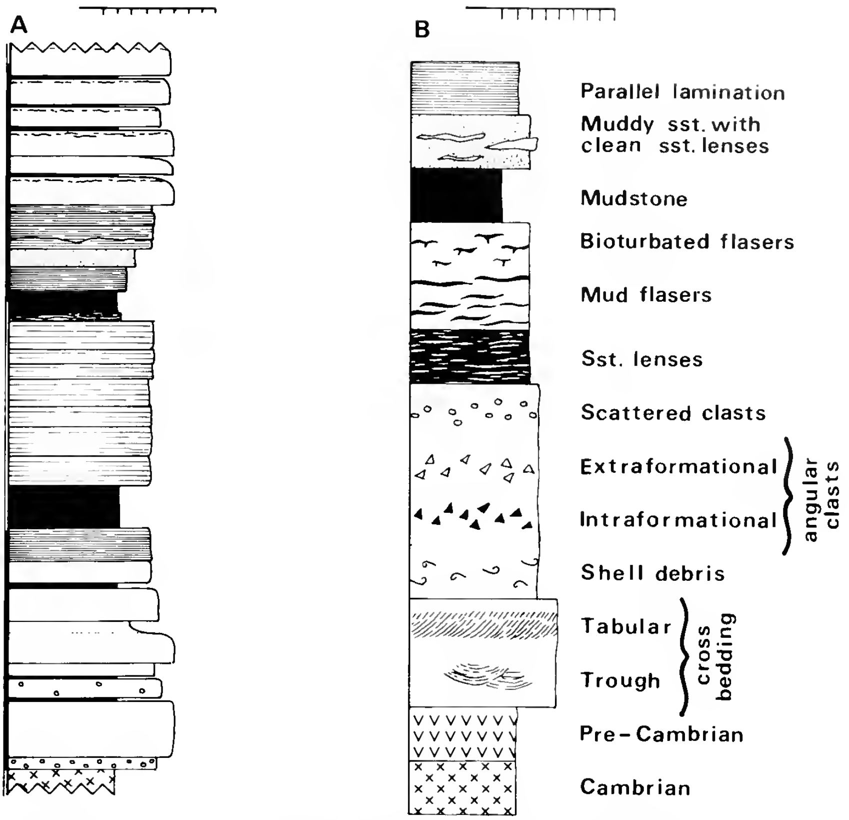


Fig. 5 A: Sedimentary log of the base of the Maes y Geirchen Sandstone Member inland from Penrhyn dock. B: Key to symbols used in sedimentary logs. Clean sandstones unshaded. At top, grain size scale from left to right: clay; silt; fine, medium, coarse sand; gravel; pebble; cobble; boulder. Vertical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

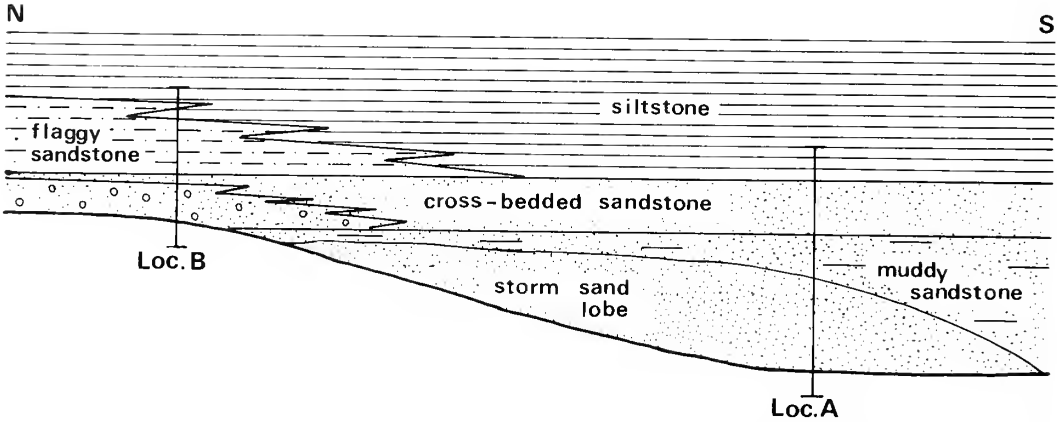


Fig. 6 Schematic depositional model for the Maes y Geirchen Sandstone Member in the Bangor area.

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

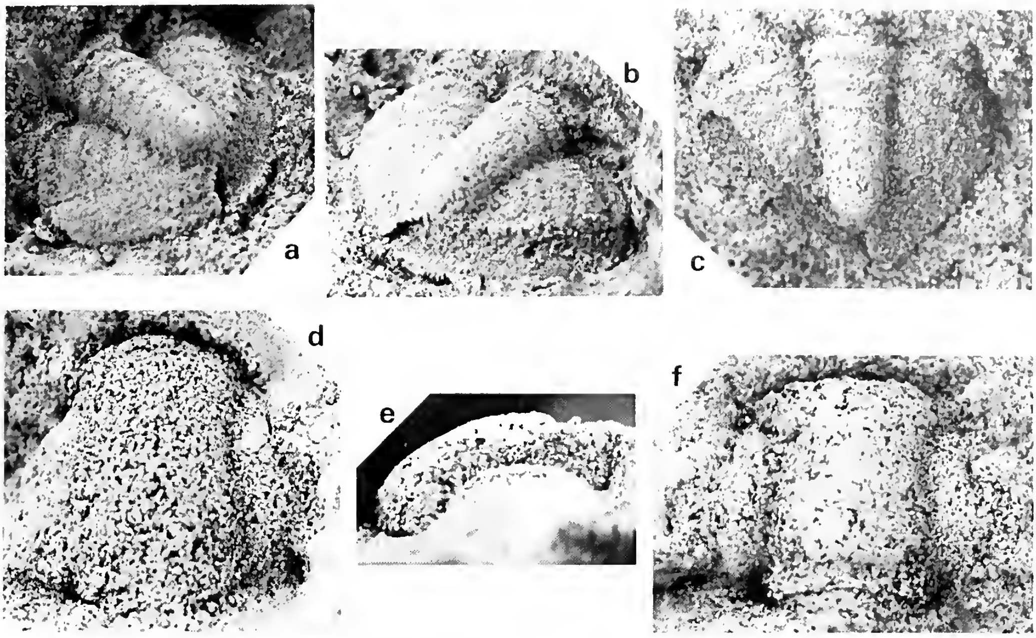


Fig. 7 *Annamitella sinesulcata* sp. nov. All material from Loc. A. a, b: It19840 (×3), oblique views of internal mould of pygidium. Note flat border and concave doublure. c: It19817a (×5), internal mould of pygidium. d: It19818 (×5), internal mould of cranidium. Note anterior border. e, f: **Holotype**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

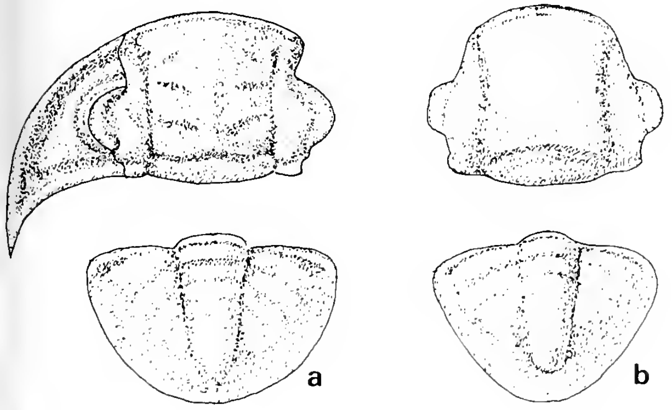


Fig. 8 a, *Annamitella perplexa* (Bates), with free cheek replaced. b, *Annamitella sinesulcata* sp. nov. (Both approx. ×3).

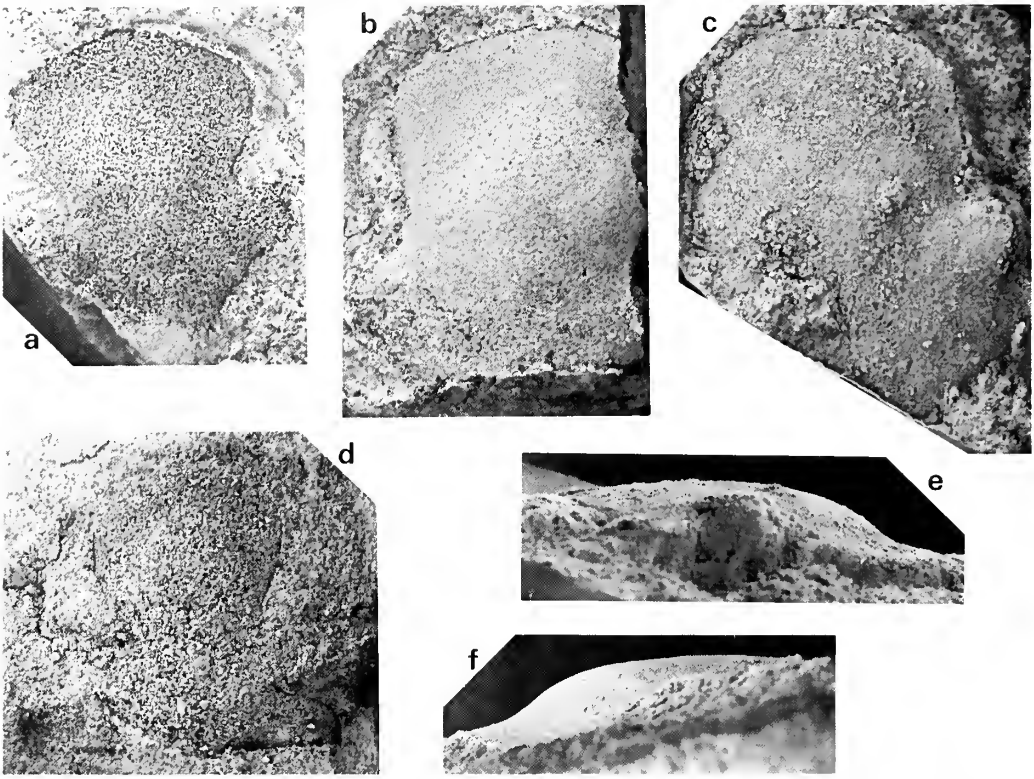


Fig. 9 *Asaphellus* cf. *graffi* (Thoral). All material from Loc.A. a: It19805 (×2). b, f: It19813d (×2). c, e: It19813c (×2). d: It19843 (×2). All are internal moulds of cranidia.

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

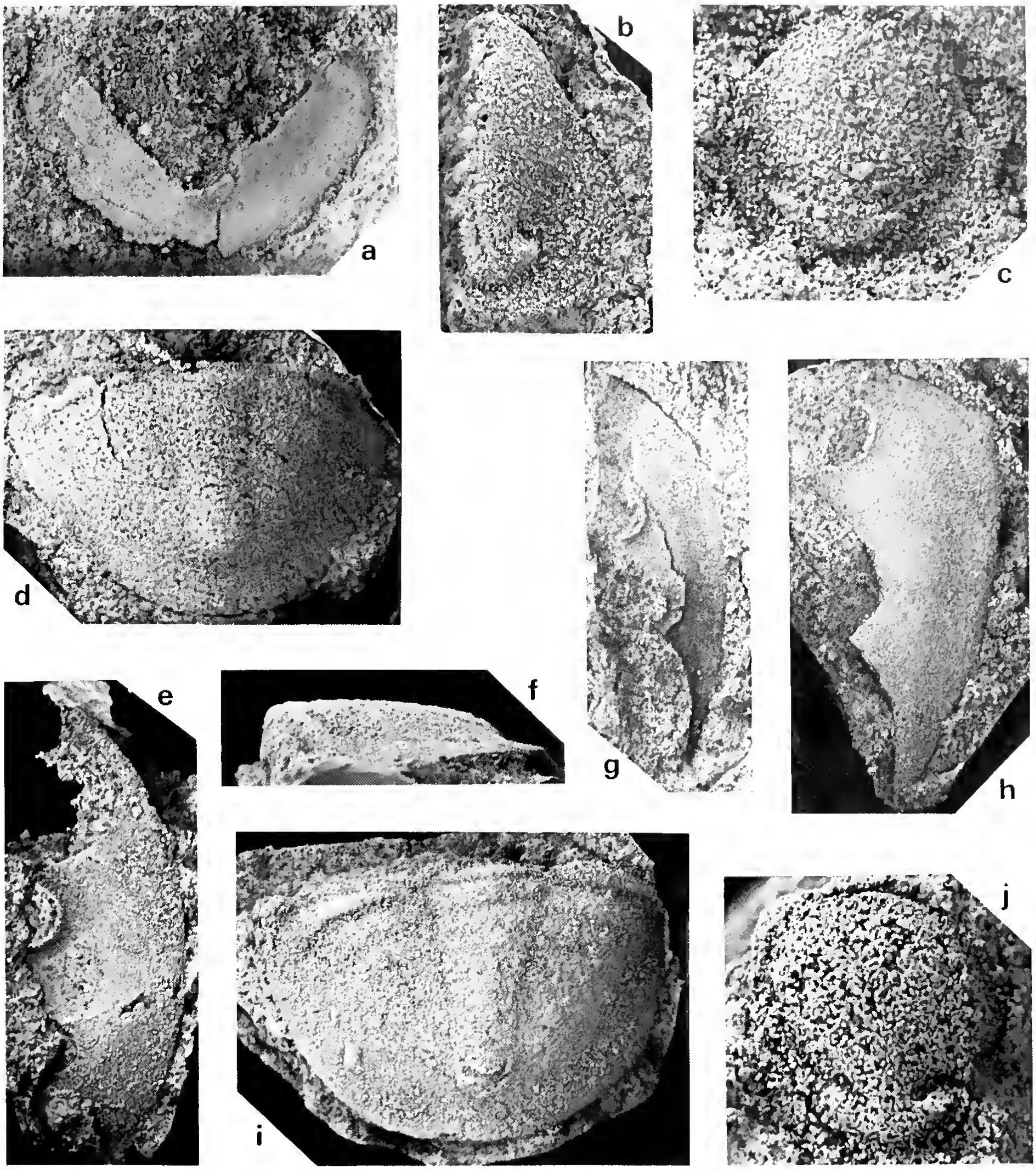


Fig. 10 *Asaphellus* cf. *graffi* (Thoral). All material from Loc. A. a: It19822 (×2), poor internal mould of pygidium showing doublure. b: It19829 (×3), latex cast of external mould of broken hypostome. c: It19831 (×7·5), internal mould of hypostome. d: It19827 (×1·25), latex cast of external mould 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.

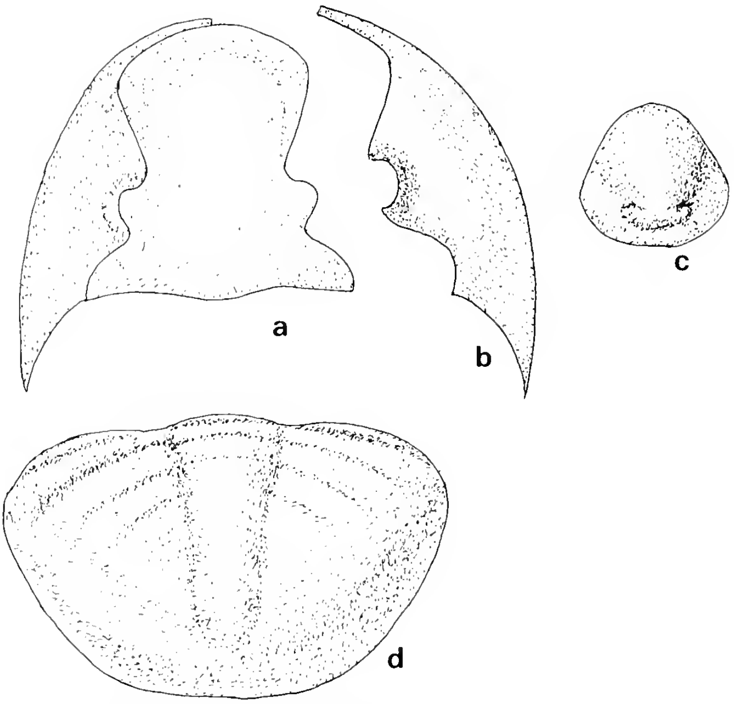


Fig. 11 *Asaphellus* cf. *graffi* (Thoral). a, cranidium with free cheek replaced. b, free cheek in plan view. c, hypostome. d, pygidium. (All approx. x1).

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.

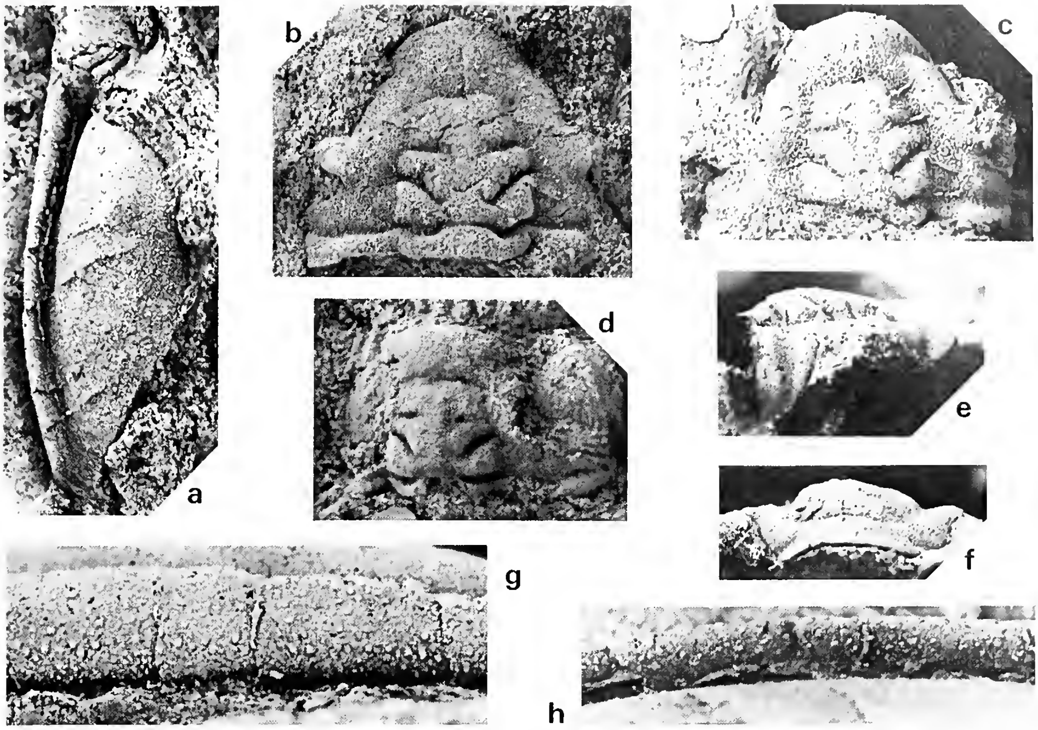


Fig. 12 *Neseuretus monensis* (Shirley). All material from Carmel Formation, central Anglesey; British Geological Survey colln. a; Af.831 (× 2·5), internal mould of free cheek. b: Af.832 (×2·5), holotype; latex cast of external mould of cranidium. c, e, f: Af.831 (×2·5), holotype; internal mould of cranidium.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

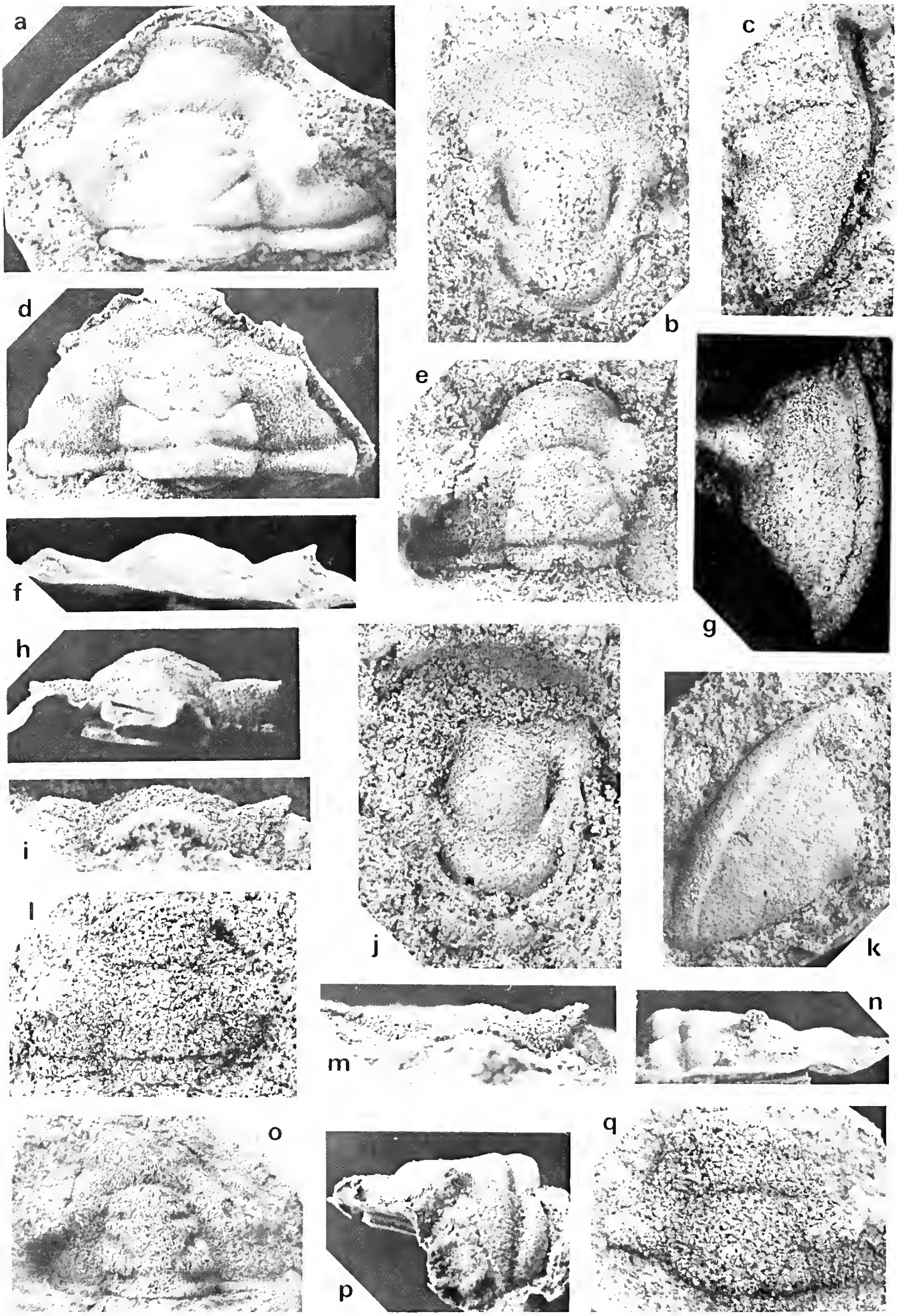


Fig. 13 *Neseuretus caerhunensis* sp. nov. All material from Loc. A. a, f, n: **Holotype** It19800 (×2), latex cast of external mould of cranidium. b: It19811 (×5), latex of external mould of hypostome. c: It19809 (×2), internal mould of free cheek. d, h, p: It19839 (×2), latex cast of external mould 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.

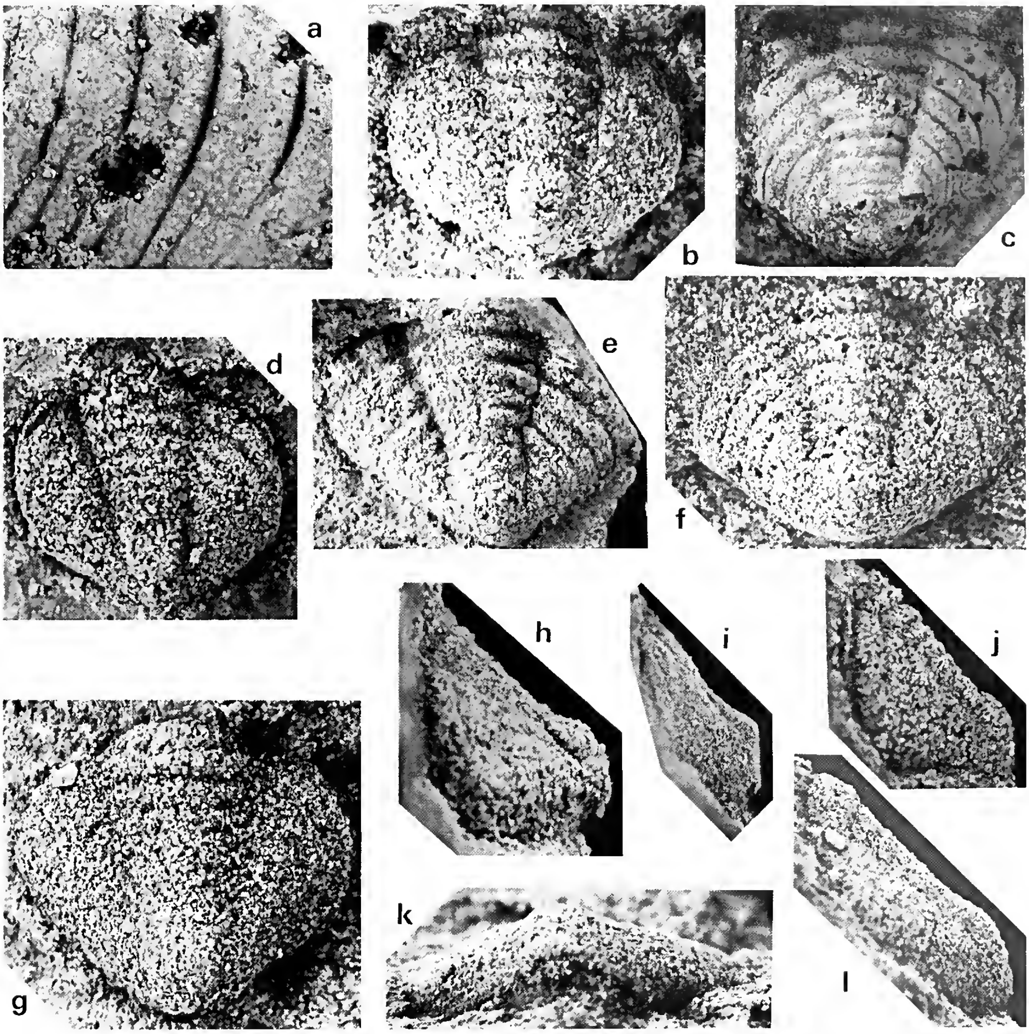


Fig. 14 *Neseuretus caerhunensis* sp. nov. All material from Loc. A. a: It19807 (×7·5), detail of ornament on internal mould of pygidium, lateral view. b, h: It19832 (×5), internal mould of pygidium. c: It19807 (×2·5), internal mould of pygidium. Note constrictions on lateral parts of axial rings. d, 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

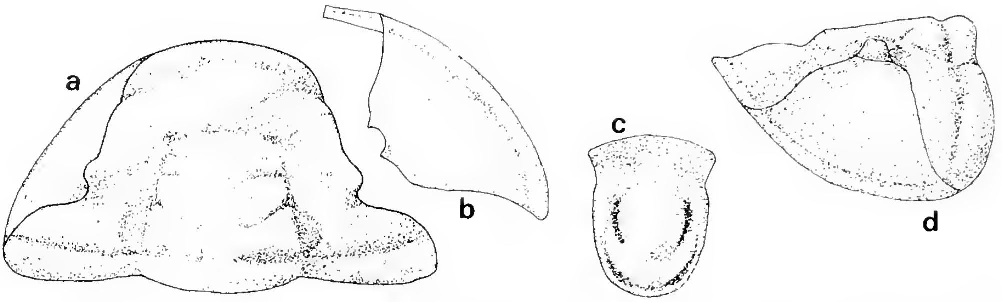


Fig. 15 *Neseuretus caerhunensis* sp. nov. a, cranidium with free cheek replaced. b, plan view of free cheek. c, hypostome. d, reconstruction of lateral view of cephalon. (All approx. ×2).

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.

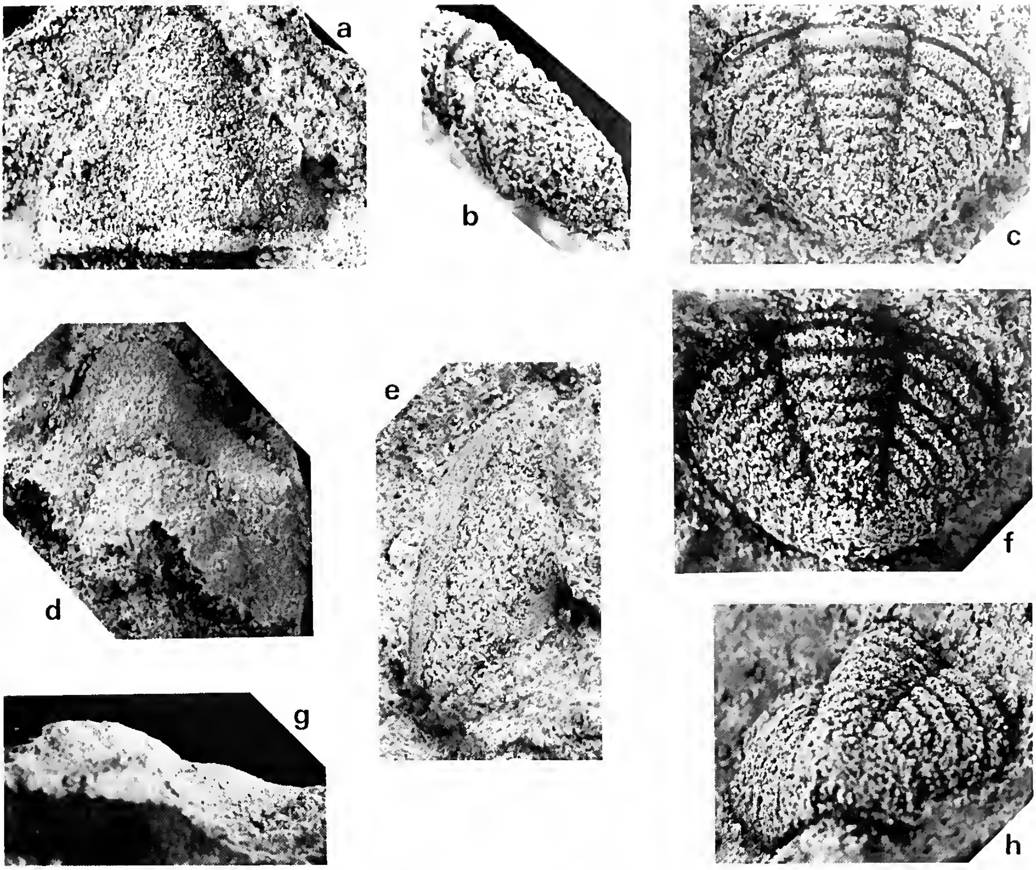


Fig. 16 *Calymenella preboiselli* sp. nov. All material from Loc. A except specimen It19844 (g) which comes from Loc. B. a: **Holotype** It19812 (×3), latex cast of external mould of cranidium. b, c: It19817 (×5), internal mould of pygidium. d, g: It19844 (×2.5), internal mould of cranidium. e: It19826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

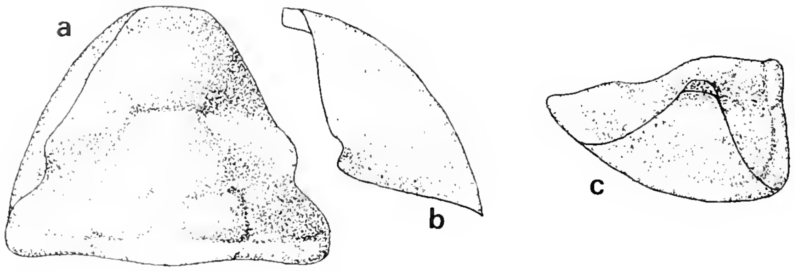


Fig. 17 *Calymenella preboiselli* sp. nov. a, cranidium with free cheek replaced. b, free cheek in plan view. c, lateral view of reconstructed cephalon. (All approx. ×3).

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.

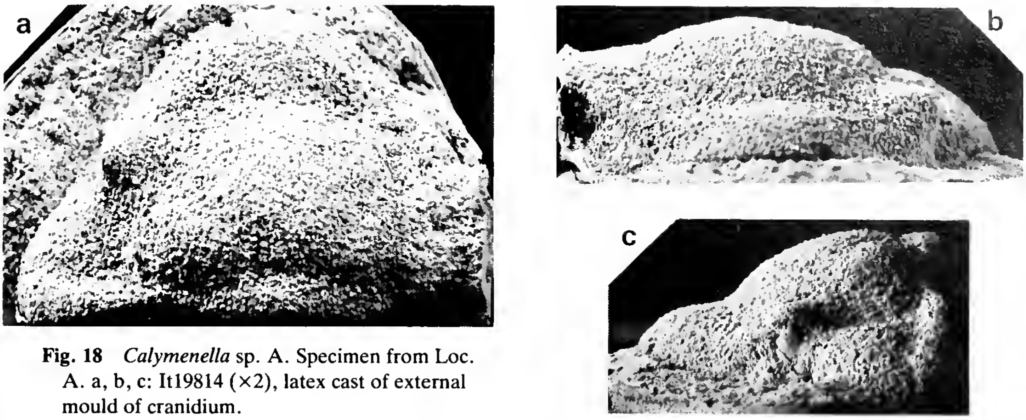


Fig. 18 *Calymenella* sp. A. Specimen from Loc. A. a, b, c: It19814 (×2), latex cast of external mould of cranidium.

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.

ACKNOWLEDGEMENTS. I am grateful to the Trustees of the British Museum (Natural History) for providing a three-year postgraduate award during which time the above work was undertaken. I thank Dr R.A. Fortey for providing guidance and encouragement during this work and for making suggestions on the improvement of the manuscript. I would also like to thank Dr A.W.A. Rushton for the loan of material in the B.G.S. collections, and Aberdeen University Chemistry Department for the use of a darkroom.

REFERENCES

Bates, D. E. B. 1968. The Lower Palaeozoic brachiopod and trilobite faunas of Anglesey. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **16** (4): 127–199, pls 1–14.

—— 1969. Some early Arenig brachiopods and trilobites from Wales. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **18** (1): 1–28, pls 1–9.

—— 1972. The stratigraphy of the Ordovician rocks of Anglesey. *Geol. J.*, Liverpool, **8**: 29–58.

Beckly, A. J. [1985.] *The Arenig Series in North Wales*. Ph.D. thesis, University of London (unpubl.).

—— 1987. Basin development in North Wales during the Arenig. *Geol. J.*, Liverpool, **22**: 19–30, 4 figs.

Brenchley, P. J. & Newall, G. 1982. Storm influenced inner-shelf sand lobes in the Caradoc (Ordovician) of Shropshire, England. *J. sedim. Petrol.*, Menasha, **52**: 1257–1269, 11 figs.

Elles, G. L. 1922. Sedgwick Museum Notes. A new *Azygograptus* from North Wales. *Geol. Mag.*, London, **59**: 299–301.

Fortey, R. A. & Cocks, L. R. M. 1986. Faunal criteria in the positioning of some Palaeozoic microcontinents. *J. geol. Soc. Lond.*, **143** (1): 151–160, 7 figs.

—— **& Morris, S.F.** 1982. The Ordovician trilobite *Neseuretus* from Saudi Arabia, and the palaeogeography of the *Nesueretus* fauna related to Gondwanaland in the earlier Ordovician. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **36** (2): 63–75, 11 figs.

—— **& Owens, R. M.** 1978. Early Ordovician (Arenig) stratigraphy and faunas of the Carmarthen district, south-west Wales. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **30** (3): 225–294, 12 figs, pls 1–11.

—— —— 1987. The Arenig Series in South Wales. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **41** (3): 69–307, 146 figs.

—— **& Shergold, J. H.** 1984. Early Ordovician trilobites, Nora Formation, Central Australia. *Palaeontology*, London, **27**: 315–366, 17 figs, pls 38–46.

Gibbons, W. 1985. Geology and paleobiology of islands in the Ordovician Iapetus Ocean: Review and implications: Discussion. *Bull. geol. Soc. Am.*, New York, **96**: 1225.

Gigout, M. 1951. Études géologiques sur la Méséta Marocaine Occidentale (arrière Pays de Casablanca, Mazagan et Safi). *Trans. Inst. scient. chérif.*, Tangier, **3**: 1–507, 18 pls.

Graham, J. R. 1919. Wave-dominated shallow-marine sediments in Lower Carboniferous of Morocco. *J. sedim. Petrol.*, Menasha, **52** (4): 1271–1276, 6 figs.

Greenly, E. 1919. The geology of Anglesey, **1**: 1–388; **2**: 389–980. *Mem. geol. Surv. U.K.*, London.

—— 1944. The Ordovician Rocks of Arvon. *Q. Jl geol. Soc. Lond.*, **100**: 75–83.

Hammann, W. 1983. Calymenacea (Trilobita) aus dem Ordovizium von Spanien; ihre Biostratigraphie, Ökologie und Systematik. *Abh. senckenb. naturforsch. Ges.*, Frankfurt a.M., **542**: 1–177, 50 figs, 25 pls.

—— **& Henry, J.-L.** 1978. Quelques espèces de *Calymenella*, *Eohomalonotus* et *Kerfornella* (Trilobita, Ptychopariida) de l'Ordovicien du Massif Armoricain et de la Péninsule Ibérique. *Senckenberg. leth.*, Frankfurt a.M., **59** (4/6): 401–429, 7 figs, pls 1–3.

Harrington, H. J. & Leanza, A. F. 1957. Ordovician trilobites of Argentina. *Spec. Publ. Dept. Geol. Univ. Kans.*, Lawrence, 1: 1–276, 140 figs.

Henry, J. L. 1980. Trilobites ordoviciens du Massif Armoricain. *Mém. Soc. géol. minér. Bretagne*, Rennes, **22**: 1–250, 48 pls.

Howells, M. F., Reedman, A. J. & Leveridge, B. E. 1985. *Geology of the country around Bangor. Explanation for 1:50 000 geological sheet* **106** (England & Wales). 36 pp., 13 figs. London, Br. Geol. Surv.

Kreisa, R. D. 1981. Storm-generated sedimentary structures in subtidal marine facies with examples from the middle and upper Ordovician of Southwestern Virginia. *J. sedim. Petrol.*, Menasha, **51** (3): 823–848.

Moore, R.C. (ed.) 1959. *Treatise on Invertebrate Paleontology*, **O** (Arthropoda 1). xix + 560 pp., 415 figs. Lawrence, Kansas.

Neuman, R. B. 1984. Geology and paleobiology of islands in the Ordovician Iapetus Ocean : Review and implications. *Bull. geol. Soc. Am.*, New York, **95**: 1188–1201, 4 figs.

—— **& Bates, D. E. B.** 1978. Reassessment of Arenig and Llanvirn age (Early Ordovician) brachiopods from Anglesey, north-west Wales. *Palaeontology*, London, **21** (3): 571–613, pls 63–68.

Reedman, A. J., Leveridge, B. E. & Evans, R. B.. 1984. The Arfon Group ('Arvonian') of North Wales. *Proc. Geol. Ass.*, London, **95**: 313–322.

——, **Webb, B. C., Addison, R., Lynas, B. D. T., Leveridge, B. E. & Howells, M. F.** 1983. The Cambrian–Ordovician boundary at Aber and Betws Garmon, North Wales. *Rep. Inst. geol. Sci.*, London, **83/1**: 7–10, 1 fig., pl. 1.

Salter, J. W. 1865–67. A Monograph of the British Trilobites from the Cambrian, Silurian and Devonian Formations, 2: 81–128, pls 7–14. *Palaeontogr. Soc. (Monogr.)*, London.

Shirley, J. 1936. Some British trilobites of the family Calymenidae. *Q. Jl geol. Soc. Lond.*, **92**: 384–422, pls 39–41.

Thoral, M. M. 1946. Cycles géologiques et formations nodulifères de la Montagne Noire. *Nouv. Archs Mus. Hist. nat. Lyon*, **1**: 1–103, pls 1–16.

Webb, B. C. 1983. Early Caledonian structures in the Cambrian slate belt, Gwynedd, North Wales. *Rep. Inst. geol. Sci.*, London, **83/1**: 1–6, 5 figs.

Whittard, W. F. 1960–64. The Ordovician trilobites of the Shelve Inlier, West Shropshire, 4: 117–162, pls 16–21 (1960); 7: 229–264, pls 34–45 (1964). *Palaeontogr. Soc. (Monogr.)*, London.

Whittington, H. B. 1966. Trilobites of the Henllan Ash, Arenig Series, Merioneth. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **11** (10): 489–505, pls 1–5.

Yin Gonsheng & Li Shanji 1978. Trilobita. In: [*Fossils of south-west China: Guizhou*], **1** (Cambrian–Devonian periods): 385–594, pls 144–192. Beijing. [In Chinese].

Bull. Br. Mus. nat. Hist. (Geol.) **45** (1):21–37 Issued 27 July 1989

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

L. R. M. COCKS

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

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).

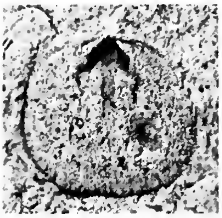
Discussion. The original specimen occurs on a slab with the common late Devonian rhynchonellide termed by Davidson *Rhynchonella inaurita* and so there is no doubt as to its age. Only a single valve is now in the Vicary Collection, although Davidson's original description speaks of two. The generic attribution 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).

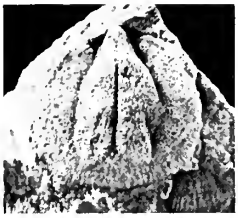
Class **ARTICULATA**
Order **ORTHIDA** Schuchert & Cooper
Suborder **ORTHIDINA** Schuchert & Cooper
Superfamily **ENTELETACEA** Waagen

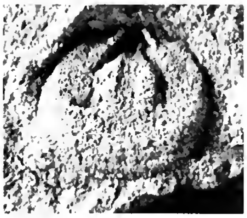
The Budleigh Salterton enteletaceans of Devonian age consist of the three species described below, two from the Lower Devonian and one from the Upper Devonian. Not revised is the species described by Davidson (1881: 344, fig. 20) as *Orthis hamoni* Rouault. Rouault's original material from the Lower 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

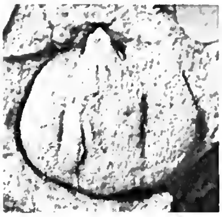

1

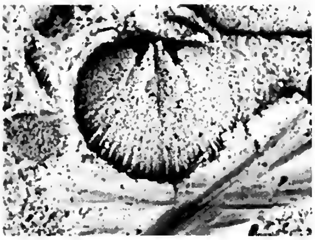

2

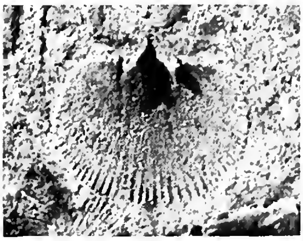

3

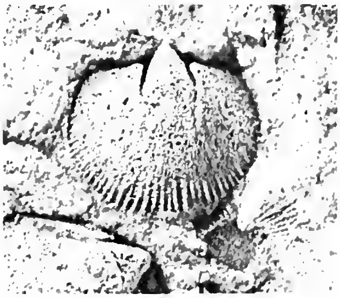

4

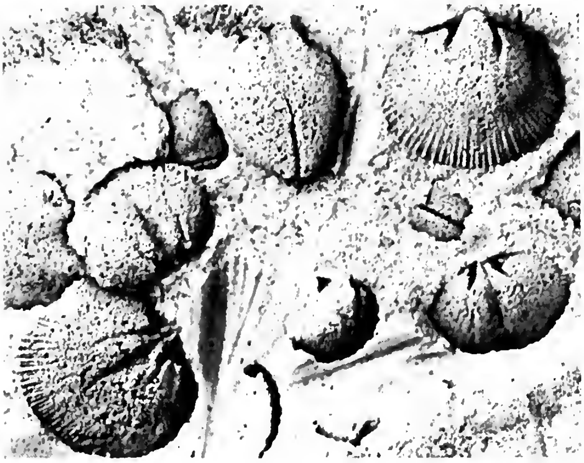

5


6


7


8a


8b


9

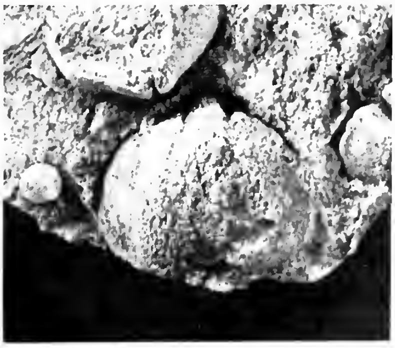

10

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.

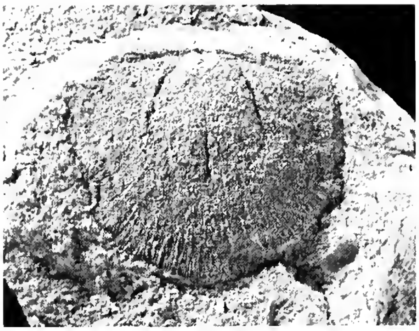
Genus ***MCLEARNITES*** Caster, 1945

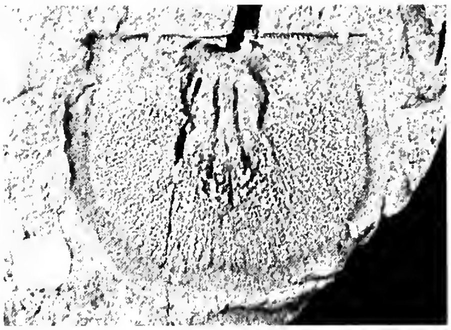
Mclearnites rouaulti (Davidson, 1870) Figs 11–12

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.

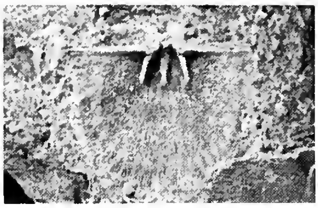
LECTOTYPE of *rouaulti* (here selected), B 21540, internal mould of a brachial valve, figured Davidson 1870: pl. 6, fig. 8 (left) and also Davidson 1881: pl. 39, fig. 9c, refigured here as Fig. 12. There is also the internal mould of a pedicle valve on the same slab.

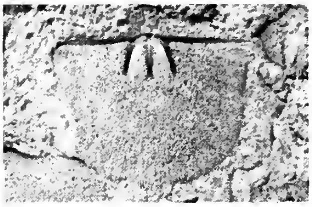
DISCUSSION. Only three pedicle valves and one brachial valve are known of this species from Budleigh Salterton; nevertheless it is distinctive and clearly attributable to *Mclearnites*. It is also the same form as that named *Douvillina (Mesodouvillina) lecaroensis* by Renouf (1972) from the Grès à *Orthis 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.

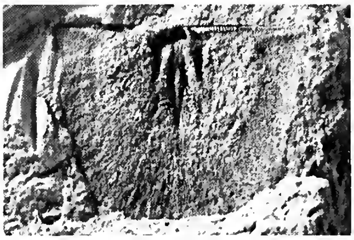

11

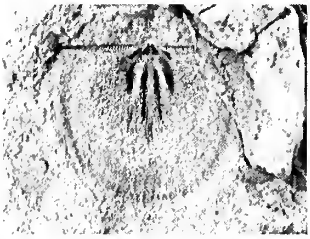

12

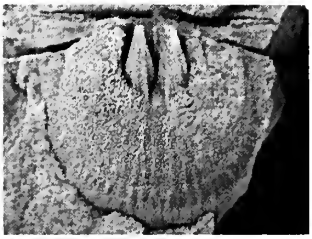

13

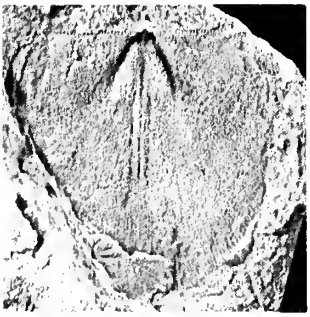

14a


14b

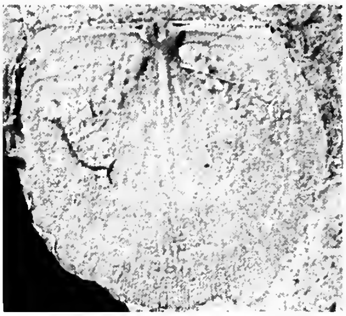

15

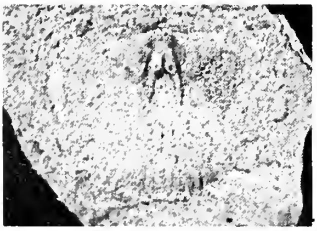

16

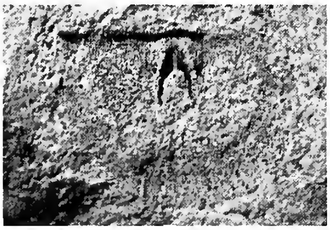

17


18


19


20


21a


21b


22

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 figures of '*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.

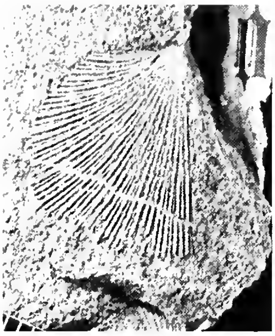
Suborder **CHONETIDINA** Muir-Wood
Superfamily **CHONETACEA** Bronn
Family **ANOPLIIDAE** Muir-Wood

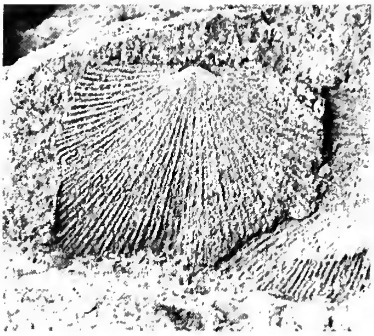
Genus *ANOPLIA* Hall & Clarke, 1892

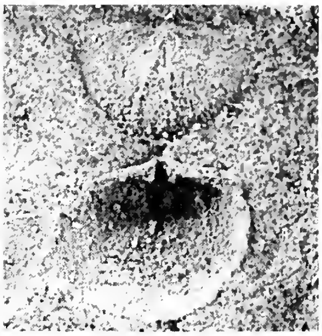
Anoplia sp. Figs 25–28

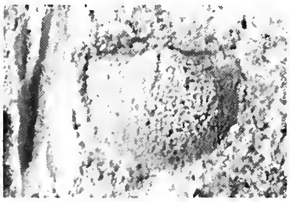
1870 *Chonetes* sp. Davidson: 87; pl. 6, fig. 13.
1881 *Chonetes* sp.? Davidson; 352; pl. 39, figs 12, 13.

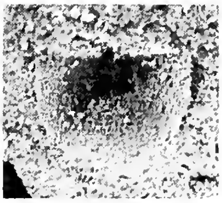
It is unfortunate that the rock in which the specimens of *Anoplia* have been found is a relatively coarse quartzite, so that the finer details of morphology and possible ornamentation are not preserved, otherwise this chonetid would warrant formal description and the creation of a new specific name. 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),

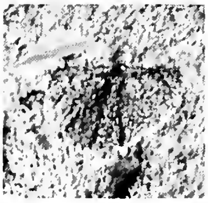

23

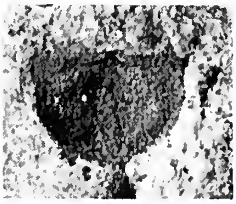

24

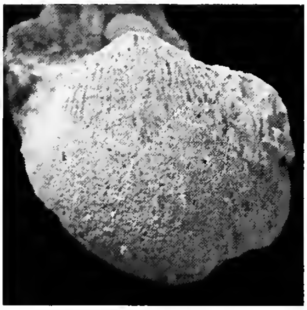

25


26a

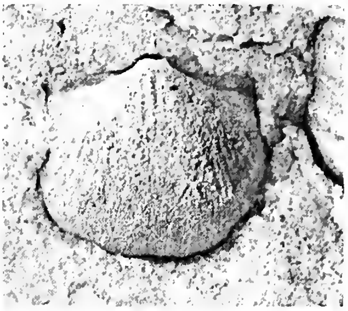

26b


27


28


29a


29b


30

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

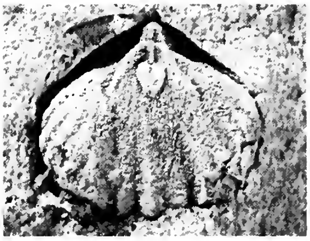
1870 *Rhynchonella Vicaryi* Davidson: 82; pl. 7, figs 7, 8.
1881 *Rhynchonella Vicaryi* Davidson; Davidson: 343; pl. 38, figs 30, 31.

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.

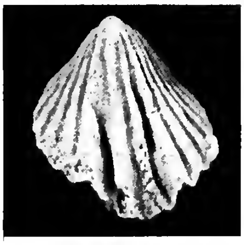

31a


31b


32

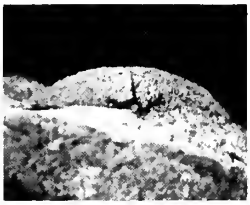

33a

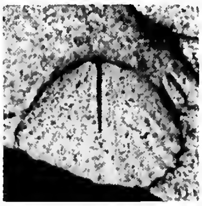

33b

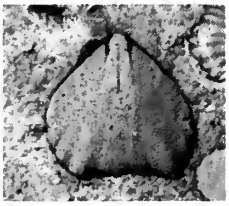

33c


33d

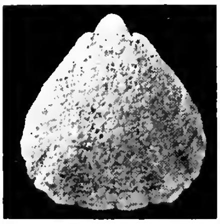

34a


34b


35


36

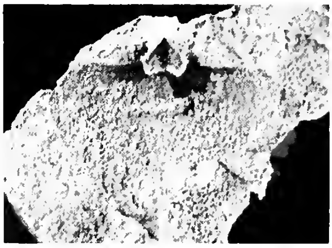

37a

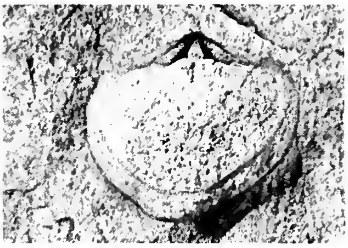

37b


37c


37d


38


39a


39b

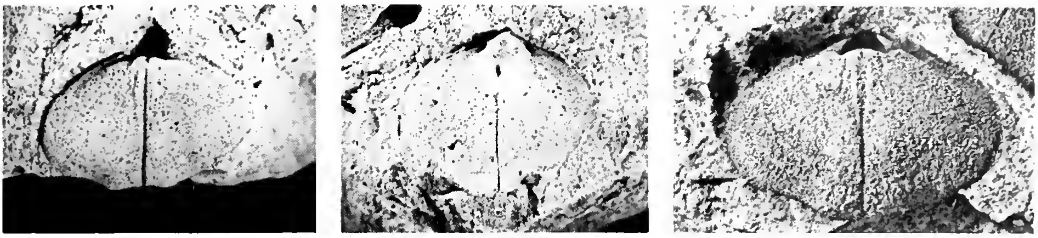
Figs 31, 32 Uncinuliform gen. et sp. indet. Fig. 31a, b, BC 6252, internal mould of conjoined valves, figured Davidson 1881: pl. 38, figs 35, 35a as *Rhynchonella inaurita*, × 2; Fig. 32, BC 21528, internal mould of pedicle valve, figured Davidson 1870: pl. 5, fig. 3 as *Rhynchonella inaurita*, × 1·5.

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.



40 41 42

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.

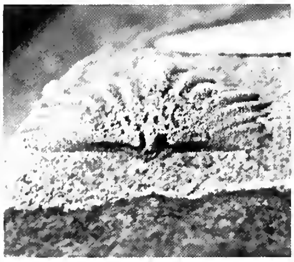
Order **SPIRIFERIDA** Waagen
Superfamily **SPIRIFERACEA** Waagen
Family **DELTHYRIDAE** Waagen
Subfamily **ACROSPIRIFERINAE** Termier & Termier

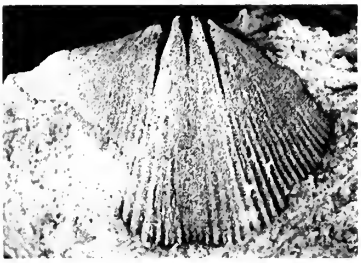
Genus ***HOWELLELLA*** Kozlowski, 1929

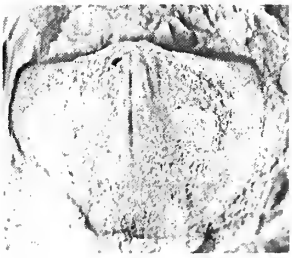
Howellella cortazari Carls, 1969 Figs 43a, b

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.

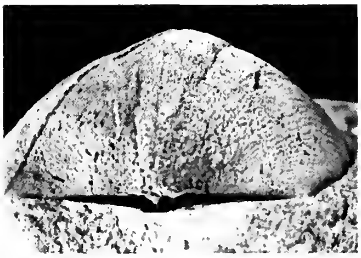

43a

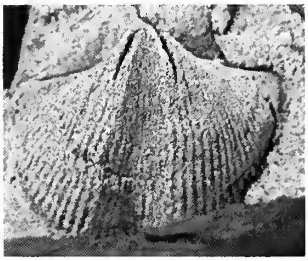

43b


44

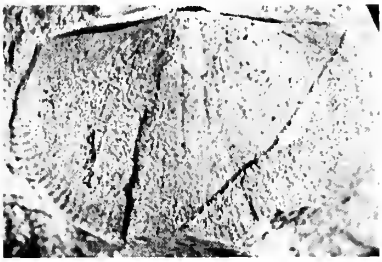

45a

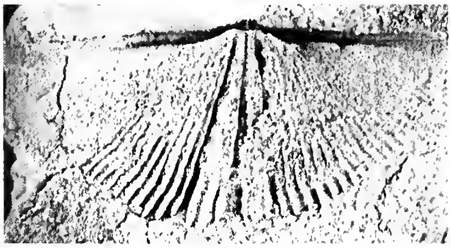

45b


46a


47


46b


46c


48


49

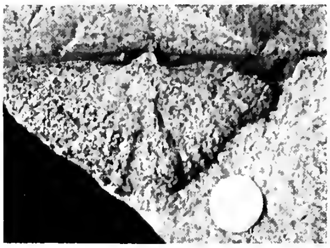

50

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.

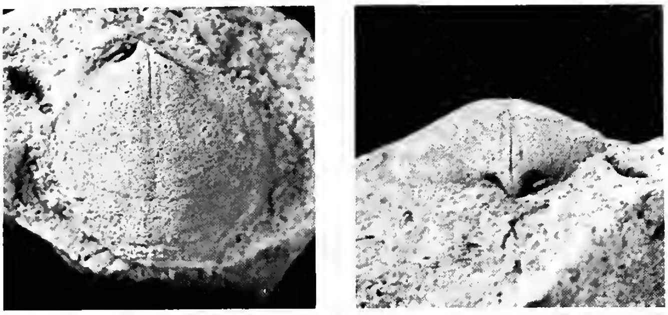
Gourvennec (1985) has revised Lower Devonian *Howellella* and concluded that the species are best differentiated both by the absolute size and by the numbers of costae. The Budleigh Salterton form never exceeds 13 mm in width (n=10) and has 6–9 costae per flank, indicating in Gourvennec's terms a transition 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

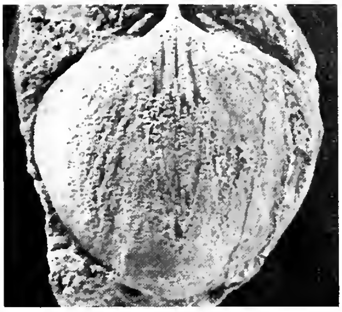
Genus ***CYRTOSPIRIFER*** Nalivkin, 1919

Cyrtospirifer verneuili (Murchison, 1840) Figs 44–47

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



51a 51b



52

53

54a 54b 54c

55

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).

ACKNOWLEDGEMENTS. I am most grateful to A.J. Boucot, C.H.C. Brunton, K.M. Evans, and P.R. Racheboeuf for comments upon generic identifications, and to Dr Brunton for reading the initial manuscript. It is a pleasure to acknowledge the help given by other museum curators: A.W.A. Rushton and D. Butler at the British Geological Survey, D. Price at the Sedgwick Museum, Cambridge, M.L.K. Curtis at Bristol City Museum, K.J. Boot at the Royal Albert Museum, Exeter, and G. Shrimpton at the Royal Geological Society of Cornwall, Penzance.

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.

REFERENCES

Asselberghs, E. 1930. Description des faunes marines du Gedinnien de l'Ardenne. *Mémoires du Musée Royal d'Histoire naturelle de Belgique*, Brussels, **41**: 1–73, pls 1–6.

Bassett, M.G. 1981. The Ordovician brachiopods of Cornwall. *Geological Magazine*, Cambridge, **118**: 647–664, pls 1–4.

Boucot, A.J. 1960. Lower Gedinnian brachiopods of Belgium. *Mémoires de l'Institut géologique de l'Université de Louvain*, **21**: 281–324, pls 9–18.

—— **& Harper, C.W.** 1968. Silurian to lower Middle Devonian Chonetacea. *Journal of Paleontology*, Tulsa, **42**: 143–176, pls 27–30.

——, **Johnson, J.G. & Staton, R.D.** 1964. On some atrypoid, retzioid and athyridoid Brachiopoda. *Journal of Paleontology*, Tulsa, **38**: 805–822, pls 125–128.

——, —— **& Walmsley, V.G.** 1965. Revision of the Rhipidomellidae (Brachiopoda) and the affinities of *Mendacella* and *Dalejina*. *Journal of Paleontology*, Tulsa, **39**: 331–340, pls 45, 46.

Brunton, C.H.C. 1982. British Dinantian (Lower Carboniferous) terebratulid brachiopods. *Bulletin of the British Museum (Natural History)*, London, (Geology) **36**: 45–57.

Carls, P. 1969. Die conodonten des tieferen Unter-Devons der Guadarrama (Mittel-Spanien) und die Stellung des Grenzbereiches Lochkovium/Pragium nach der rheinischen Gliederung. *Senckenbergiana Lethaea*, Frankfurt a.M., **50**: 303–355, pls 1–4.

Chatterton, B.D.E. 1973. Brachiopods of the Murrumbidgee Group, Taemas, New South Wales. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics*, Canberra, **137**: 1–146, pls 1–35.

Cocks, L.R.M. 1978. A review of British Lower Palaeozoic brachiopods, including a synoptic revision of Davidson's monograph. *Palaeontographical Society [Monograph]*, London. 256 pp.

—— 1979. A silicified brachiopod fauna from the Silurian of Iran. *Bulletin of the British Museum (Natural History)*, London, (Geology) **32**: 25–42.

—— **& Lockley, M.G.** 1981. Reassessment of the Ordovician brachiopods from the Budleigh Salterton Pebble Bed, Devon. *Bulletin of the British Museum (Natural History)*, London, (Geology) **35**: 111–124, figs 1–35.

Davidson, T. 1866–71. A Monograph of the British Fossil Brachiopoda. Part VII. The Silurian Brachiopoda. *Palaeontographical Society [Monograph]*, London: 1–397, pls 1–50.

—— 1870. Notes on the Brachiopoda hitherto obtained from the 'Pebble-bed' of Budleigh Salterton, near Exmouth, in Devonshire. *Quarterly Journal of the Geological Society of London*, **26**: 70–90, pls 4–6.

—— 1880. On the species of Brachiopoda that characterize the 'Grès Armoricain' of Brittany, together with a few Observations on the Budleigh Salterton 'Pebbles'. *Geological Magazine*, London, (2) **7**: 337–343, pl. 10.

—— 1881. Monograph of the British Fossil Brachiopoda. Vol. IV, Part IV. Devonian and Silurian Brachiopoda that occur in the Triassic Pebble Bed of Budleigh Salterton in Devonshire. *Palaeontographical Society [Monograph]*, London: 317–368, pls 38–42.

—— 1882–3. Monograph of the British Fossil Brachiopoda. Vol. V. Devonian and Silurian Supplements. *Palaeontographical Society [Monograph]*, London: 1–242, pls 1–17.

Drevermann, F. 1902. Die Fauna der Untercoblenzschichten von Oberstadtfeld bei Daun in der Eifel. *Palaeontographica*, Stuttgart, **49** (2): 72–120, pls 9–14.

Gourvennec, R. 1985. Le genre *Howellella* (Brachiopoda, Spiriferida) en Europe de l'Ouest au Siluro-Dévonien. *Géobios*, Lyon, **18**: 143–170, pls 1–3.

Harper, C.W. & Boucot, A.J. 1978. The Stropheodontacea. *Palaeontographica*, Stuttgart, A **161**: 55–118, pls 1–18; 119–175, pls 19–35; **162**: 1–80, pls 36–50.

Havlíček, V. 1977. Brachiopods of the order Orthida in Czechoslovakia. *Rozpravy Ustředního Ustavu Geologického*, Prague, **44**: 1–327, pls 1–56.

Isaacson, P.E. 1977. Devonian stratigraphy and brachiopod paleontology of Bolivia. Part A: Orthida and Strophomenida. *Palaeontographica*, Stuttgart, A **155**: 133–192, pls 1–6.

Johnson, J.G., Boucot, A.J. & Murphy, M.A. 1973. Pridolian and Early Gedinnian age brachiopods from the Roberts Mountains Formation of Central Nevada. *University of California Publicatons in Geological Sciences*, Berkeley, **100**: 1–75, pls 1–31.

—— —— ——1976. Wenlockian and Ludlovian age brachiopods from the Roberts Mountains Formation of Central Nevada. *University of California Publications in Geological Sciences*, Berkeley, **115**:1–102, pls 1–55.

Murchison, R.I. 1840. Sur les roches devoniennes, type particulier de l'old red sandstone des géologues anglais, qui se trouvent dans le Boulonnais et les pays limitrophes. *Bulletin de la Societé géologique de France*, Paris, (1) **11**: 229–264, pls 2, 3.

Paeckelmann, W. 1942. Beiträge zur Kenntnis devonisches Spiriferen. *Abhandlungen des Reichsamts für Bodenforschung*, Berlin, **197**: 1–188, pls 1–8.

Renouf, J.T. 1972. Brachiopods from the Grès à *Orthis monnieri* Formation of northwestern France and their significance in Gedinnian/Siegenian stratigraphy of Europe. *Palaeontographica*, Stuttgart, A **139**: 89–113, pls 21–26.

Rong Jia-yu & Yang Xue-chang 1981. Middle and late early Silurian brachiopod faunas in southwest China. *Memoirs of Nanjing Institute of Geology and Palaeontology*, **13**: 163–270.

Rouault, M. 1850. Note préliminaire sur une nouvelle formation découverte dans le terrain silurien inferéur de la Bretagne. *Bulletin de la Societé géologique de France*, Paris, (2) **7**: 724–744.

—— 1851. Fossiles du terrain silurien. *Bulletin de la Societé géologique de France*, Paris, (2) **8**: 358–359.

Salter, J.W. 1864. Note on the Fossils from Budleigh Salterton Pebble-bed. *Quarterly Journal of the Geological Society of London*, **20**: 286–302, pls 15–17.

Sandberger, G. & Sandberger, F. 1855. Die Brachiopoden des Rheinischen Schichtensystems in Nassau. In: *Versteinerungen des rheinischen Schichtensystems in Nassau*: 297–374 (1–78), pls 31–34. Wiesbaden.

Sheehan, P.M. 1976. Late Silurian brachiopods from northwestern Utah. *Journal of Paleontology*, Tulsa, **50**: 710–733.

Strusz, D.L. 1982. Wenlock brachiopods from Canberra, Australia. *Alcheringa*, Adelaide, **6**: 105–142.

Tachibana, K. 1976. Silurian brachiopods from the Kesen district of the Kitakami mountainland, northeast Japan. *Annual Report of the Faculty of Education of the University of Iwate*, **36**: 31–44.

—— 1980. Silurian brachiopods from the Kitakami mountainland, north Japan. *Annual Report of the Faculty of Education of the University of Iwate*, **40**: 29–54.

Tromelin, G. le G. de 1876. Étude de la Faune du grès Silurien de May, Jurques, Campandré, Mont-Robert etc. (Calvados), avec des observations sur divers fossiles paléozoiques de l'ouest de la France. *Bulletin de la Societé Linnéene de Normandie*, Caen, (3) **1**: 5–82.

Ushatinskaya, G.T. & Nilova, N.V. 1975. Brachiopods *in* Menner, V.V. (ed.), [*Outline of the fauna of the boundary strata of the Silurian and Devonian in Central Kazakhstan*.] 248 pp. Nedra, Moscow [In Russian].

Vandercammen, A. 1959. Essai d'étude statistique des *Cyrtospirifer* du Frasnien de la Belgique. *Mémoires de l'Institut Royal des Sciences naturelles de Belgique*, Brussels, **145**: 1–175, pls 1–5.

Wallace, P. 1969. The sedimentology and palaeoecology of the Devonian of the Ferques inlier, northern France. *Quarterly Journal of the Geological Society of London*, **125**: 83–124, pls 6–7.

Walmsley, V.G. 1965. *Isorthis* and *Salopina* (Brachiopoda) in the Ludlovian of the Welsh Borderland. *Palaeontology*, London, **8**: 454–477, pls 61–65.

—— , **Boucot, A.J. & Harper, C.W.** 1969. Silurian and Lower Devonian salopinid brachiopods. *Journal of Paleontology*, Tulsa, **43**: 492–516, pls 71–80.

Xu Han-kui 1979. Brachiopods from the Tangxiang Formation (Devonian) in Nandan of Guangxi. *Acta palaeontologia sinica*, Beijing, **18**: 362–382.

Bull. Br. Mus. nat. Hist. (Geol.) **45** (1): 39–55 Issued 27 July 1989

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

T. S. ENGESER

Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, Bundesstrasse 55, 2000 Hamburg 13, West Germany

P. D. TAYLOR

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

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

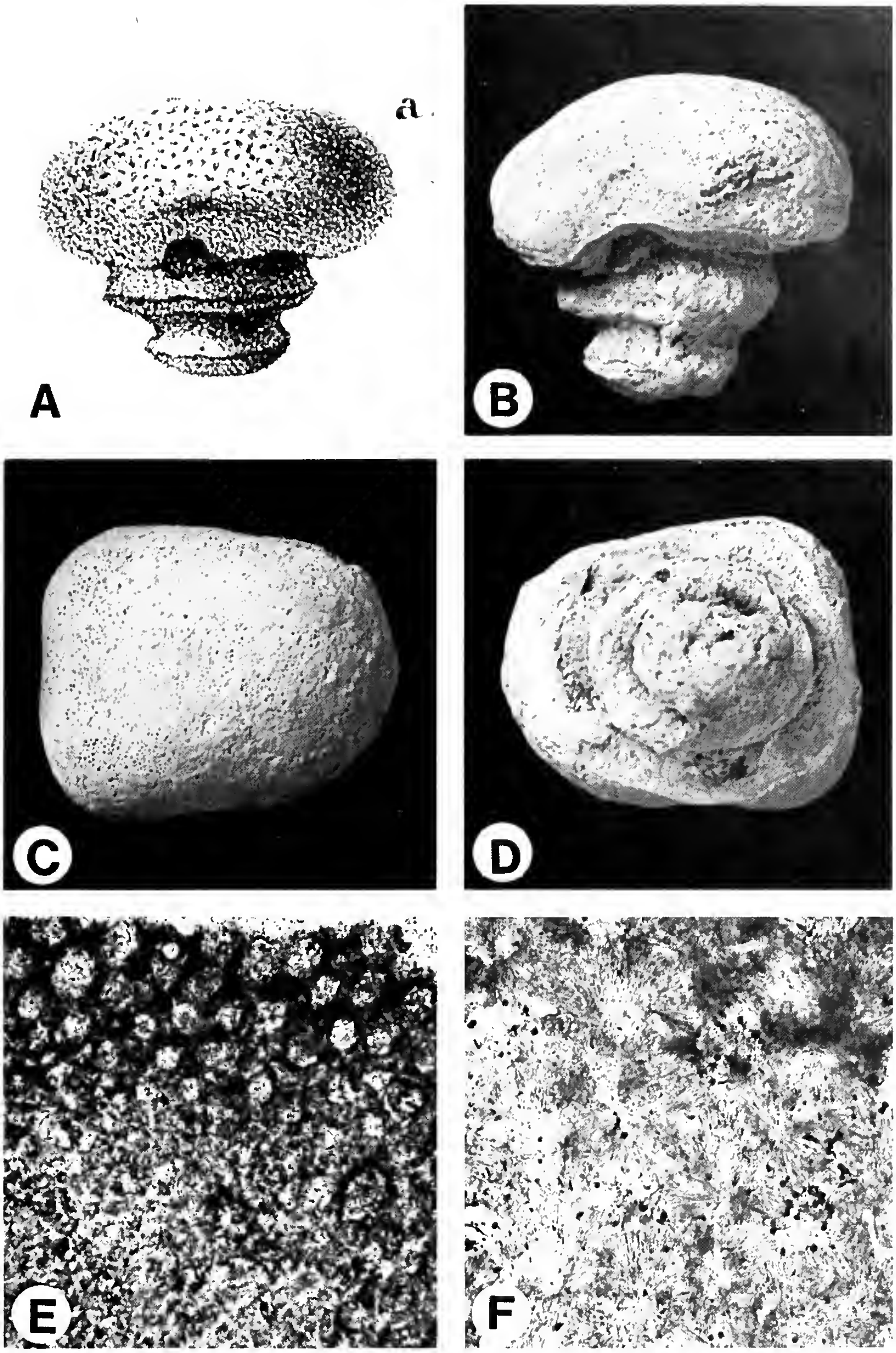


Fig. 1 *Leiospongia alpina* (Klipstein). Cassian Fm., St Cassian. Holotype, S10462. A, reproduction of pl.19, fig.17a of Klipstein (1845). B, side view, × 3·9. C, top view, × 3·9. D, underside showing epitheca, × 3·9. E, transverse sections of calicles, × 35. F, spherulitic wall structure, × 130.

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).

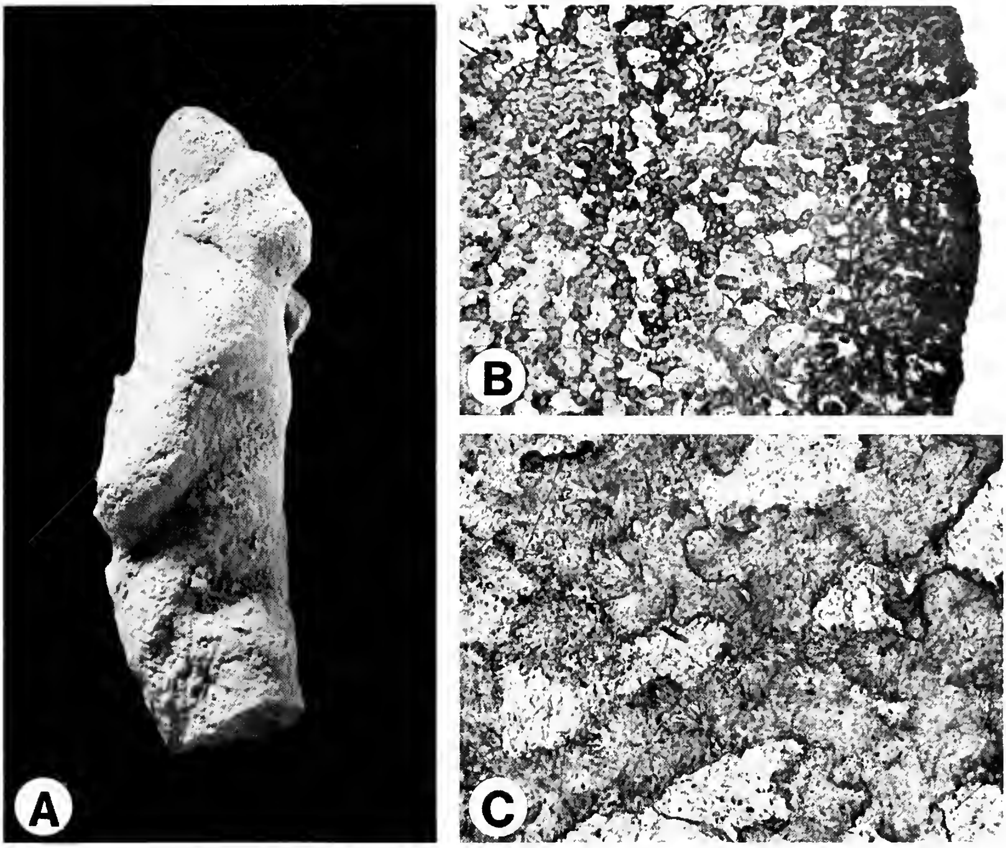


Fig. 2 *Leiospongia polymorpha* (Klipstein). Cassian Fm., St Cassian. Holotype, S9540. A, side view, × 2·5. B, transverse section, showing incomplete calicle walls, × 21. C, spherulitic wall structure, × 190.

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*

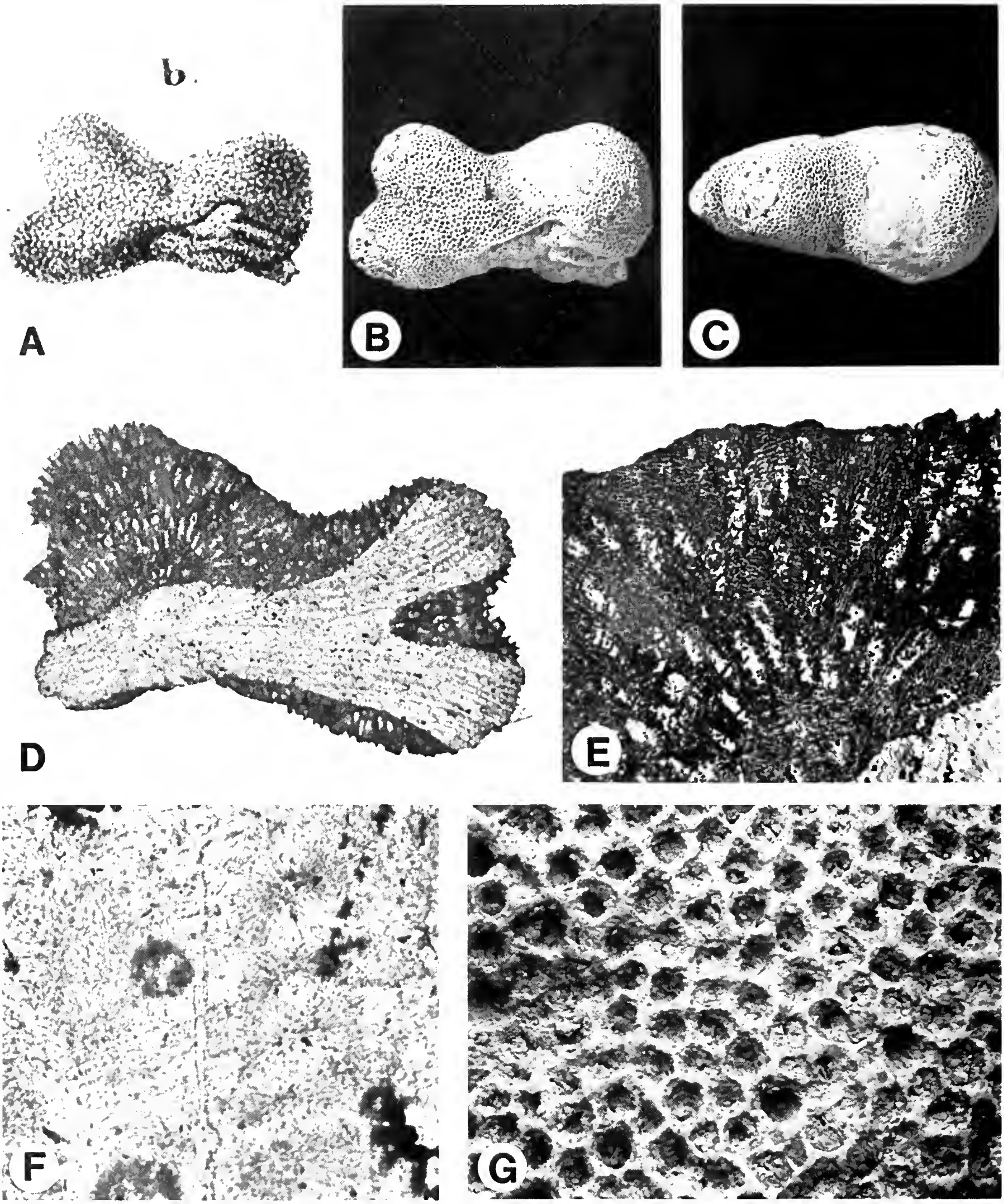


Fig. 3 *Leiospongia* sp. Cassian Fm., St Cassian. Specimen figured as *Calamopora* (?) *gnemidium* by Klipstein (1845: pl. 19, fig. 15b), S10464. A, reproduction of Klipstein's original figure. B, side view, × 4·2. C, top view, × 4·2. D, section showing dark-coloured *Leiospongia* sp. encrusting pale-coloured 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].

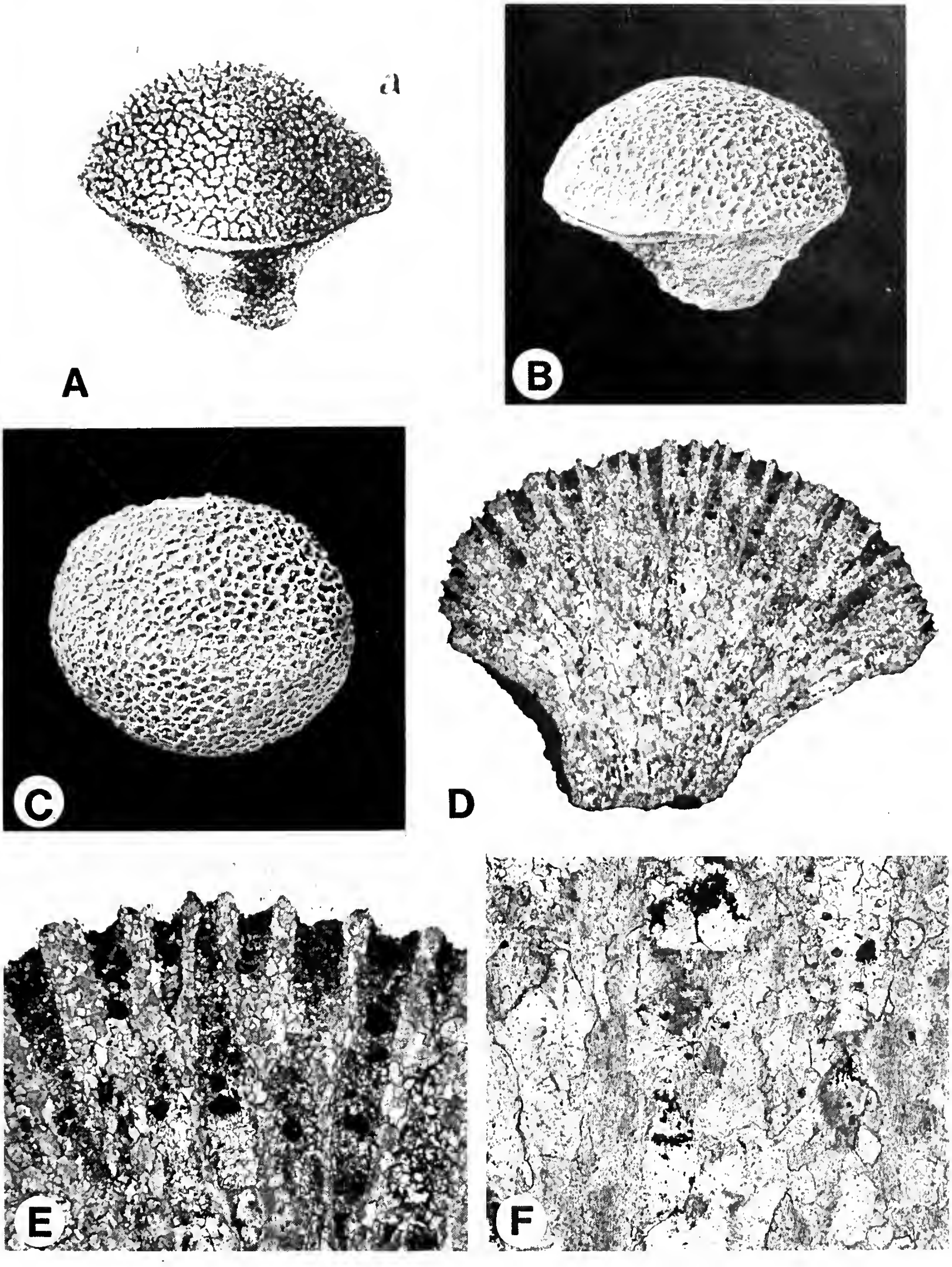


Fig. 4 *Cassianochaetetes orbignyanus* (Klipstein). Cassian Fm., St Cassian. Holotype, S10465. A, reproduction of pl. 19, fig. 20a of Klipstein (1845). B, side view showing basal epitheca, × 4·4. C, top view of thecal surface, × 4·4. D, longitudinal section, × 7·3. E, longitudinal section of calicles,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

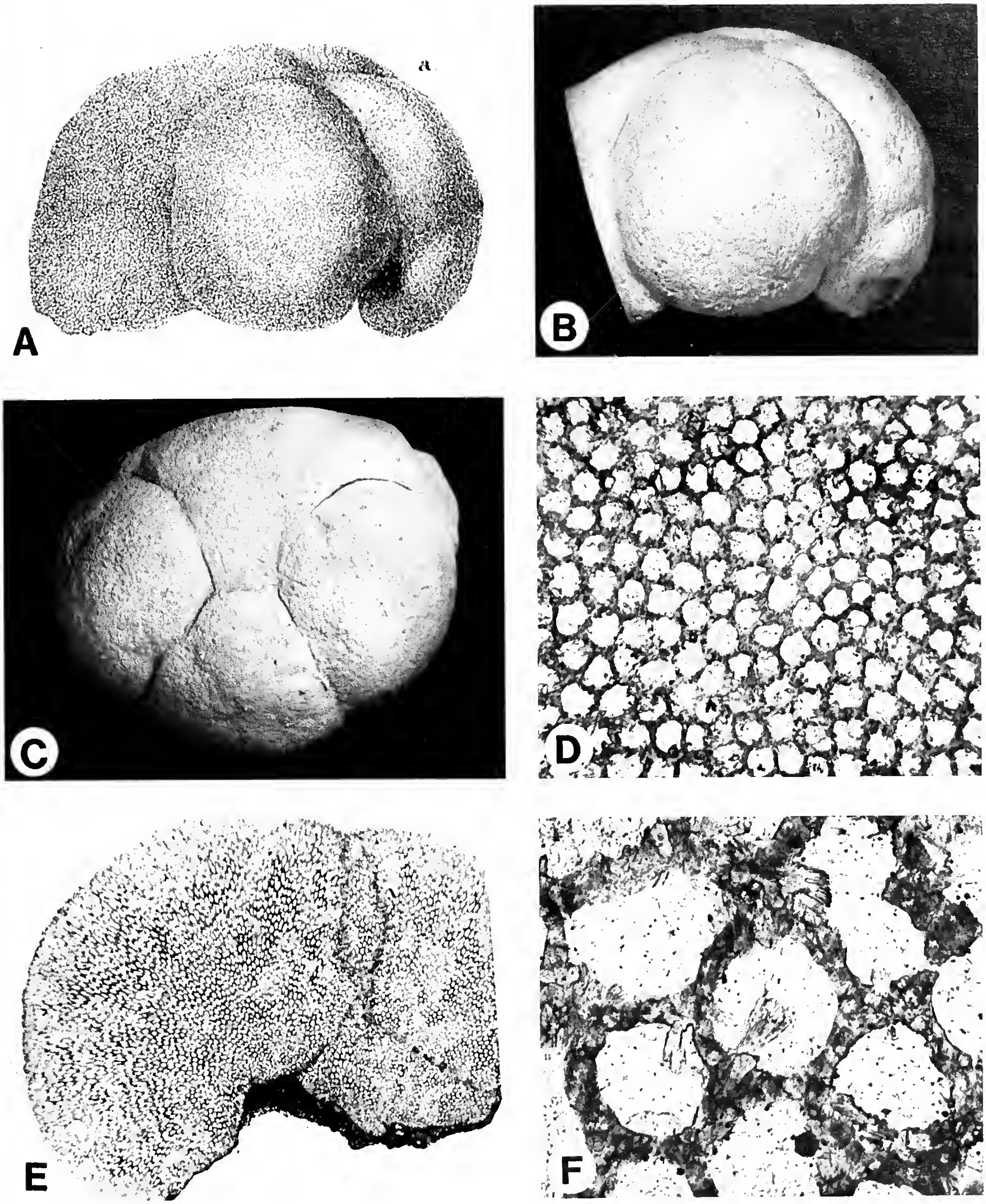


Fig. 5 *Cassianochaetetes gnemidius* (Klipstein). Cassian Fm., St Cassian. **Lectotype,** selected herein, S10466. A, reproduction of pl. 19, fig. 15a of Klipstein (1845). B, side view (bottom left corner of specimen has been cut off since Klipstein's figure was drawn), × 1·7. C, top view, × 1·6. D,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

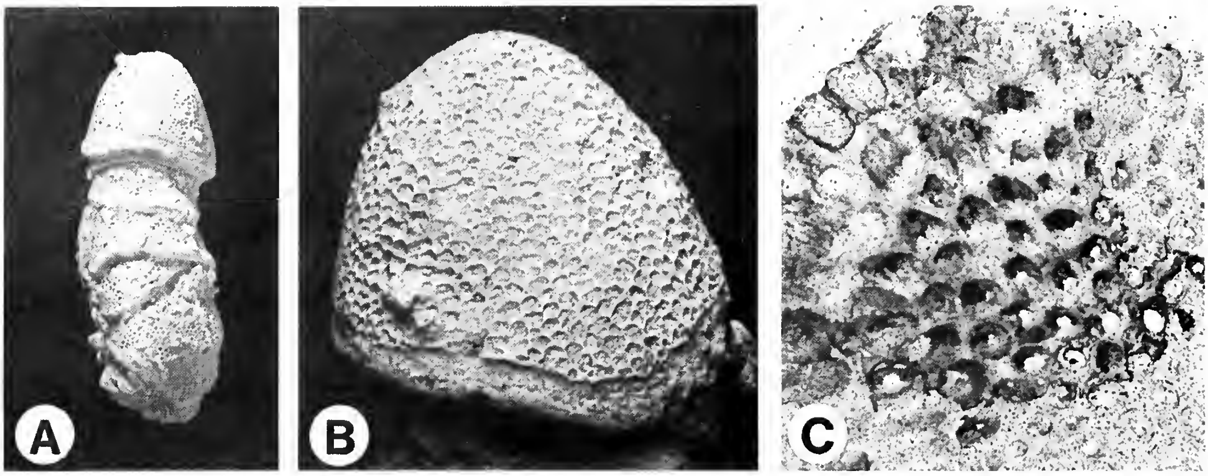


Fig. 6 ?*Cassianochaetetes milleporatus* (Münster). Cassian Fm., St Cassian. S10468. A, side view showing columnar form and multiple epithecae, × 3·8. B, scanning electron micrograph of thecal surface, × 16. C, section, × 32.

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

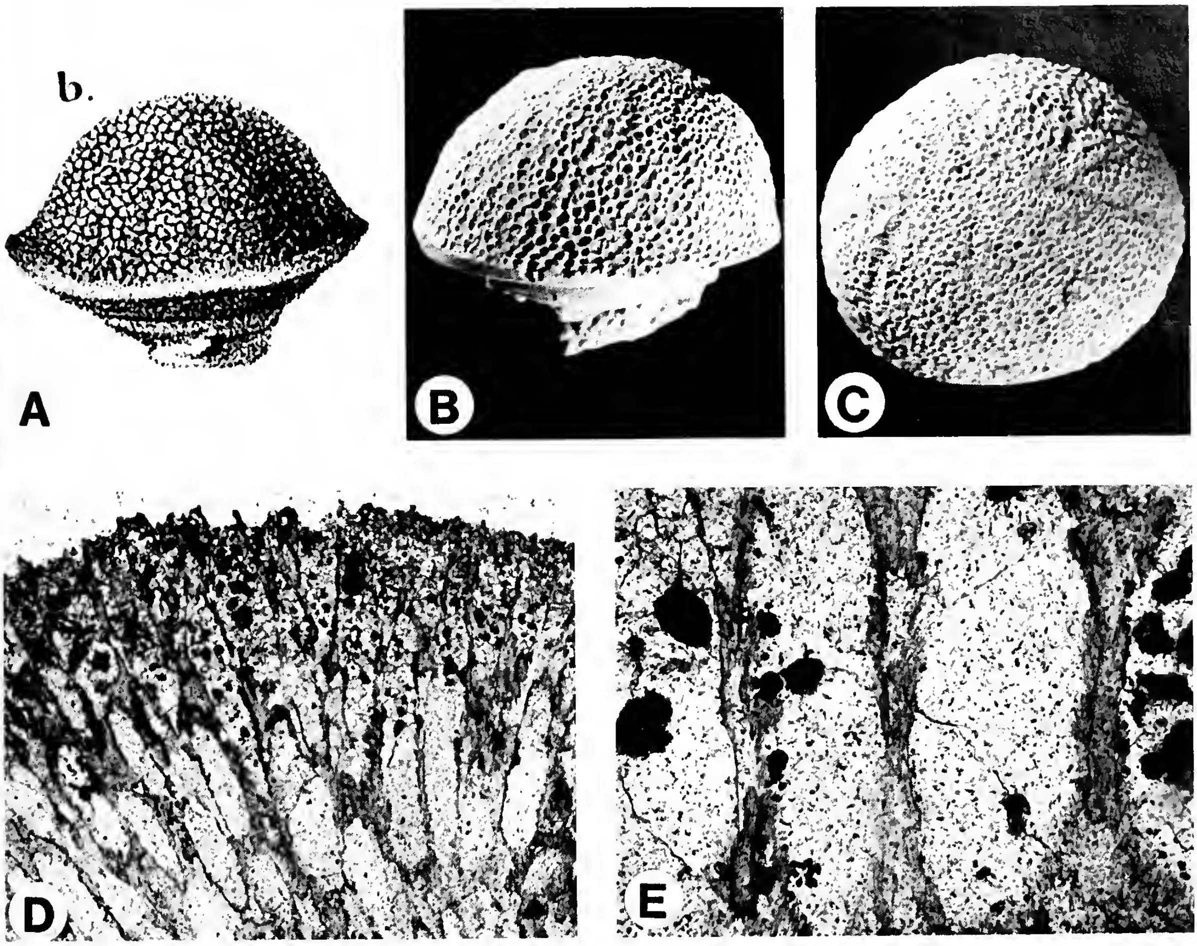


Fig. 7 *Cassianochaetetes* sp. Cassian Fm., St Cassian. Specimen figured as *Calamopora* (?) *gnemidium* by Klipstein (1845: pl. 19, figs 16a, b), S10467. A, reproduction of Klipstein's fig. 16b. B, side view, × 5·9. C, top view showing astrorhizae, × 5·9. D, oblique longitudinal section, × 21. E, calicle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

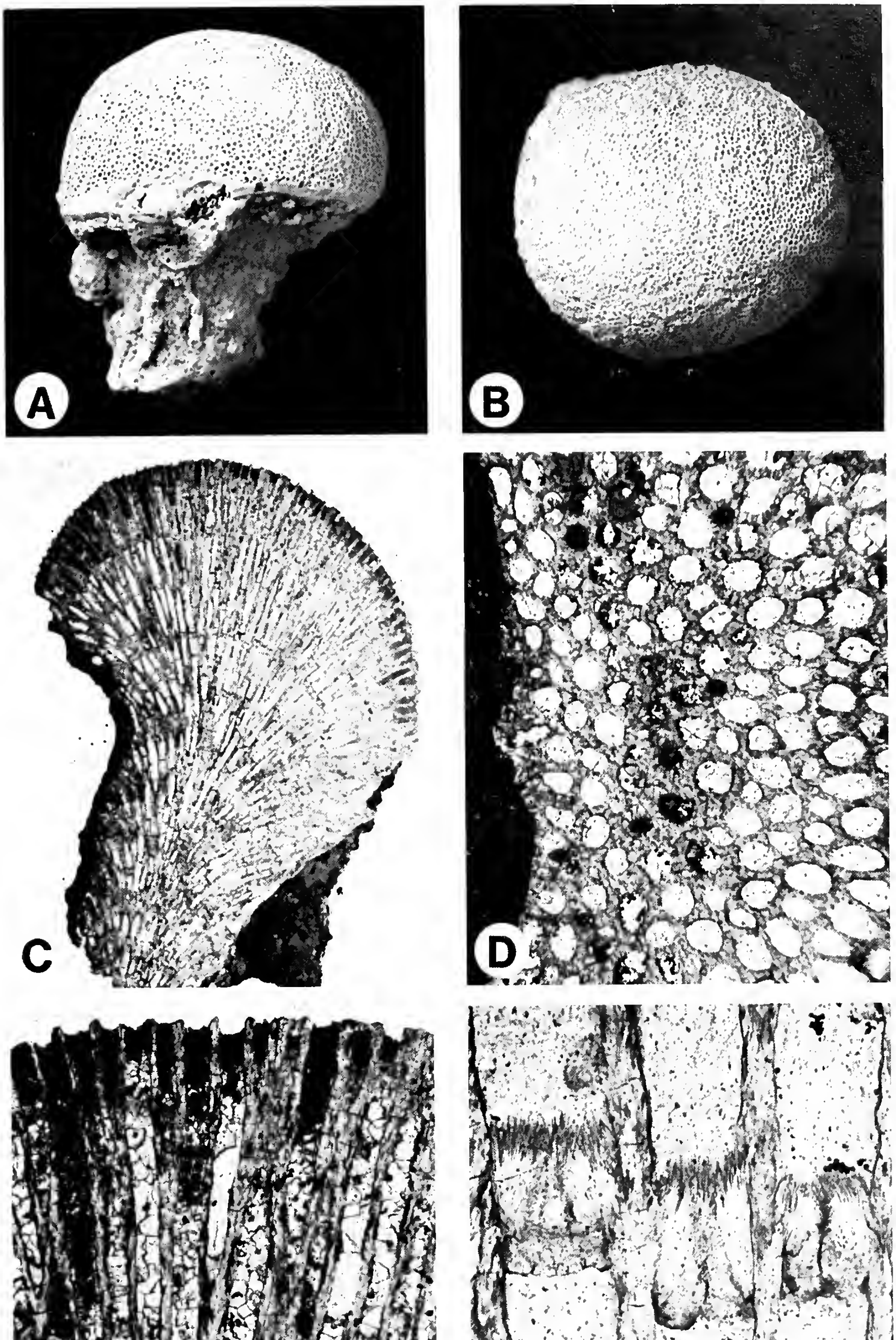


Fig. 8 *Atrochaetetes lagaaiji* (Bizzarini & Braga). Cassian Fm., St Cassian. S10469. A, side view, × 3·3. B, top view showing astrorhizae, × 3·3. C, longitudinal section showing bands of tabulae, × 4·9. D, transverse sections of calicles and epitheca (left), × 21. E, longitudinal section of calicles,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

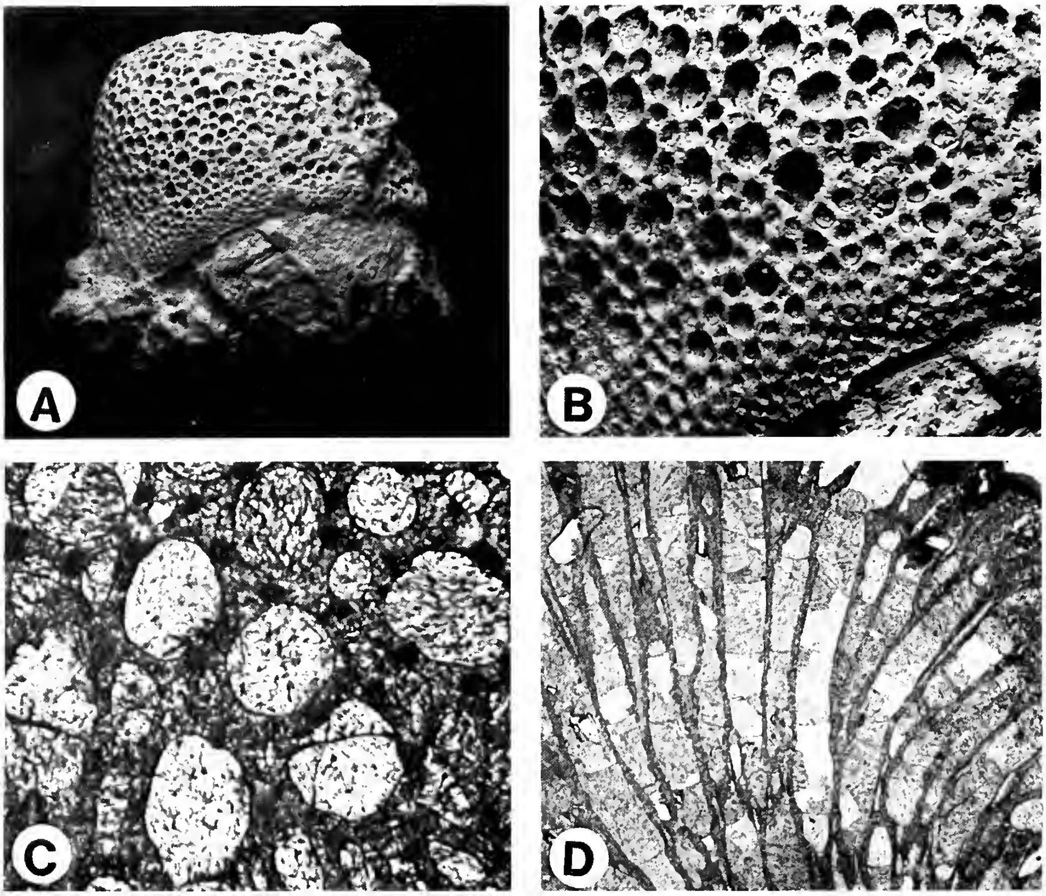


Fig. 9 *Dyscritella zardinii* Schäfer & Fois. Cassian Fm., St Cassian. D54220. A, scanning electron micrograph of colony, × 13. B, micrograph of growing edge, × 41. C, tangential acetate peel showing autozooecia, exilazooecia and styles, × 89. D, oblique longitudinal peel of zooecia, × 31.

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.

ACKNOWLEDGEMENTS. The authors wish to express their thanks to Dr J. Reitner (Berlin) and Dr Rachel Wood (Cambridge and London) for discussions. T.S.E. is greatly indebted to the scientists and curators of the British Museum (Natural History) for their kindness and cooperation during a one-year visit made possible through a grant of the NATO scientific committee awarded by the German Academic Exchange Service. This also is gratefully acknowledged.

REFERENCES

Anstey, R. L. & Perry, T. G. 1972. Eden Shale bryozoans : a numerical study (Ordovician, Ohio Valley). *Publs Mich. St. Univ. Mus.*, East Lansing, (Pal.) **1:** 1–80.

Astrova, G. G. 1965. [The morphology, evolution, and system of the Ordovician and Silurian Bryozoa]. *Trudy̆ paleont. Inst.*, Moscow, **106:** 1–431. [In Russian].

Bergquist, P. R. 1978. *Sponges*. 268 pp., Berkeley and Los Angeles.

Bizzarini, F. & Braga, G. 1978. Upper Triassic new genera and species of fair and questionable Bryozoa and Chaetetida from the S. Cassiano Formation of the Dolomites (Eastern Alps). *Boll. Soc. Paleont. Ital.*, Modena, **17:** 28–48.

—— —— 1982. The Triassic Bryozoa of the Western Tethyan Basin. *Boll. Soc. Paleont. Ital.*, Modena, **21:** 223–234.

—— —— 1985. *Braiesopora voigti* n. gen. n. sp. (cyclostome bryozoan) in the S. Cassiano Formation in the Eastern Alps (Italy). *In* Nielsen, C. & Larwood, G. P. (eds), *Bryozoa : Ordovician* to *Recent*: 25–33. Fredensborg.

Boardman, R. S. 1984. Origin of the post-Triassic Stenolaemata (Bryozoa): a taxonomic oversight. *J. Paleont.*, Lawrence, **58:** 19–39.

—— ***et al.*** 1983. Bryozoa. *In* Robison, R.A. (ed.), *Treatise on Invertebrate Paleontology*, **G.** 253 pp. Lawrence, Kansas.

Borg, F. 1926. Studies on Recent cyclostomatous Bryozoa. *Zool. Bidr. Uppsala*, **10:** 181–507.

Boule, M. 1923. Types du prodrôme de paléontologie stratigraphique universelle d'Alcide d'Orbigny. *Annls. Paléont.*, Paris, **12:** 177–189.

Cuffey, R. L., Basile, L. L. & Lisenbee, A. L. 1979. A bryozoan-like chaetetid (possible sclerosponge) from Jurassic–Cretaceous limestones near Orhaneli, northwestern Turkey. *Geobios*, Lyon, **12:** 473–479.

Cuif, J. J. & Fischer, J.-C. 1974. Étude systematique sur les Chaetetida du Trias de Turquie. *Annls. Paléont.*, Paris, (Invert.) **60:** 3–14.

Dieci, G., Russo, A. & Russo, F. 1975. Revisione del genere *Leiospongia* d'Orbigny (Sclerospongiae triassica). *Boll. Soc. Paleont. Ital.*, Modena, **13:** 135–146.

—— —— —— **& Marchi, M. S.** 1977. Occurence of spicules in Triassic Chaetetids and Ceratoporellids. *Boll. Soc. Paleont. Ital.*, Modena, **16:** 229–238.

Dunaeva, N. N. & Morozova, I. P. 1967. [Evolutional features and the systematic position of some late Palaeozoic trepostomes]. *Paleont. Zh.*, Moscow, **4:** 86–94. [In Russian].

Flügel, E. 1961. Bryozoen aus den Zlambach-Schichten (Rhät) des Salzkammergutes, Österreich. *Abh. Österr. Akad. Wiss., math.-nat. Kl.*, Vienna, **170:** 265–272.

—— 1963. Revision der triadischen Bryozoen und Tabulaten. *Sitz.-Ber. Österr. Akad. Wiss.*, Vienna, (1) **172:** 225–252.

Fromentel, M. E. 1859. Introduction à l'étude des ésponges fossiles. *Mém. Soc. linn. Normandie*, Caen, **9:** 1–50.

Hu Zhao-Xun 1984. Triassic Bryozoa from Xixang (Tibet) with reference to their biogeographical provincialism in the world. *Acta palaeont. sin.*, Peking, **23:** 568–577. [In Chinese; Engl. summ.].

International Commission on Zoological Nomenclature 1976. Opinion 1059. *Bull. zool. Nomencl.*, London, **33:** 24–26.

Klipstein, A. von 1843–45. *Beiträge zur geologischen Kenntnis der östlichen Alpen*. 311 pp. Giessen.

Kühn, O. 1936. Die Anthozoen, Hydrozoen, Tabulaten und Bryozoen der Trias von Braşov (Kronstadt). *Anuar Inst. geol. Rom.*, Bucharest, **17:** 109–132.

Laube, G. C. 1865. Die Fauna der Schichten von St. Cassian. *Denkschr. Akad. Wiss. Wien*, **24:** 223–296.

Laubenfels, M. W. de 1955. Porifera. *In*: Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology*, **E** (Archaeocyatha and Porifera): E21– E112.

McKinney, F. K. 1975. Autozooecial budding patterns in dendroid stenolaemate bryozoans. *Doc. Lab. Geol. Fac. Sci. Lyon*, (h.s.) **3** (1): 65–76.

—— 1977. Autozooecial budding patterns in dendroid Paleozoic bryozoans. *J. Paleont.*, Tulsa, **51:** 303–329.

Migliorini, C. I. & Venzo, S. 1933. Il Ladinico Superiore dell'Isola di Rodi (Egeo). *Palaeontogr. Ital.*, Siena, **34:** 137–170.

Morozova, I. P. 1986. Bryozoa. *In*: Oleinikov, A.N. & Zhamoida, A.I. (eds), [Parastratigraphic groups of flora and fauna of the Triassic]. *Trudy̆ vses. nauchno-issled. geol. Inst.*, Leningrad, **334:** 67–78. [In Russian].

—— **& Zharnikova, N. K.** 1984. [On some new Triassic bryozoans.] *Paleont. Zh.*, Moscow, **1984** (4): 73–79. [In Russian; Engl. transl. *Paleont. J.*, Washington, **18** (4): 72–78].

Münster, G. Graf zu 1841. Beiträge zur Geognosie und Petrefakten-kunde des südöstlichen Tirol's vorzüglich der Schichten von St. Cassian. *Beiträge zur Petrefakten-kunde* **4**. 152 pp., 16 pls. Bayreuth.

Neave, S. A. (ed.) 1939. *Nomenclator zoologicus*, **2.** 1025 pp. London.

Nye, O. B. 1976. Generic revision and skeletal morphology of some cerioporid cyclostomes (Bryozoa). *Bull. Am. Paleont.*, Ithaca, **69:** 1–222.

Orbigny, A. d' 1849. Note sur la classe de Amorphozoaires. *Rev. Mag. Zool.*, Paris, (2) **1:** 545–550.

—— 1850. *Prodrôme de paléontologie* . . . (etc). **1.** 394 pp. Paris.

Podell, M. E. & Anstey, R. L. 1979. The interrelationship of early colony development, monticules and branches in Palaeozoic bryozoans. *Palaeontology*, London, **22:** 965–982.

Poluzzi, A. & Sartori, R. 1975. Report on the carbonate mineralogy of Bryozoa. *Docum. Lab. Geol. Fac. Sci. Lyon*, (h.s.) **3** (1): 193–210.

Quenstedt, F. A. 1876–78. Korallen, Schwämme. *In: Petrefaktenkunde Deutschlands*, Tübingen, (1) **5:** 1–612.

Royal Society of London (comp.) 1870. *Catalogue of Scientific Papers (1800–1863)*, **4.** 1006 pp. London.

Sakagami, S. 1985. Palaeogeographic distribution of Permian and Triassic Ectoprocta (Bryozoa). *In* Nakazawa, K. & Dickins, J. M. (eds), *The Tethys*: 171–183. Tokyo.

Schäfer, P. & Fois-Erickson, E. 1986. Triassic Bryozoa and the evolutionary crisis of Paleozoic Stenolaemata. *In* Walliser, O. (ed.), *Global Bio-events*: 251–255. Berlin.

—— **& Fois, E.** 1987. Systematics and evolution of Triassic Bryozoa. *Geologica Palaeont.*, Marburg, **21:** 173–225.

Schnorf, A. 1960. Quelques Hydrozoaires du Sénonien de Martigues (Bouches-du-Rhône). *Ecl. geol. Helv.*, Basle, **53:** 427–437.

Scrutton, C. T. 1987. A review of favositid affinities. *Palaeontology*, London, **30:** 485–492.

Soule, J. D. & Soule, D. F. 1970. New species of *Thalamoporella* (Ectoprocta) from Hawaii, examined by scanning electron microscopy. *Am. Mus. Novit.*, New York, **2417:** 1–18.

Tavener-Smith, R. & Williams, A. 1972. The secretion and structure of the skeleton of living and fossil Bryozoa. *Phil. Trans. Roy. Soc.*, London, (B) **264:** 97–159.

Taylor, P. D. 1986. Scanning electron microscopy of uncoated fossils. *Palaeontology*, London, **29:** 685–690.

Ulrich, E. O. 1882. American Paleozoic Bryozoa. *J. Cincinn. Soc. nat. Hist.*, Cincinnati, **5:** 121–175.

Urlichs, M. 1974. Zur Stratigraphie und Ammonitenfauna der Cassianer Schichten von Cassian (Dolomiten, Italien). *SchrReihe erdwiss. Komm. öst. Akad. Wiss.*, Vienna, **2:** 207–222.

Vacelet, J. 1985. Coralline sponges and the evolution of Porifera. *Spec. Vol. Syst. Assoc.*, Oxford, **28:** 1–13.

Vinassa de Regny, P. 1911. Neue Schwämme, Tabulaten und Hydrozoen aus dem Bakony. *Result. Wiss. Erforsch. Balatonsees*, Budapest, (Palaeont.) **1** (3): 1–17, 4 pls.

Woehrmann, S. von 1889. Die Fauna der sogenannten Cardita- und Raibler-Schichten in den Nordtiroler und bayerischen Alpen. *Jb. k.k. geol. Reichsanst.*, Vienna, **39:** 181–258.

Wood, R. 1987. Biology and revised systematics of some late Mesozoic stromatoporoids. *Spec. Pap. Palaeont.*, London, **37:** 1–89.

Zittel, K. A. 1879. Studien über fossile Spongien, 3. Monactinellidae, Tetractinellidae und Calcispongiae. *Abh. k. bayer. Akad. Wiss.*, Munich, (2) **13** (2): 1–48.

Bull. Br. Mus. nat. Hist (Geol.) **45** (1): 57–69 Issued 27 July 1989

Larval shells of four Jurassic bivalve molluscs

C. P. PALMER

9 Upton Dene, Grange Road, Sutton, Surrey SM2 6TA

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.

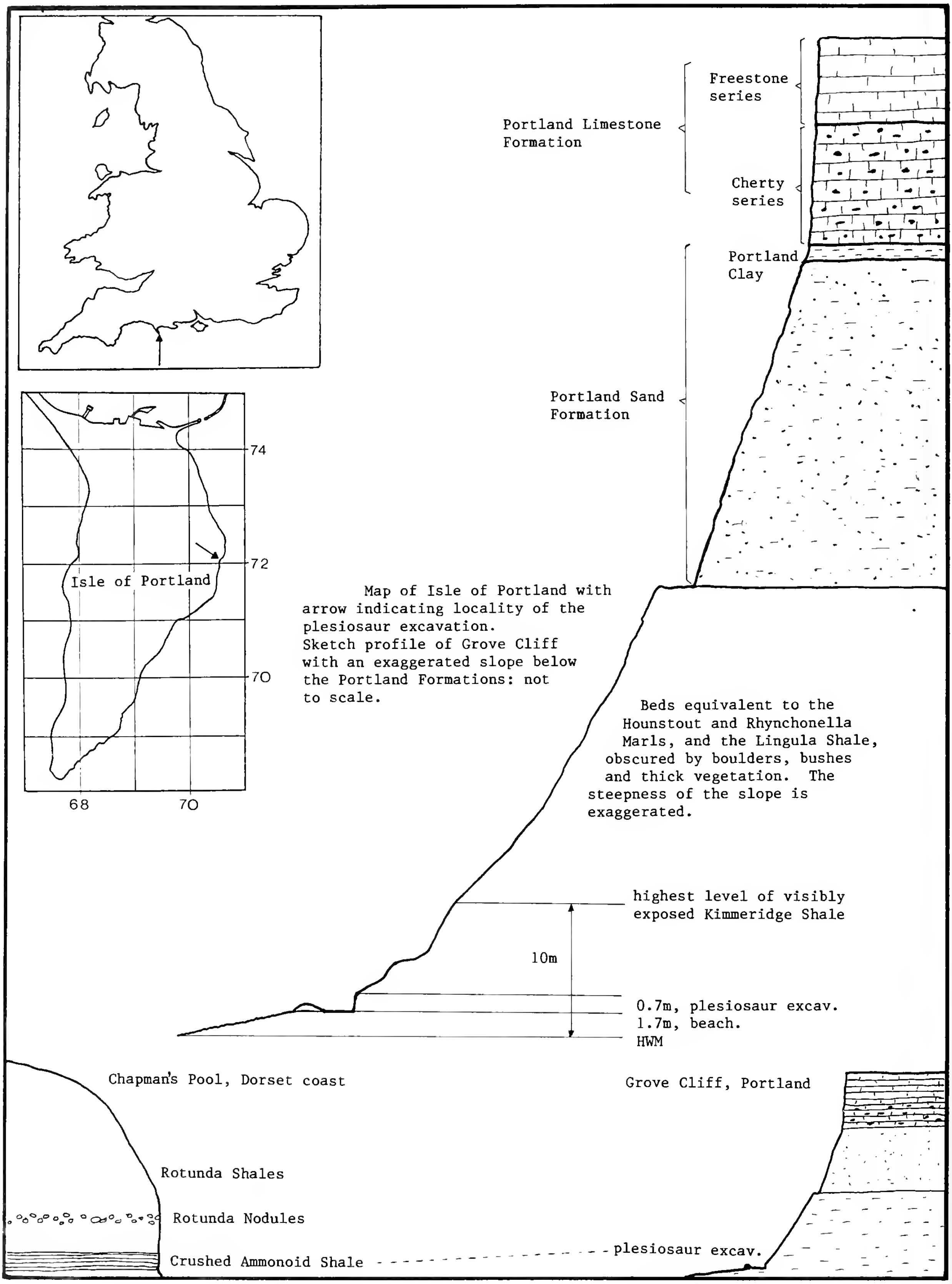
Some of the better-preserved spat were selected for photography under the scanning electron microscope (SEM) of the BM(NH) EM Unit, using low magnification of uncoated specimens as recommended by Taylor (1986). The SEM micrographs form the basis of Plates 1–5 of this report, except Plate 2, figs 9–11. 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 antero-ventral 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.

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

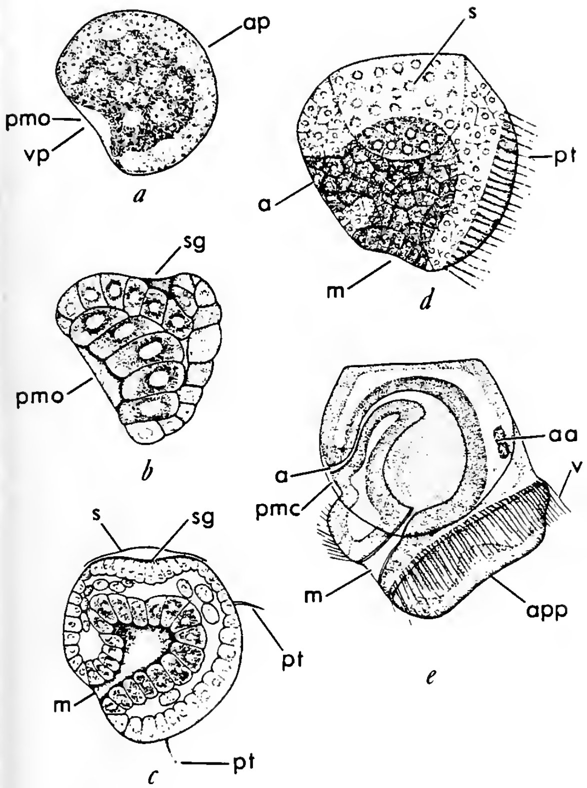


Fig. 2 Early development of *Ostrea edulis*, redrawn from Horst (1882), with presumptive dorsal region (shell gland and later the hinge) at top and anterior to right: *a*, gastrula; *b*, early trochophore; *c*, middle trochophore; *d*, late trochophore; *e*, early veliger. (a = anus, aa = anterior adductor, 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).

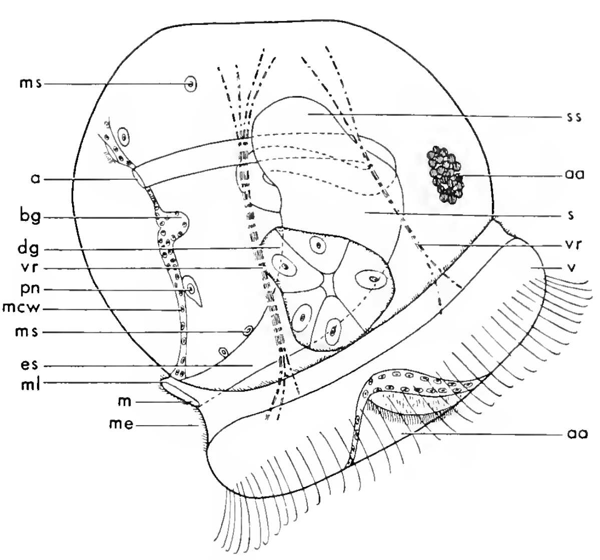


Fig. 3 Anatomy of a young, newly released, six-day-old veliger larva of *Ostrea edulis*, redrawn from Erdmann (1935). (a = anus, aa = anterior adductor, ao = apical organ, bg = primordial byssal gland, dg = digestive gland, es = esophagus, m = mouth, mcw = mantle cavity wall, me = mouth embayment, ml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

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.

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

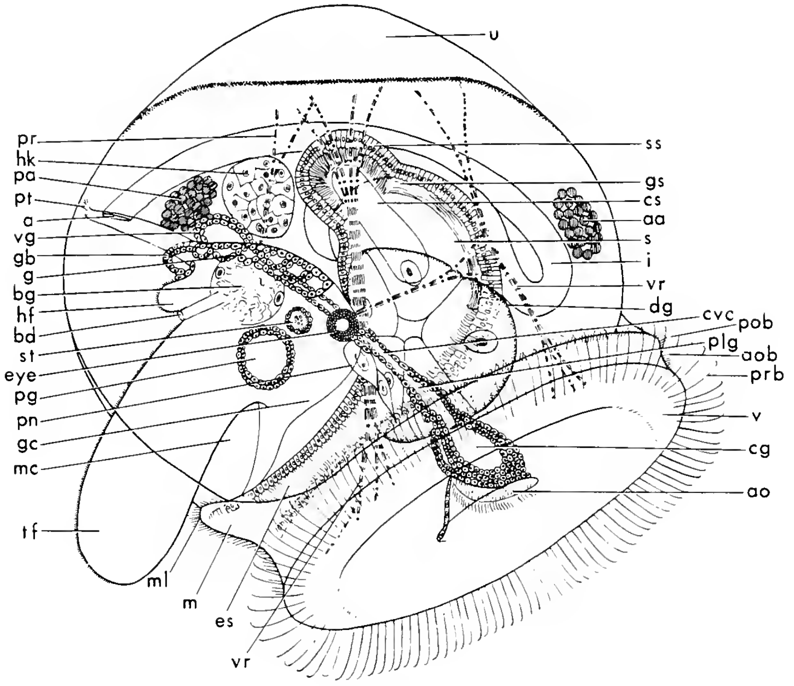


Fig. 4 Anatomy of a pediveliger larva of *Ostrea edulis*, redrawn from Erdmann (1935). (a = anus, aa = anterior adductor, ao = apical organ, acb = adoral ciliary band, bd = byssal gland duct, bg = byssal gland, cg = cerebral ganglion, cs = crystalline style, cvc = cerebropleural–visceral connective, 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.)

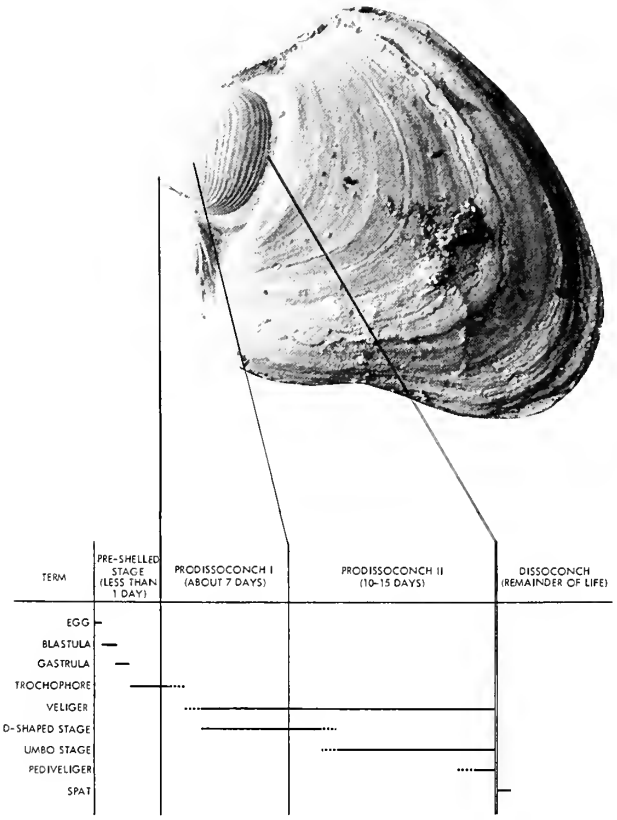


Fig. 5 Correlation of development stages of *Ostrea edulis* with *Liostrea plastica*. (Modified after fig. 4 of Waller, 1981.)

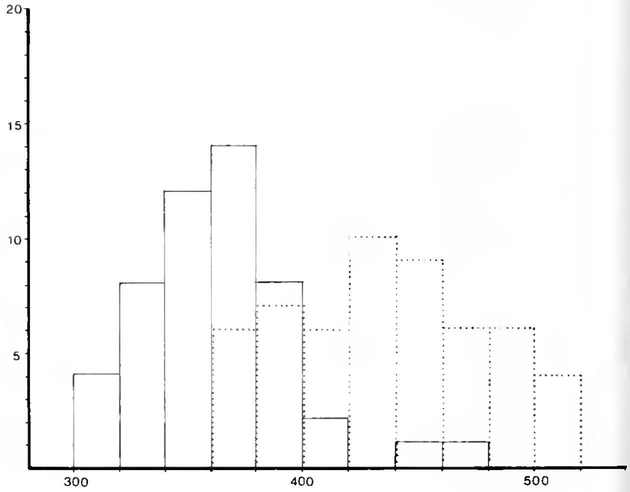
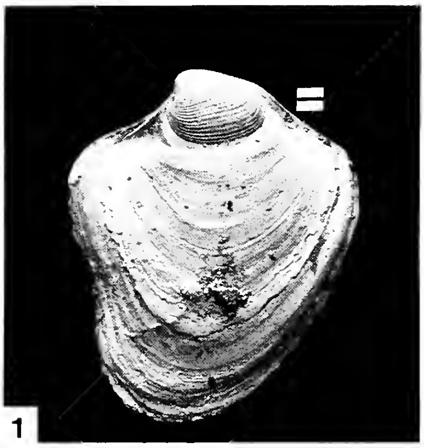


Fig. 6 Frequency distribution of height and length of pediveliger of *Liostrea plastica* at metamorphosis. The *x* axis represents dimensions in microns μ; *y* axis represents frequency; solid lines = height; dotted lines = length.

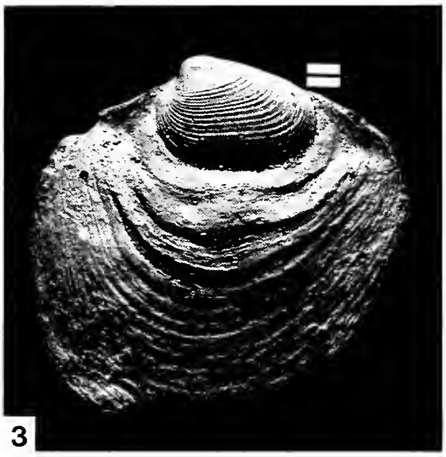
a relatively large Prod. 1 development (Waller 1981: figs 90–96) compared with Prod. II.

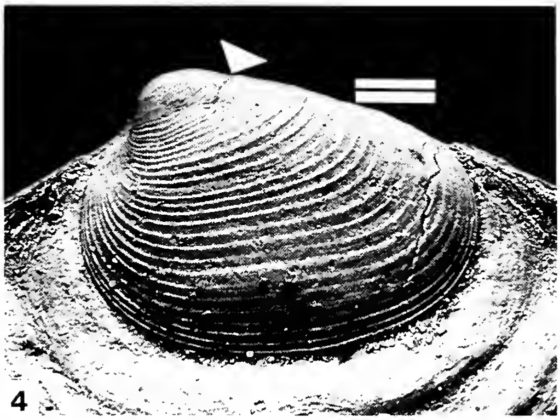
Ostrea edulis does not release gametes into the sea where external fertilization can take place, but employs a more advanced reproductive strategy. Instead, nearby males release sperm into the sea which is drawn into the female mantle cavity by feeding currents, where it fertilizes eggs contained in 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*


1


2


3


4


5

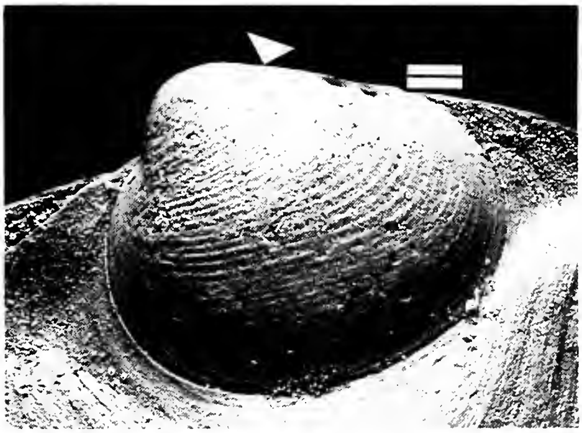


PLATE 1 *Liostrea plastica.*

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.

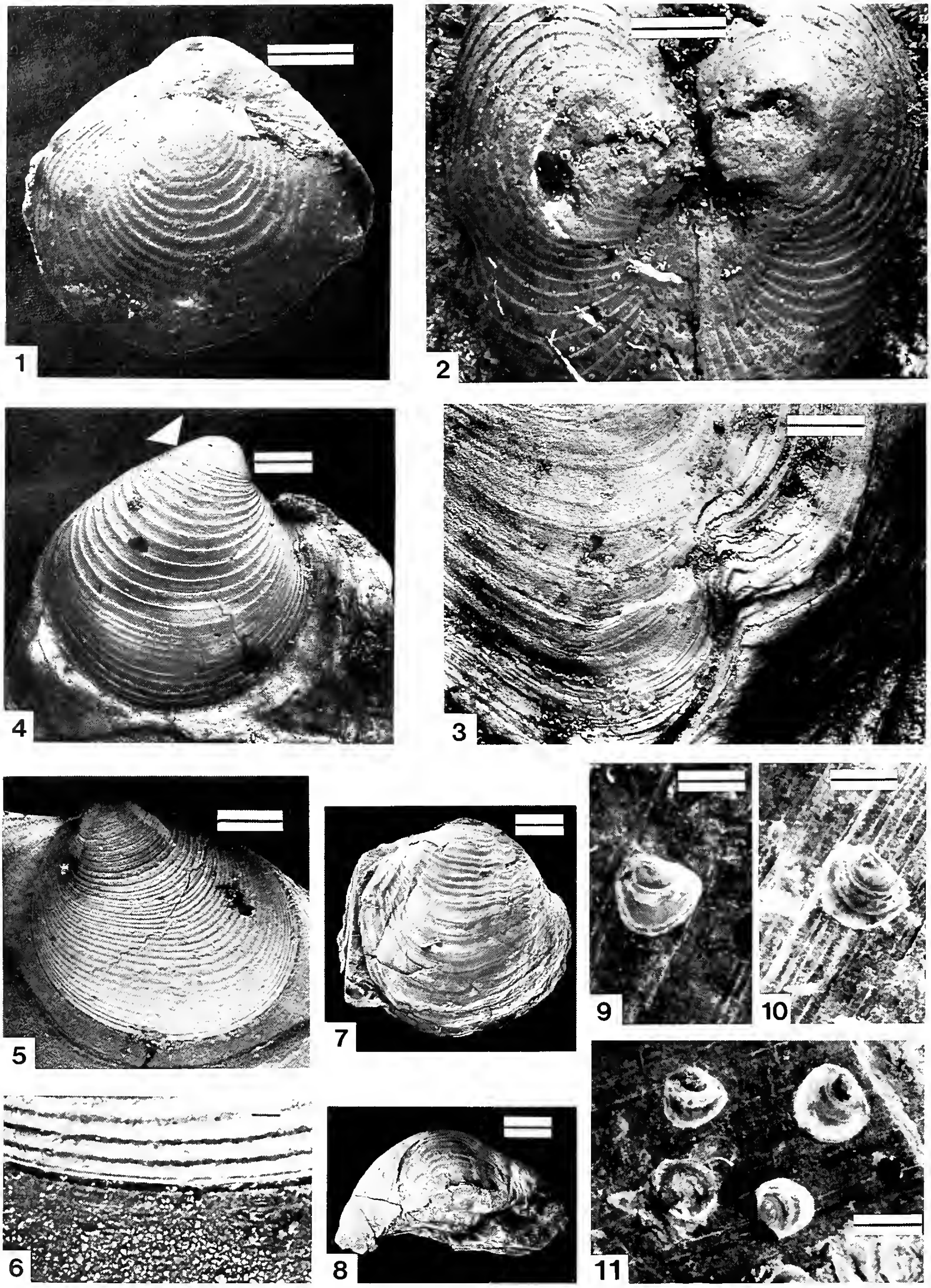


PLATE 2 *Liostrea plastica*, figs 1–8; *Liostrea irregularis*, figs 9–11.

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.

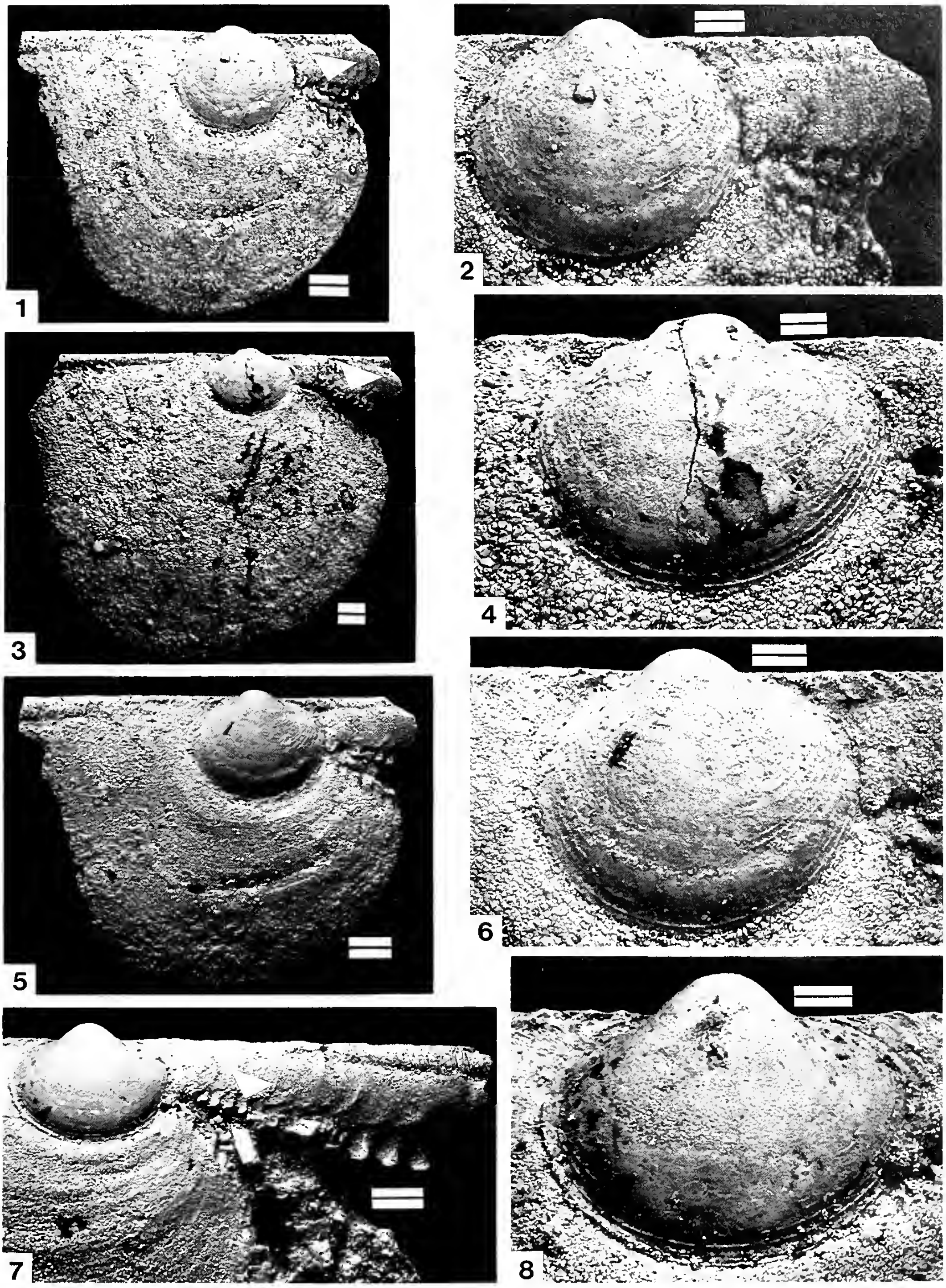


PLATE 3 *Oxytoma* sp., right valves only.

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).

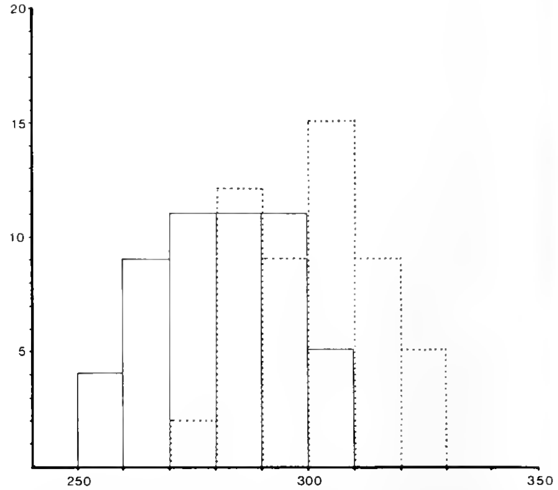


Fig. 7 Frequency distribution of height and length of prodissoconch of *Oxytoma* sp. at metamorphosis. The *x* axis represents dimensions in microns µ; *y* axis represents frequency; solid lines = height; dotted lines = length.

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.

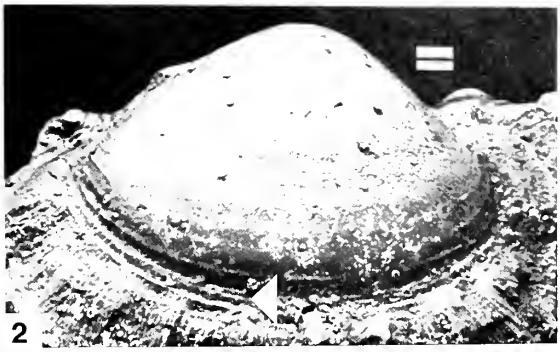
	Mean	Max.	Min.	SD
height µm	276·5	300	250	14·8
length µm	295·9	320	270	13·7
h/l %	93·68	103·57	84·97	3·76

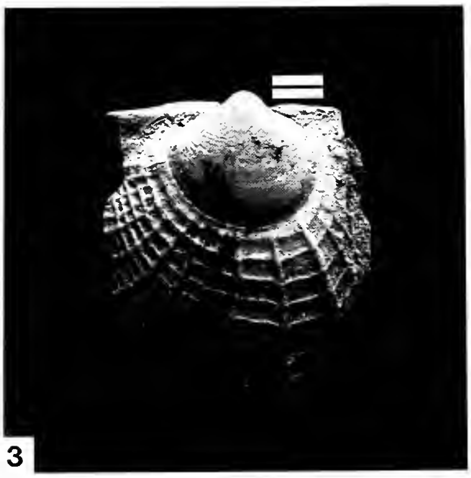
A histogram showing the frequency distribution of height and length is given in Fig. 7.

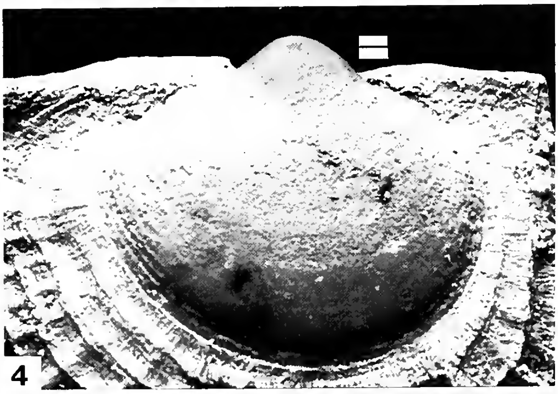
DISCUSSION. An unresolved difficulty lies in assigning these juvenile *Oxytoma* to an adult named form. L. R. Cox held the view that *O. inequivalvis* ranged almost throughout the Jurassic: W. J. Arkell held that it was confined to the Lower Jurassic. Until the stratigraphical taxonomics of this group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

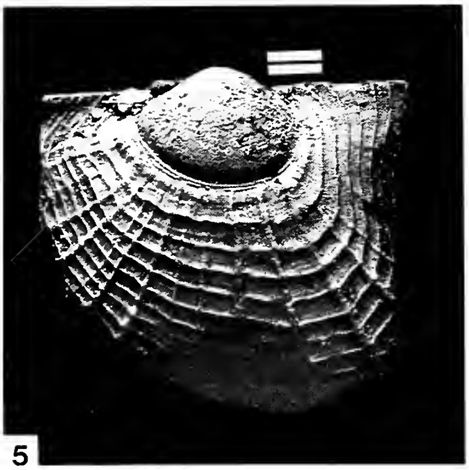
Waller (1984) reminds us of three forms of ctenolium structures to be distinguished. A true ctenolium is formed by the mantle along the margin of the disc beneath the auricular notch. It is composed of lathic calcite, part of the internal structure of the shell. He compares this with the callus, or


1


2


3


4


5


6

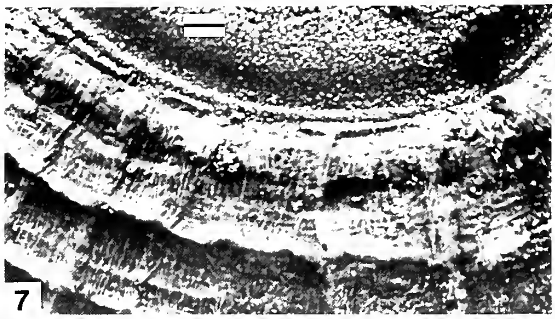

7

PLATE 4 *Oxytoma* sp., left valves only.

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

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

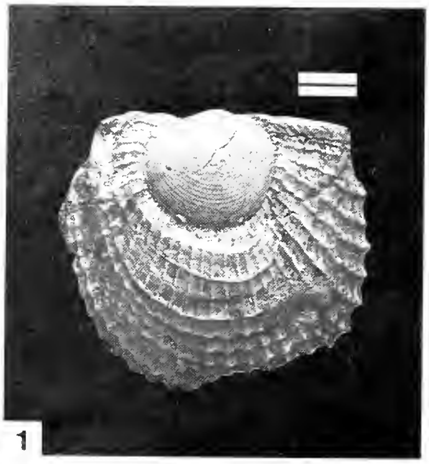
ig. 3 Broken juvenile with prodissoconch, LL41340; scale bar = 100 μ.

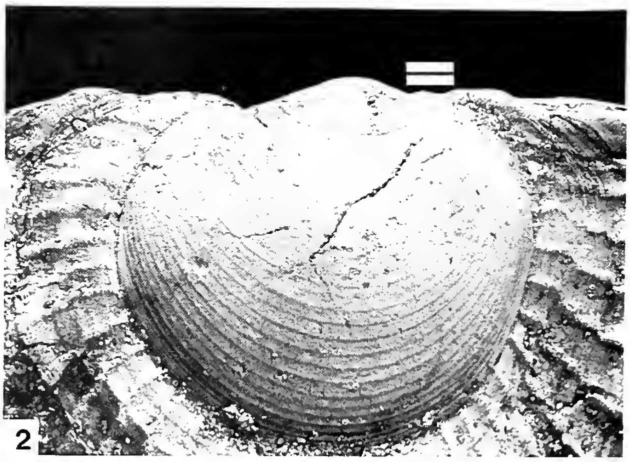
ig. 4 Enlarged view of prodissoconch in fig. 3, showing growth halts at prodissoconch/dissoconch boundary and immediate fine divaricate 'ornament' ventral to the boundary; scale bar = 20 μ.

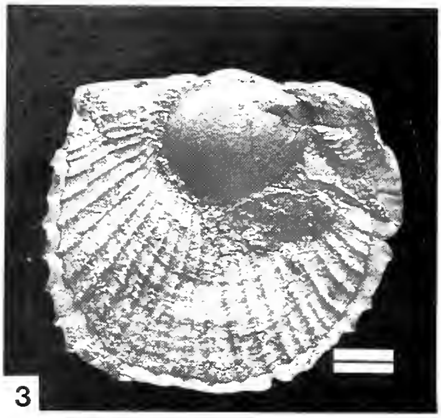
ig. 5 Juvenile with prodissoconch, LL41341; scale bar = 100 μ.

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

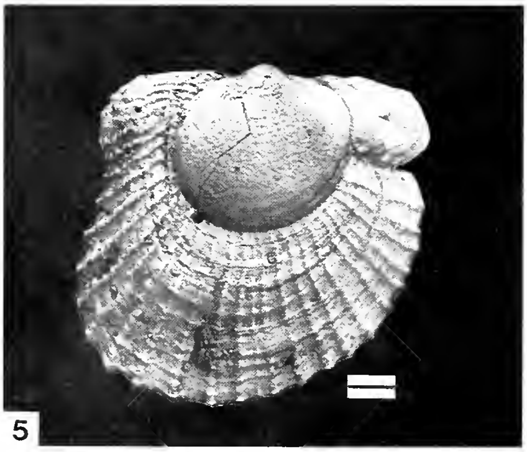
ig. 7 Enlarged view of fig. 5 showing immediate formation of radial ribs and divaricate 'ornament' ventral to prodissoconch/dissoconch boundary; scale bar = 20 μ.


1


2


3


4


5

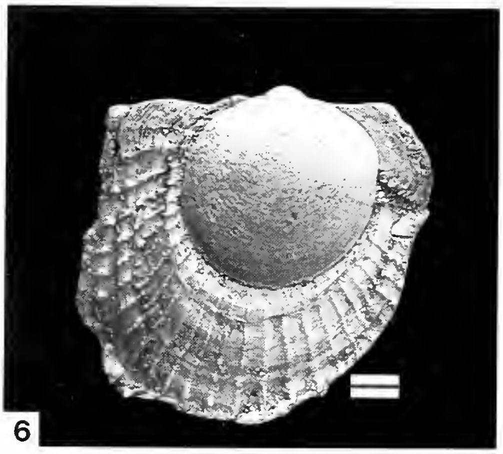

6

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.

nductura, 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 ine 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.

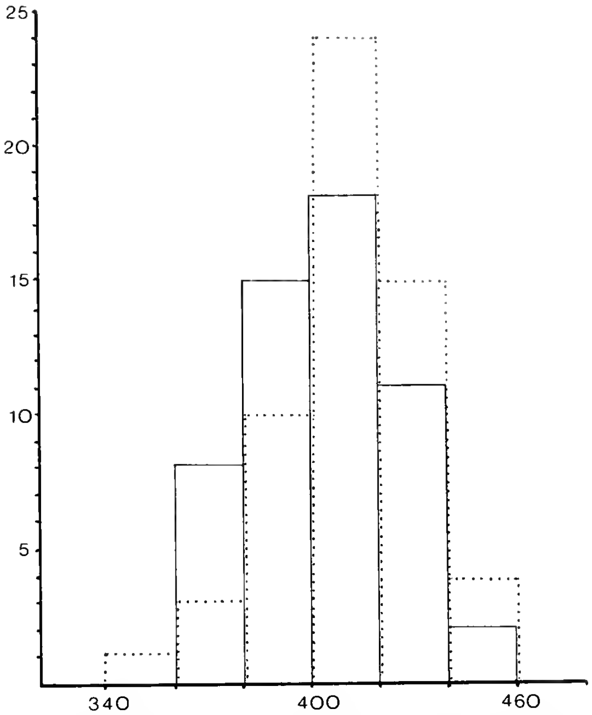


Fig. 8 Frequency distribution of height and length of prodissoconch of *Meleagrinella* sp. at metamorphosis. The x axis represents dimensions in microns µ; y axis represents frequency; solid lines = height; dotted lines = length.

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

echnique; to my colleague Noel Morris for helpful discussions oncerning larval development; and to Tom Waller for permission to eproduce his text-figures.

EFERENCES

rown, D. S. 1984. Discovery of a specimen of the plesiosaur *Colymbosaurus trochanterius* (Owen) on the Island of Portland. *Proceedings of the Dorset Natural History and Archaeological Society*, Dorchester, **100**: 170.

asey, R. 1967. The position of the Middle Volgian in the English Jurassic. *Proceedings of the Geological Society of London*, **1640**: 128–133.

ope, J. C. W. 1968. Epizoic oysters on Kimmeridgian ammonites. *Palaeontology*, London, **11** (1): 19–20.

—— 1978. The ammonite faunas and stratigraphy of the upper part of the Upper Kimmeridge Clay of Dorset. *Palaeontology*, London, **21** (3): 469–533.

rdmann, W. 1935. Untersuchungen über die Lebensgeschichte der Auster, 5. Über die Entwicklung und die Anatomie der 'ansatzreifen' Larve von *Ostrea edulis* mit Bemerkungen über die Lebensgeschichte der Auster. *Wissenschaftliche Meeresuntersuchungen der Kommission zur Wissenschaften Untersuchung der Deutschen Meere (Helgoland)*, Kiel & Leipzig, n.s. **19** (6), 25 pp., 5 figs, 8 pls.

orst, R. 1882. Bijdrage tot de kennis van de ontwikkelingsgeschiedenis van der oester (*Ostrea edulis*). *Tijdschrift der Nederlandsche Dierkundige Vereeniging*, Leiden, **6**: 25–34, pl. 3. (Engl. transl. Jacobson, H. 1886, *Report United States Commissioner of Fisheries*, Washington, **1884** (34): 891–910, 2 pls.)

Jablonski, D. & Lutz, R. A. 1983. Larval ecology of marine benthic invertebrates: palaeobiological implications. *Biological Review of the Cambridge Philosophical Society*, **58** (1): 21–89.

Kelly, A. R. A. 1984. Bivalvia of the Spilsby Sandstone and Sandringham Sands (Late Jurassic–Early Cretaceous) of Eastern England. Part 1: 1–94, 20 pls. *Monograph of the Palaeontographical Society*, London.

Lloyd, A. J., Savage, R. J. G., Stride, A. H. & Donovan, D. T. 1973. The geology of the Bristol Channel floor. *Philosophical Transactions of the Royal Society of London*, (A) **274** (1244): 595–626.

Palmer, C. P. 1988. The Kimmeridgian fauna associated with the Portland plesiosaur. *Proceedings of the Dorset Natural History and Archaeological Society*, Dorchester, **109** (1987): 109–112.

Stenzel, H. B. 1971. Oysters. *In* Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology*, **N** (Mollusca 6, Bivalvia 3): N953–N1224. Geol. Soc. Amer. and Univ. Kansas Press.

Taylor, P. D. 1986. Scanning electron microscopy of uncoated fossils. *Palaeontology*, London, **29** (4): 685–690.

Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates. *Meddelelser fra Kommissionen for Danmarks Fiskeri og Havundersøgelser*, Copenhagen, (Plankton) 4 (1). 523 pp.

—— 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Review of the Cambridge Philosophical Society*, **25**: 1–45.

Waller, T. R. 1981. Functional morphology and development of veliger larvae of the European oyster *Ostrea edulis* Linné. *Smithsonian Contributions to Zoology*, Washington, **328**. 70 pp.

—— 1984. The ctenolium of scallop shells: functional morphology and evolution of a key family-level character in the Pectinacea (Mollusca: Bivalvia). *Malacologia*, Ann Arbor, **25** (1): 203–219.

Bull. Br. Mus. nat. Hist. (Geol.) **45** (1): 71–76 Issued 27 July 1989

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

C.H. SHUTE

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

C.J. CLEAL

37 Lipscombe Close, Newbury, Berkshire RG14 5JW

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.

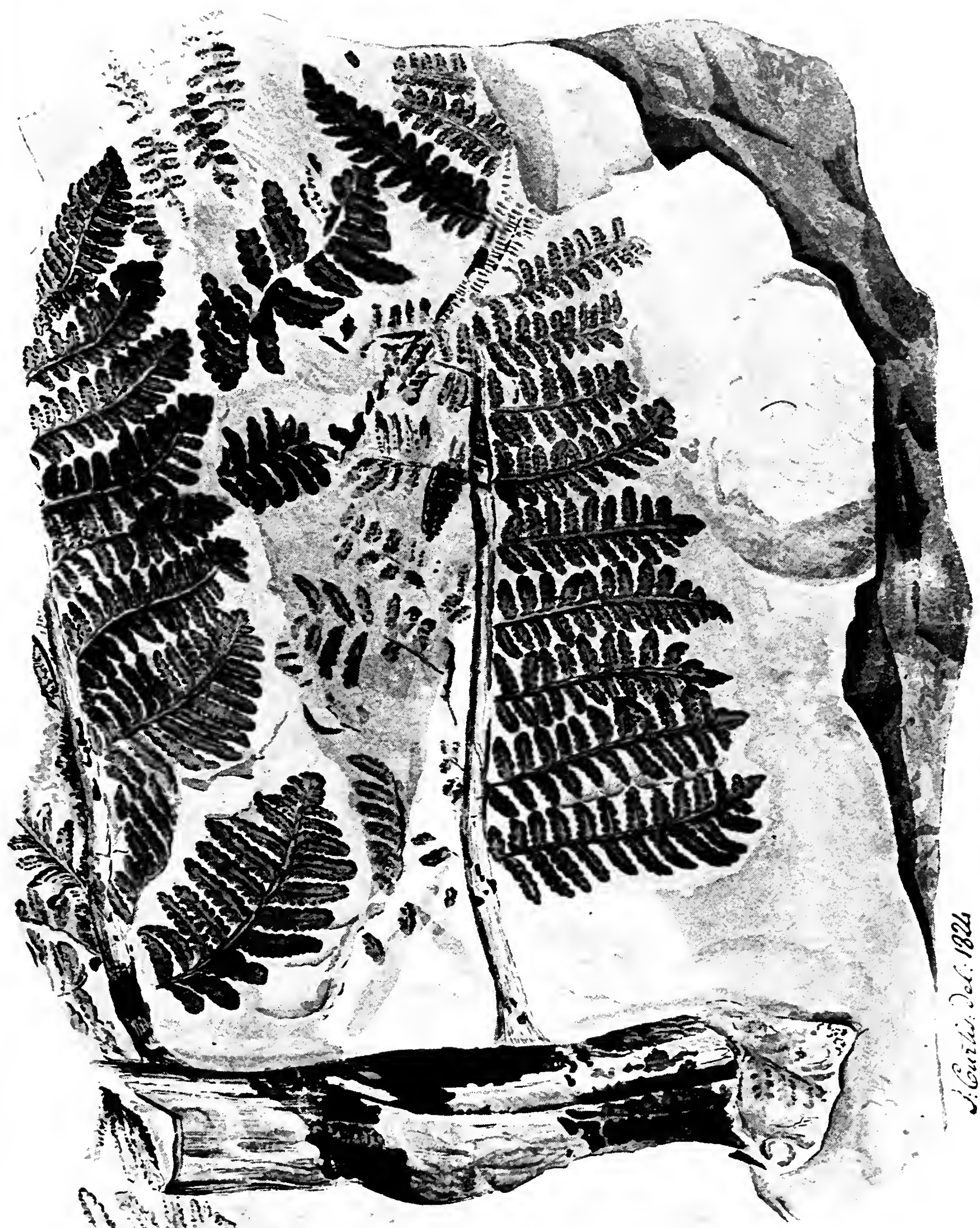
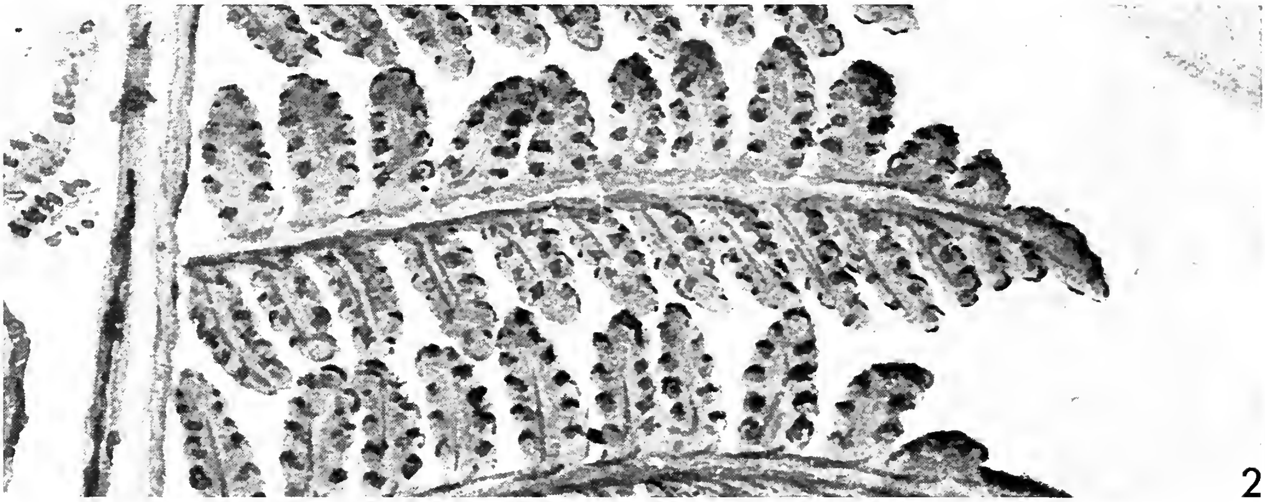


Plate 2 *Lobatopteris miltoni* (Artis) Wagner. Wash drawing of the holotype, made by J. Curtis, used as the basis for Artis' (1825: pl. 14) engraving. Natural size.


1


2

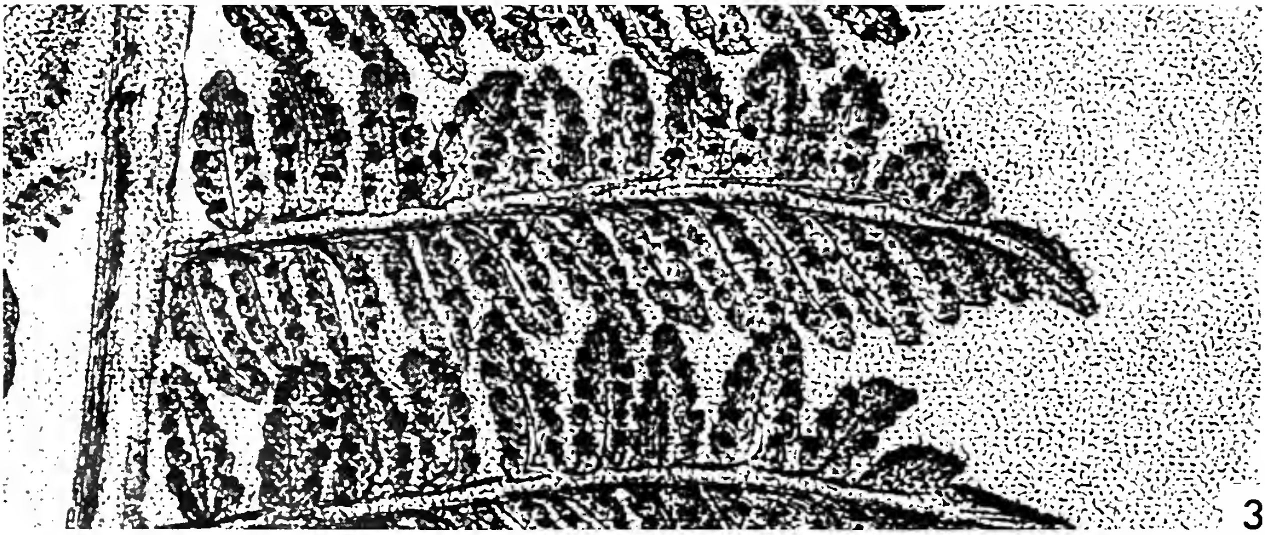

3

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.

ACKNOWLEDGEMENT. The photographs illustrating this paper were taken by the Photographic Department of the British Museum (Natural History).

REFERENCES

Artis, E.T. 1825. *Antediluvian phytology, illustrated by a collection of the fossil remains of plants peculiar to the coal formations of Great Britain.* xiii + 24 pp., 24 pls. London (reprinted 1838).

Cleal, C.J. 1984. The Westphalian D floral biostratigraphy of Saarland (Fed. Rep. Germany) and a comparison with that of South Wales. *Geological Journal*, Liverpool, **19**: 327–351.

Corsin, P. 1955. Sur les *Pecopteris* et leur position systématique. *Annales des Sciences Naturelles*, Paris, (Bot.) **11**: 493–501.

Dalinval, A. 1960. Contribution à l'étude des Pécoptéridées. Les *Pecopteris* du Bassin Houiller du Nord de la France. *Études Géologiques pour l'Atlas de Topographie Souterraine*, Lille, **1** (3): 1–222, 61 pls.

Hill, C. R. & Camus, J. M. 1986. Evolutionary cladistics of marattialean ferns. *Bulletin of the British Museum (Natural History)*, London, (Bot.) **14**: 219–300.

Kidston, R. 1924. Fossil plants of the Carboniferous rocks of Great Britain. Part 5. *Memoirs of the Geological Survey of Great Britain*, London, (Pal.) **2**: 377–522.

Laveine, J.-P. 1967. Les Neuroptéridées du Nord de la France. *Études Géologiques pour l'Atlas de Topographie Souterraine*, Lille, **1** (5): 1–344, 14 + 84 pls.

—— 1970. Quelques Pécoptéridinées houillères à la lumière de la palynologie (11). Implications paléobotaniques et stratigraphiques. *Pollen et Spores*, Paris, **12**: 235–297.

Mosbrugger, V. 1983. Organische Zusammenhörigkeit zwei Fossil-Taxa als taxonomisches Problem und Beispiel der jungpaläozoischen Farnfruktifikationen *Scolecopteris* und *Acitheca*. *Review of Palaeobotany and Palynology*, Amsterdam, **40**: 191–206.

Wagner, R. H. 1959. Some Stephanian pecopterids from N. W. Spain. *Mededelingen van de Geologische Stichting*, Maastricht, (N.S.) **12**: 5–23.

—— 1971. The Westphalian D floras of the Olloniego and Esperanza formations in the Central Asturian Coalfield. *Trabajos de Geologia, Facultad de Ciencias, Universidad de Oviedo*, **4**: 461–505.

Bull. Br. Mus. nat. Hist. (Geol.) **45** (1): 77–163 Issued 27 July 1989

Classification and review of the brachiopod superfamily Plectambonitacea

L. R. M. COCKS

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

RONG JIA-YU

Nanjing Institute of Geology and Palaeontology, Academia Sinica, Chi-Ming-Ssu, Nanjing, People's Republic of China

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

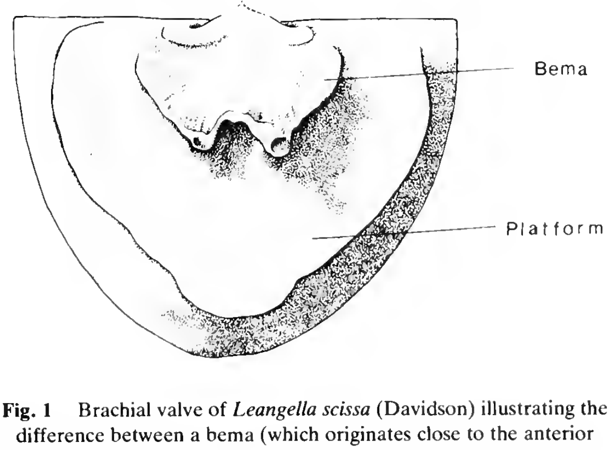


Fig. 1 Brachial valve of *Leangella scissa* (Davidson) illustrating the difference between a bema (which originates close to the anterior end of the socket plates) and a platform (which originates laterally to the structures surrounding the cardinal process).

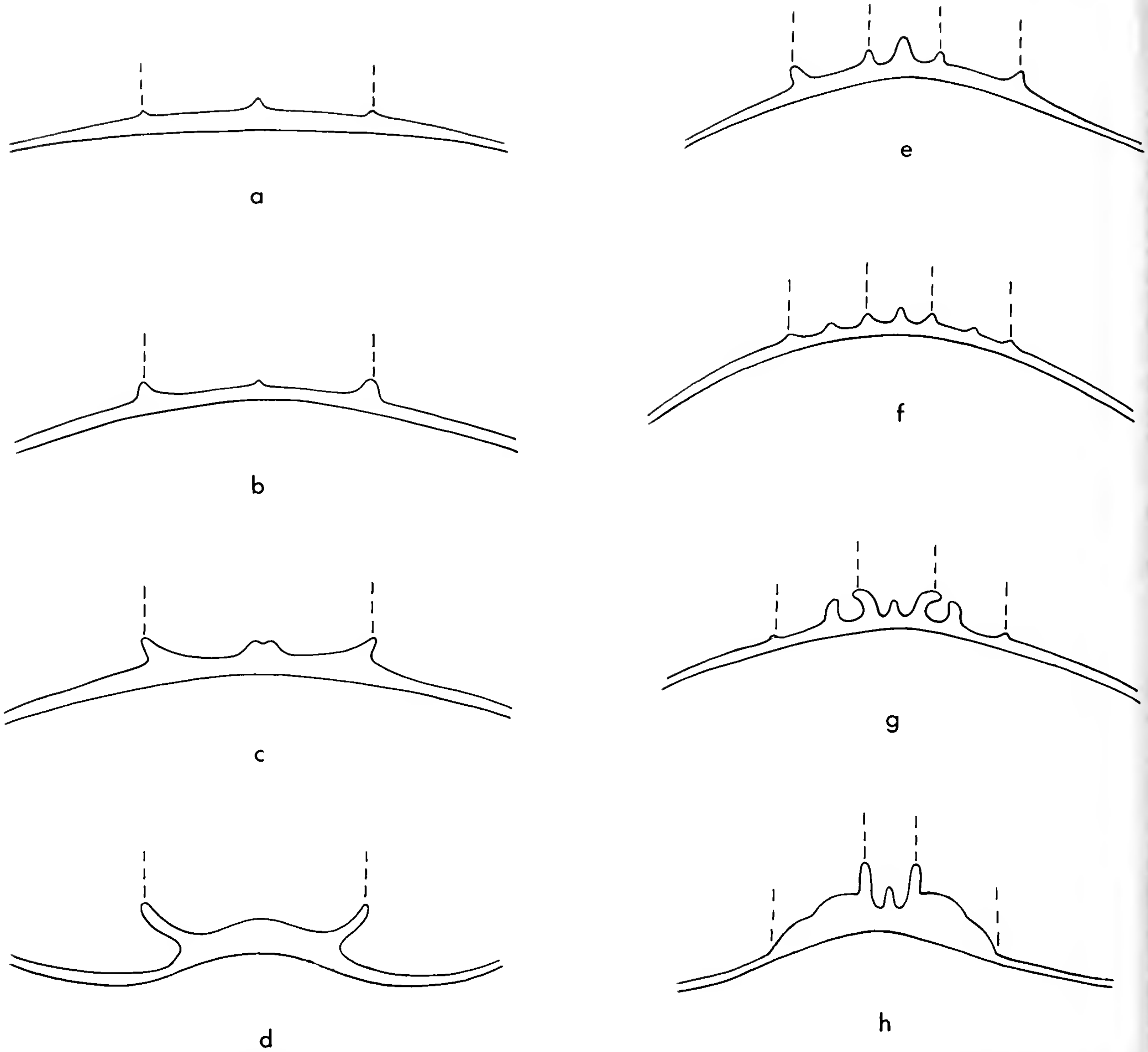


Fig. 2 Cross-section through various brachial valves to illustrate the different types of bema. The dotted lines indicate the limits of the bema, a–d are entire and e–h are divided; c and d are elevated; g and h illustrate the more extreme modifications. a, *Aegiria*; b, *Rurambonites*; c, *Leangella*;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

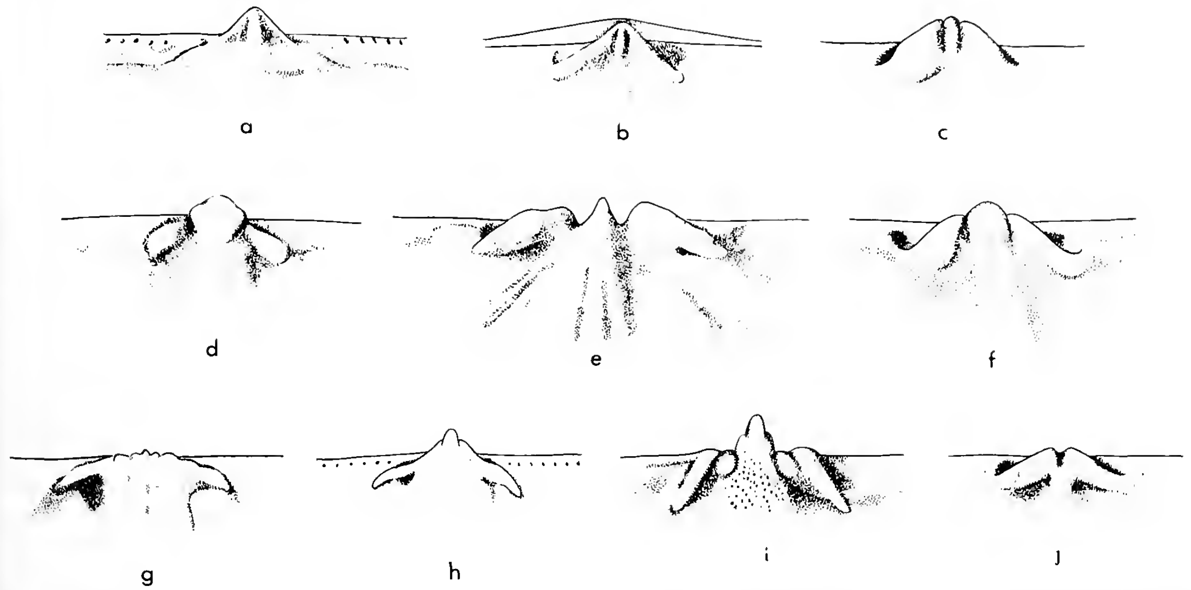
In general we follow the nomenclature used by Williams (*in* Williams *et al.* 1965), but the following terms need further elucidation.

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)



ig. 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).

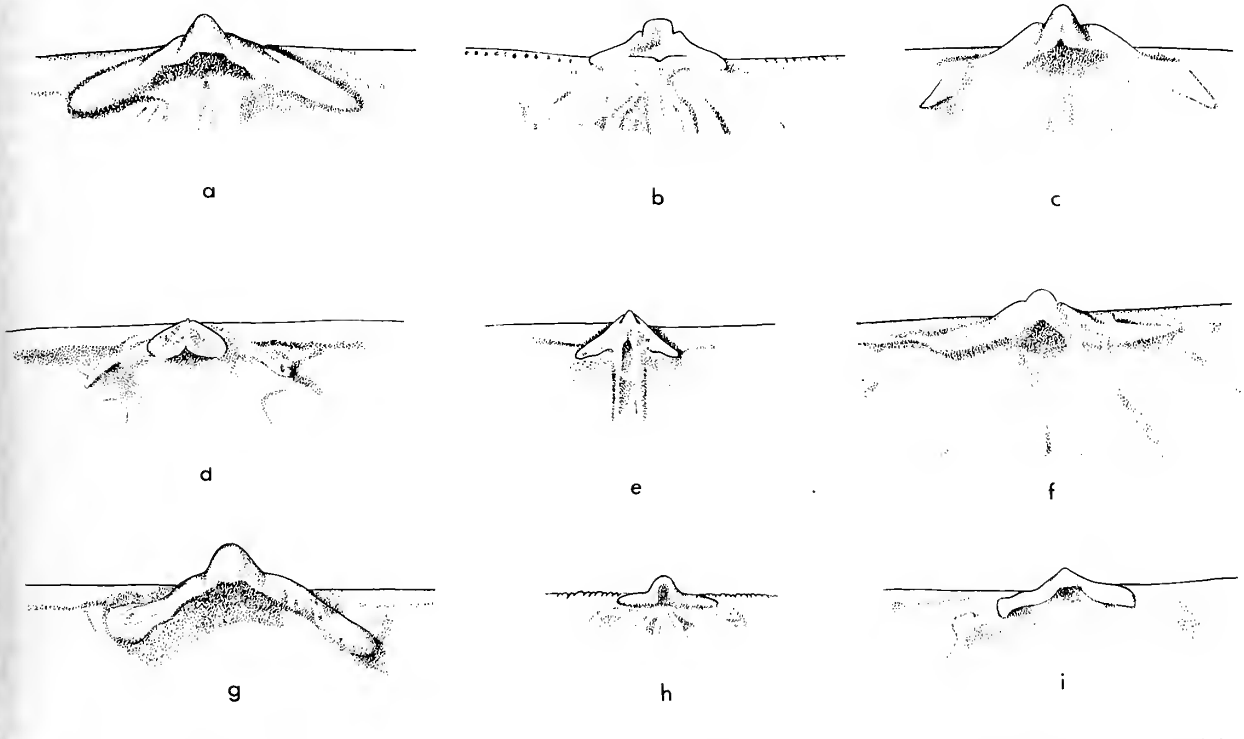


Fig. 4 Different types of cardinal process within the Plectambonitacea; all are trifid and undercut. a, *Sowerbyella eximia* Cooper, × 10 (after Cooper 1956: pl. 204, fig. 32); b, *Eoplectodonta duvalii* (Davidson), × 6 (from BB 31837); c, *Sowerbyella liliifera* Öpik, × 12 (from BB 5149); d, *Ptychoglyptus 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 lightly inclined. However, many of the more advanced genera, in particular the later Sowerbyellidae such as *Eoplecodonta*, did not have functional pedicles in adult life, and hus can only have lived freely on the sea floor, obviously with heir concave sides upwards to keep the valve gape clear of he substrate.

Ultrastructural studies (Brunton 1972) have shown hat the plectambonitacean primary layer is similar to both chonetaceans and strophomenaceans. However, the econdary shell layer differs within the Plectambonitacea: he sowerbyellids have standard fibrous secondary shell tructure, 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, t 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 hat 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 n 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

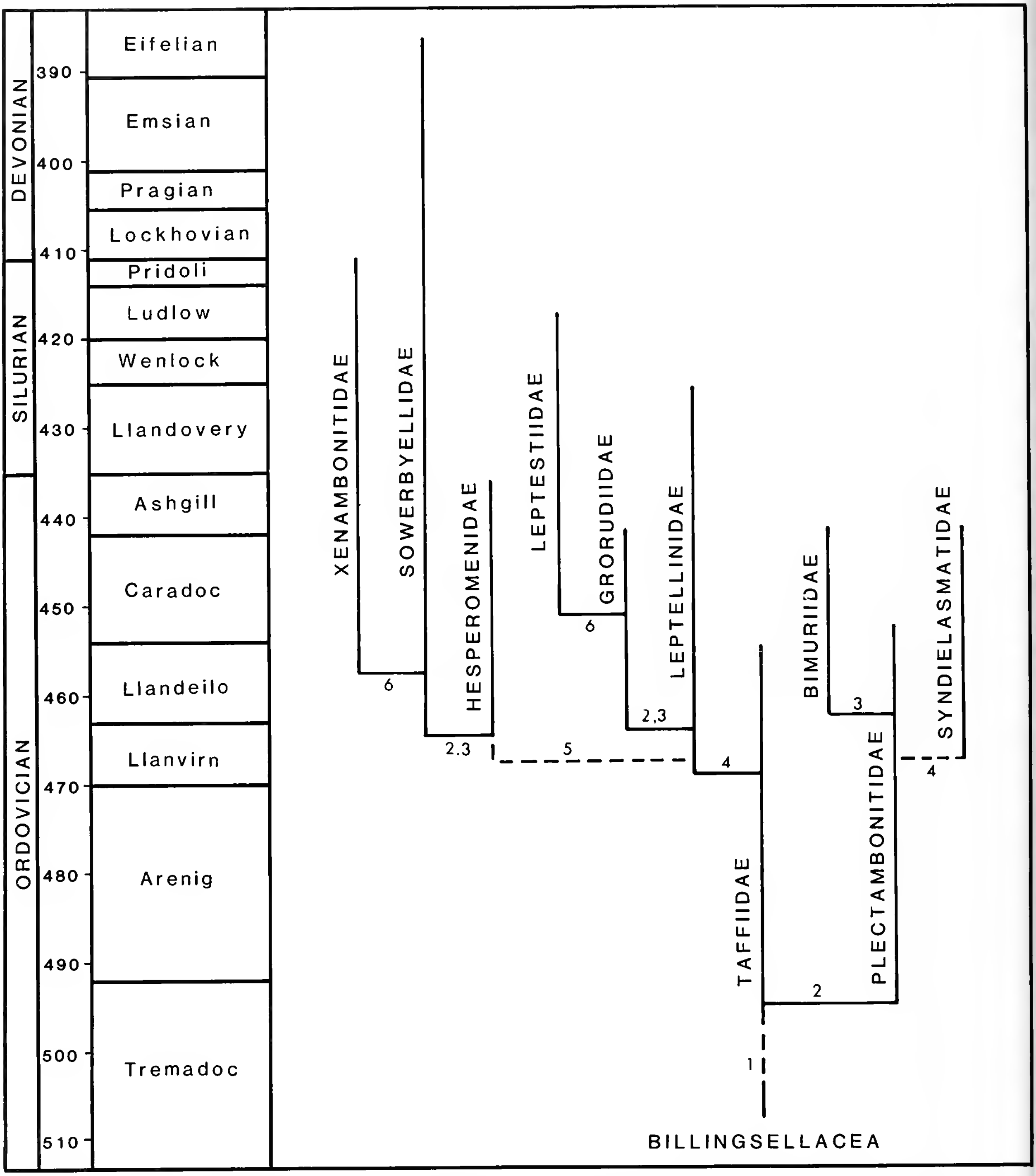


Fig. 5 Range chart and phylogeny of the families of the Plectambonitacea. The numbers indicate the acquisition or loss of critical characters as follows: 1. acquisition of pseudopunctae; 2. acquisition of side septa; 3. acquisition of bema; 4. acquisition of trifid cardinal process; 5. acquisition of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

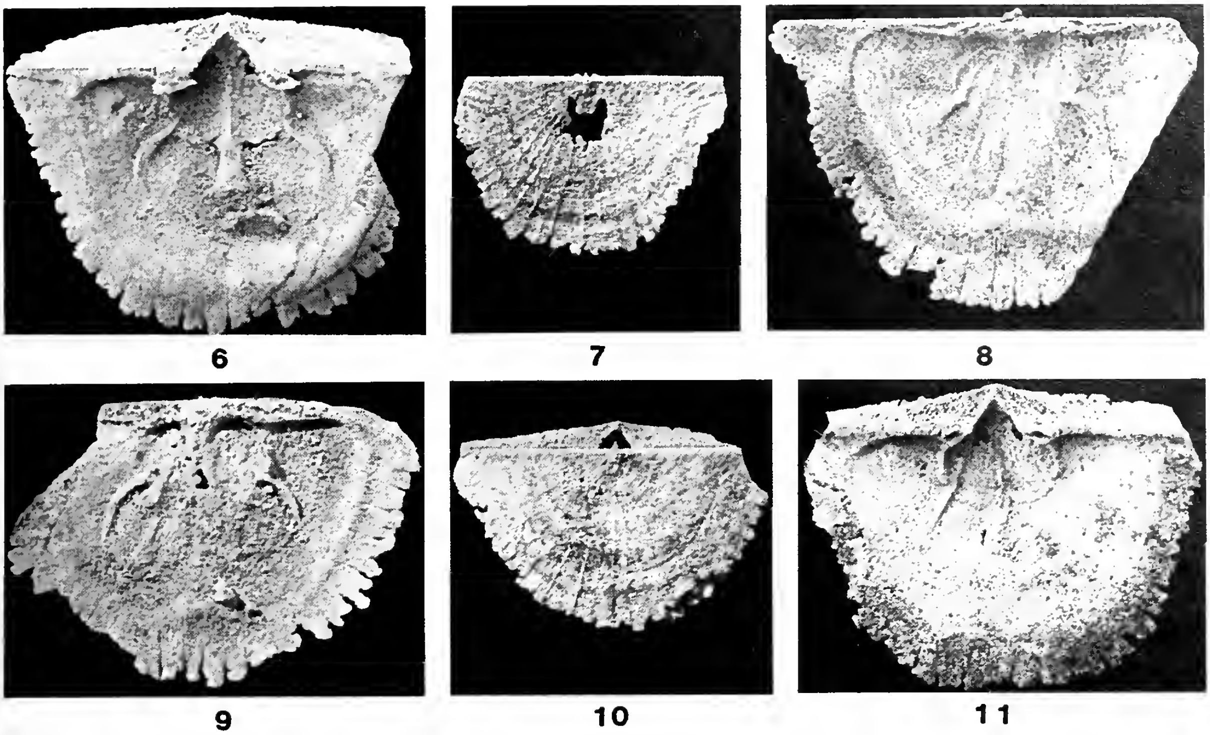
REMARKS. *Ingria* is a very variable genus, for example side septa are usually well developed, but the type species *Ingria nefedyevi* (Eichwald) almost lacks them (Öpik 1932: pl. 6, fig. 32). Because of this variability, we accept Cooper's (1938: 185) synonymy of *Ingria* with *Palinorthis* from Nevada.

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.

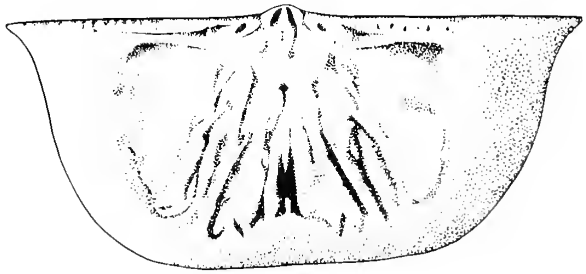


Fig. 12 *Plectambonites planissimus* Pander, 1830, from C_1 Beds (Llanvirn–Llandeilo), Baltic, USSR (after Williams 1965: fig. 237.2c), × 4.

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.

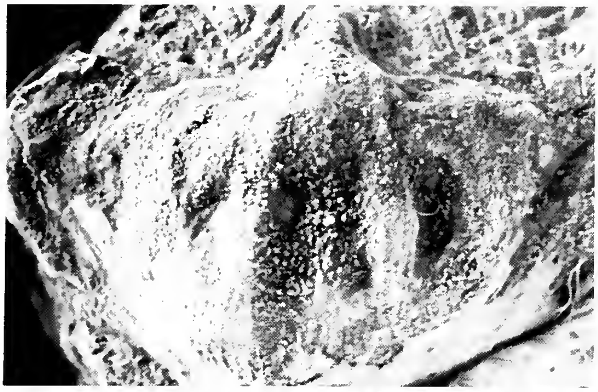
?***AKELINA*** Severgina, 1967
Figs 13–17

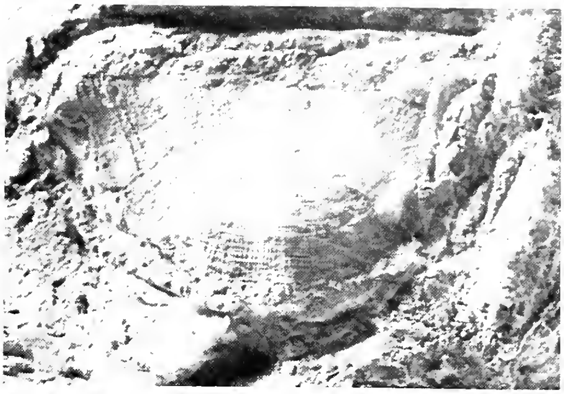
1967 *Akelina* Severgina: 133
1984*b* *Akelina* Severgina: 49

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.

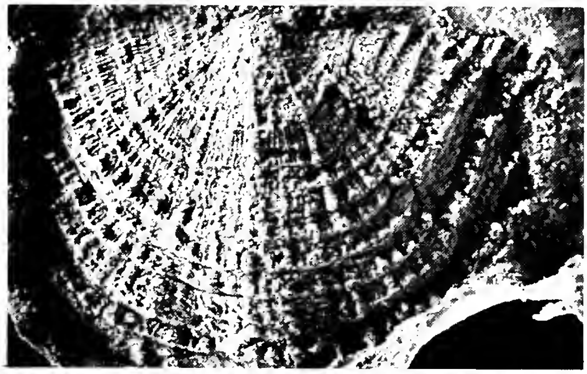
We are privileged in being able to examine and reillustrate the type specimens of the genus. They are preserved in a variety of lithologies, a partly exfoliated pedicle valve (Fig. 13) and a brachial valve exterior (Fig.14) in limestone; two

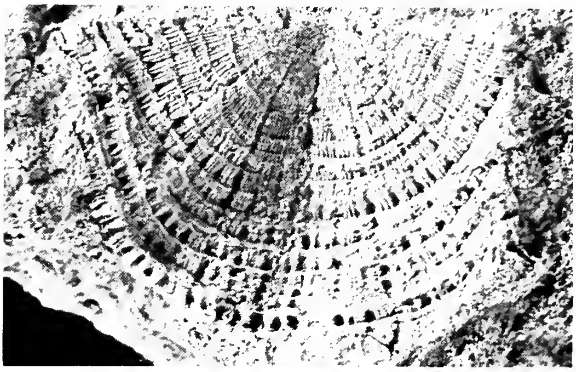

13


14

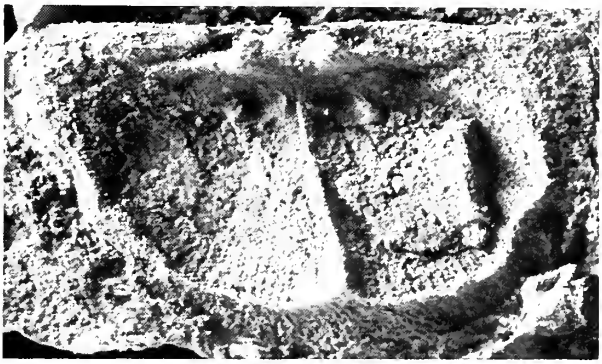

a


15b


16a


16b


7a


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.

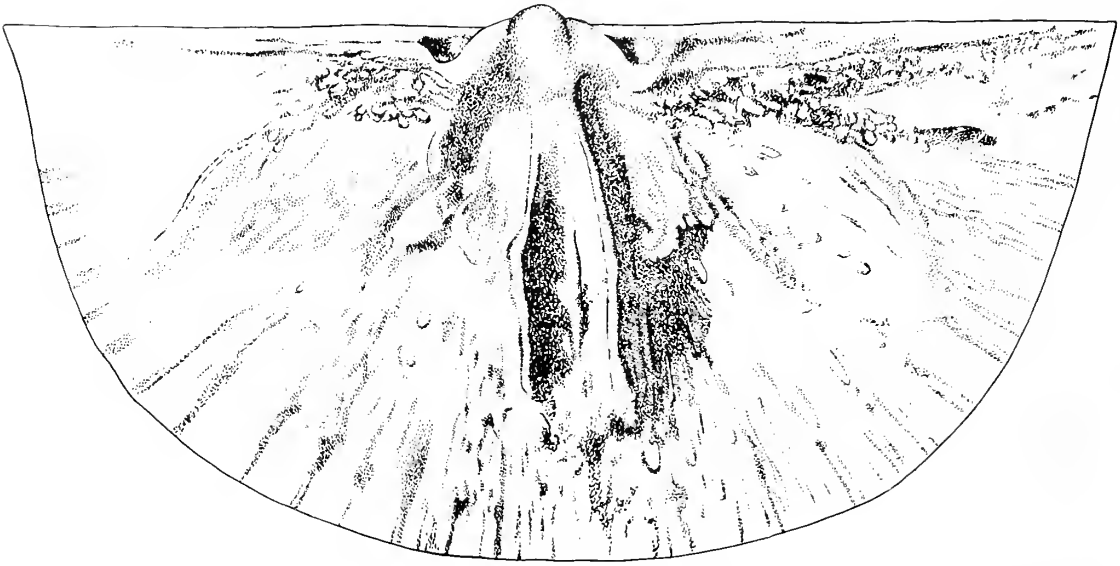


Fig. 18 *Isophragma ricevillense* Cooper, 1956, from base of Athens Formation (L. Caradoc), 4 km SSE of Riceville, Tennessee, USA, interior of brachial valve, based on BC 7211, × 12.

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.

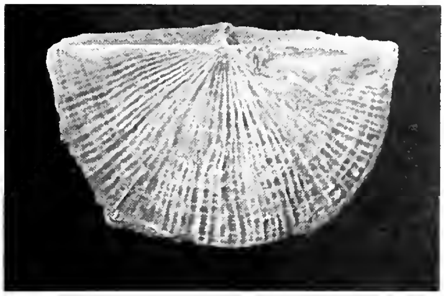
REMARKS. It is difficult to find a precise term for the structure seen in the central part of the brachial valve in some taphrodontids. We term it a double septum, but the space between the two septa does not reach the valve floor, and thus the two side septa become united to form what might be termed 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.

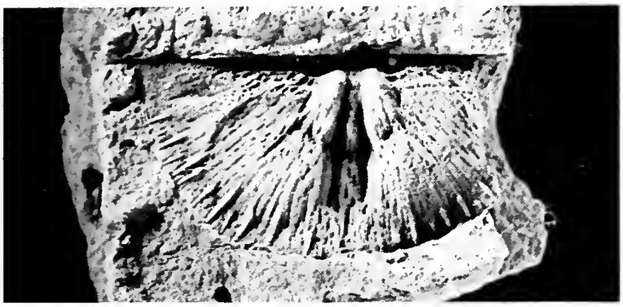
RANGE. Llanvirn (*Nanambonites paucus*) to L. Caradoc (*Isophragma* spp.).

19a

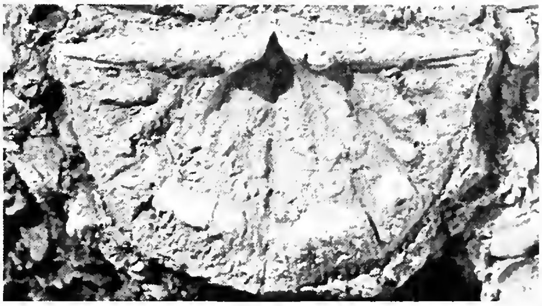


20a

20b



19b



21

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*).

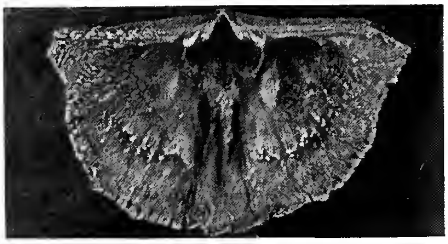
TAPHRODONTA (TAPHRODONTA) Cooper, 1956
Figs 22, 23

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

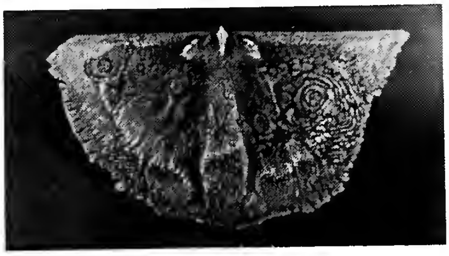
TYPE SPECIES. *Taphrodonta parallela* Cooper, 1956.

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.



22



23

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*).

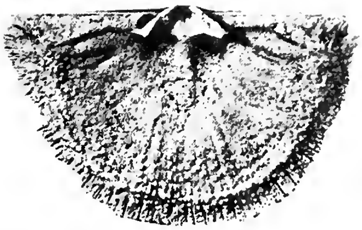
APORTHOPHYLA Ulrich & Cooper, 1936

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

24a

25



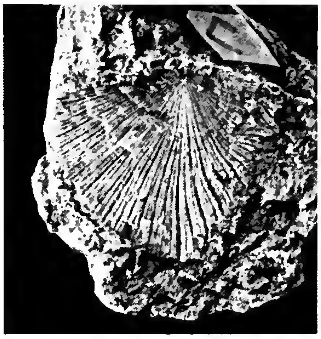
24b

26

27

28

29



30

igs 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.

igs 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.

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

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

EMARKS. *Aporthophyla* is very close to *Taffia*, particularly ince 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.

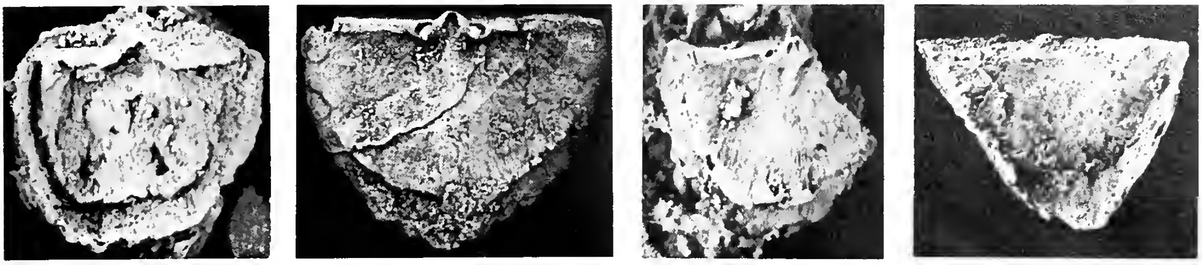
REMARKS. Even though the cardinal process is clearly that of a taffiid, nevertheless the rest of the morphology (apart from the interesting pedicle valve platform) is very close to *Leptellina* and its relatives in the Leptellinidae, and some form related to *Tourmakeadia* was probably the ancestor of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



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 he 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 mpersistent 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 n 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, $B_{iii\gamma}$ (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).

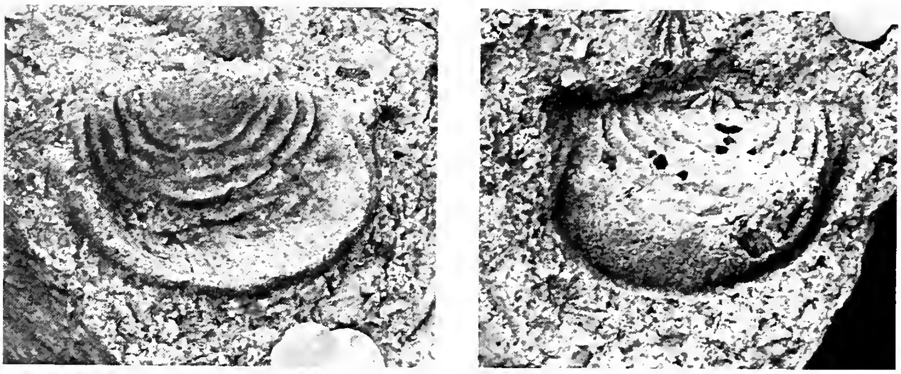
BORUA Williams & Curry, 1985

Figs 31–34

1985 *Borua* Williams & Curry: 250

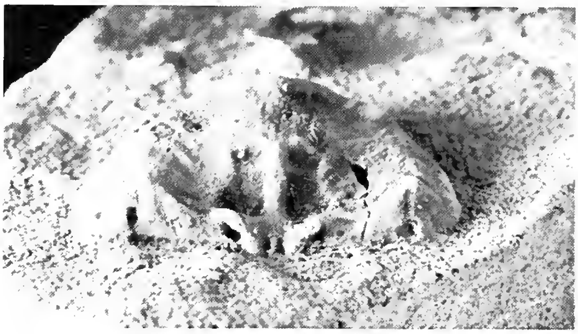
TYPE SPECIES. *Borua modesta* Williams & Curry, 1985.

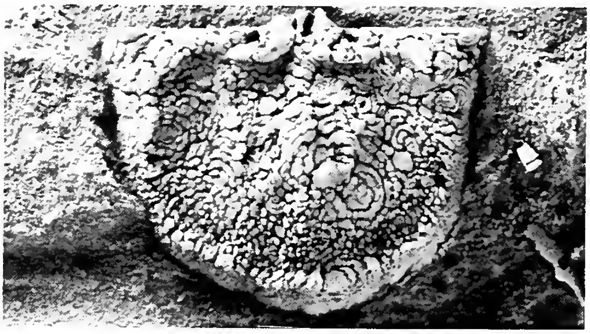
DIAGNOSIS. Smooth apart from faint peripheral parvicostellae and occasional impersistent rugae in some specimens. Short

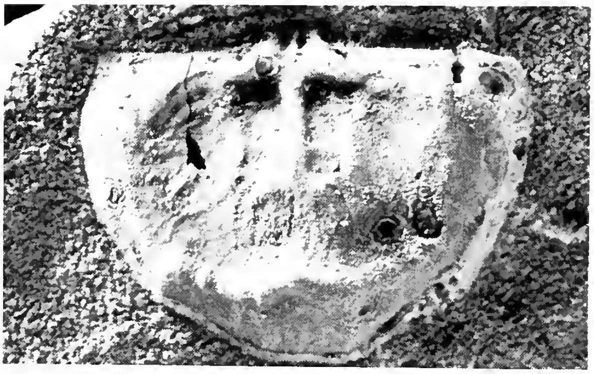

35a

35b


36


37a


38


37b


39

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 enerally absent in the Taffiidae; nevertheless we prefer to ssign the genus here.

PECIES ASSIGNED

uttasella gutta Neuman, 1977: 31; pl. 5, figs 1–5 from Llanvirn age rocks, Virgin Arm, Newfoundland, Canada.

INVERSELLA (INVERSELLA) Öpik, 1933

933 *Inversella* Öpik: 21
965 *Inversella* Williams: H372

YPE SPECIES. *Inversella borealis* Öpik, 1933.

IAGNOSIS. No median septum in brachial valve. Persistent ugae over valve and strongly geniculate in a ventral direction.

PECIES ASSIGNED

nversella angulata Öpik, 1933: 23; pl. 3, fig. 3 from $B_{iii\beta}$ (L. Llanvirn), Toila, Estonia, USSR.

nversella borealis Öpik, 1933: 23 (figured as *Palaeostrophomena concava* by Öpik 1932: pl. 4, fig. 24) from the Echinosphaeriten Limestone C_ia (U. Llanvirn), Eesti, Estonia, USSR.

nversella sp. of Neuman 1977: 34; pl. 6, figs 1–4 from Llanvirn age rocks, Virgin Arm, New World Island, Canada.

PECIES QUESTIONABLY ASSIGNED

nversella 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

968 *Reinversella* Bates: 169

YPE SPECIES. *Reinversella monensis* Bates, 1968.

IAGNOSIS. Like *Inversella* (*Inversella*) with second deflection f the anterior and lateral borders. With continuous rugae.

EMARKS. The close similarity between *Inversella* and *Reinersella* leads us to place the latter as a subgenus within the ormer.

PECIES ASSIGNED

einversella 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.

einversella monensis Bates, 1968: 169; pl. 8, figs 10–17 from Treiorwerth Formation (Arenig), Ffynnon-y-mab, Anglesey, Wales.

RUTRUMELLA Harper, 1981

981 *Rutrumella* Harper *in* Bruton & Harper 1981: 163

YPE SPECIES. *Rutrumella implexa* Harper, 1981.

IAGNOSIS. Resupinate. Differs from *Schedophyla* in having iscontinuous rugae, not geniculate. Relatively large socket lates.

EMARKS. This resupinate genus has a distinctive ornament of iscontinuous 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.

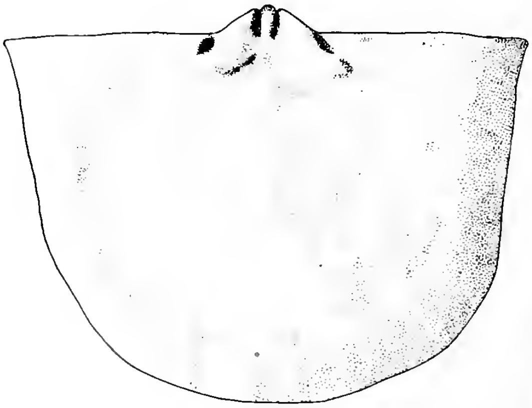


Fig. 40 *Spanodonta hoskingiae* Prendergast, 1935, from Gap Creek Formation (Middle Ordovician), south side of Gap Spring, Price's Creek, Emmanuel Range, Western Australia, interior of brachial valve, based on BC 7238 and BC 10605, × 5.

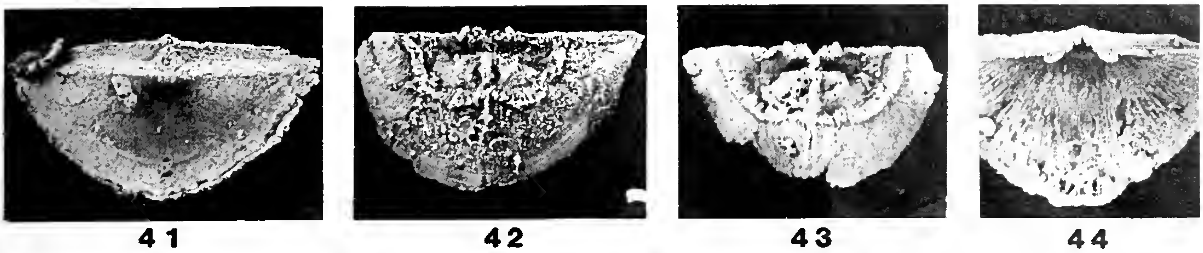
REMARKS. *Spanodonta* was originally described as a productacean from the Carboniferous of Western Australia, but was reassigned to the Plectambonitacea when the Ordovician age of the beds became known. A good new collection of topotype material made by the British Museum (Natural History) expedition 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



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.

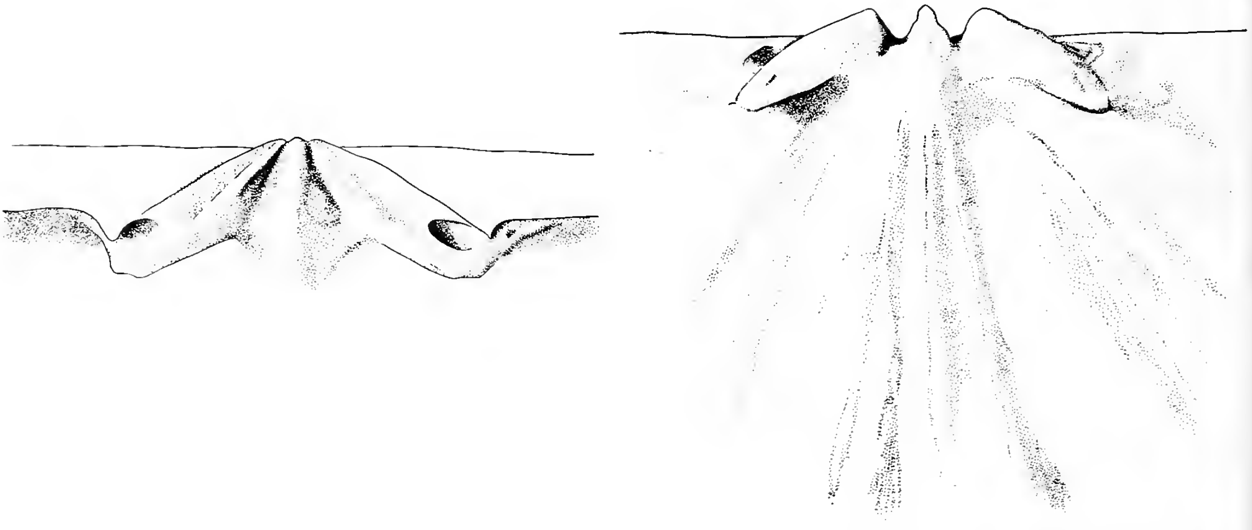


Fig. 45 *Bimuria superba* Ulrich & Cooper, 1942, from Arline Formation (Llandeilo), half mile east of Friendsville, Tennessee, USA, posterior and anterior views of the cardinal process area, based on BC 7269, × 6.

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.

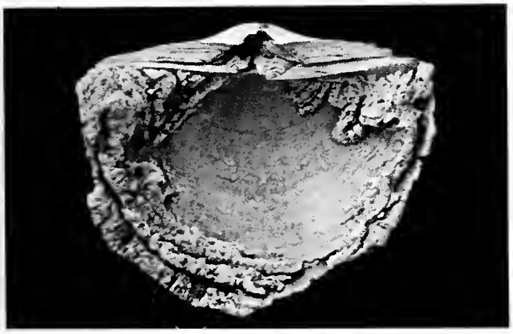
Leptaena transversalis var. *youngiana* Davidson, 1871: 320; pl. 47, figs 19, 20 from Craighead Limestone (U. Caradoc), Craighead, Girvan, Scotland (revised Williams 1962: 175; pl. 16, figs 38–41; pl. 17, figs 1–3); also subspecies *recta* Williams, 1962: 175; pl. 17, figs 4–7 from Balclatchie Mudstones (L. Caradoc), Penwhapple Burn, Girvan, Scotland.

46a

46b

46c

47a



47b

igs 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

977 *Acculina* Misius *in* Misius & Ushatinskaya: 113
986 *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 eptum.

REMARKS. Only *Acculina* and *Reversella* are resupinate within he Leptellinidae. Comparison is difficult since the type species of *Acculina* is small (maximum width 20 mm), whilst he 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

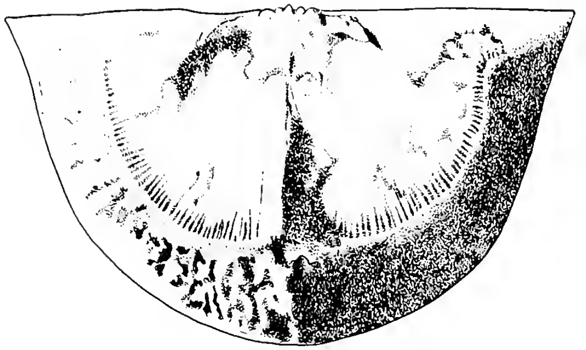


Fig. 48 *Leptellina* (*Leptellina*) *tennesseensis* Ulrich & Cooper, 1936, from Lenoir Formation (Llandeilo), quarter mile west of Friendsville, Tennessee, USA, interior of brachial valve, based on BB 1228, × 5.

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).

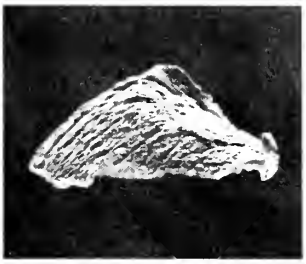
Leptellina pulchra Cooper, 1956: 753; pl. 189, figs 1–23; pl. 195, figs 9–16; pl. 219, fig. 14 from Effna–Rich Valley Formations (Llandeilo), Porterfield Quarry, Virginia, USA.

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.

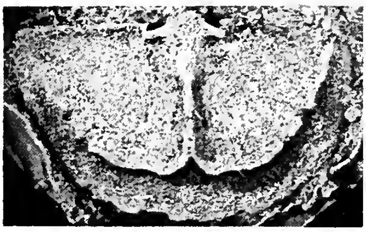
Leptellina rhacta Williams, 1962: 164; pl. 15, figs 17–19, 21,


49a


49b


49c


50


51


52a


52b


52c

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^{c}Coy, 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.

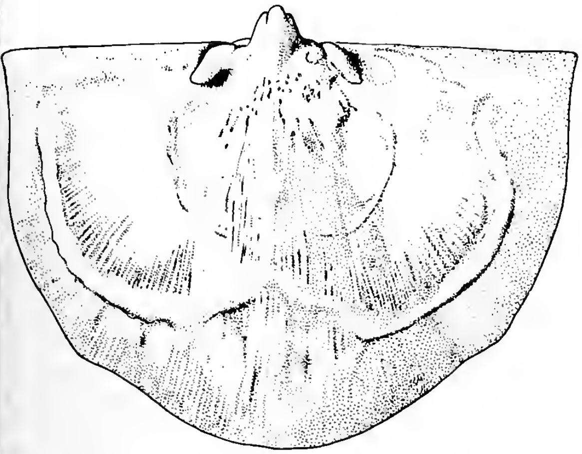


Fig. 53 *Leptelloidea leptelloides* (Bekker, 1922), from Kukruse Formation (L. Caradoc), Kohtla-Järve, Estonia, USSR, interior of brachial valve, based on BB 5169, × 6.

PECIES QUESTIONABLY ASSIGNED

eptelloidea 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).

eptelloidea (*Benignites*?) *heintzi* Spjeldnaes, 1957: 74; pl. 4, figs 10–11 from 4aα Beds (Llanvirn), Ravaldsjøelven, Sandsvaer, Norway (no brachial interiors known).

eptelloidea yaxianensis Xu & Su, 1979: 108 from Middle Ordovician iron ores, Yaxian county, Hainan Island, China (brachial valve interior uncertain).

eptelloidea 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).

PECIES REJECTED

eptelloidea 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).

eptelloidea 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).

eptelloidea 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).

eptelloidea rosendahli Spjeldnaes, 1957: 75; pl. 2, figs 4–5 from Coelosphaeridium Beds (M. Caradoc), Fangberget, Ringsaker, Norway (to *Bilobia*).

eptelloidea 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).

eptelloidea 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).

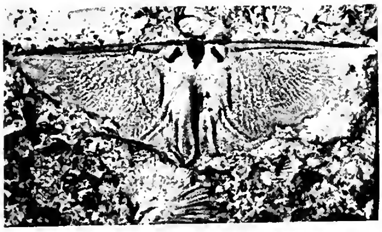
PALAEOSTROPHOMENA Holtedahl, 1916
Figs 57, 58

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

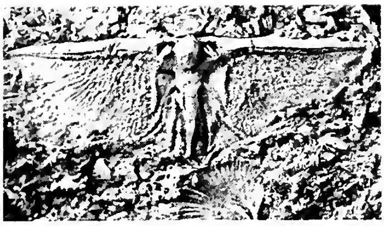
TYPE SPECIES. *Strophomena concava* Schmidt, 1858.

DIAGNOSIS. Resupinate.

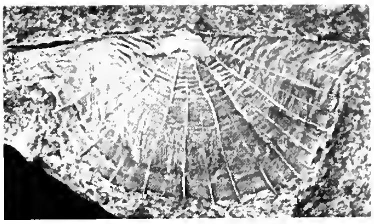
REMARKS. No brachial valve interiors of *P. concava* are known although from Öpik's (1933: pl. 4, fig. 1) illustration of the exterior, it is certain that the cardinal process is trifid. It is the only member of the subfamily which is resupinate. None of the North American species described by Cooper (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.



54a

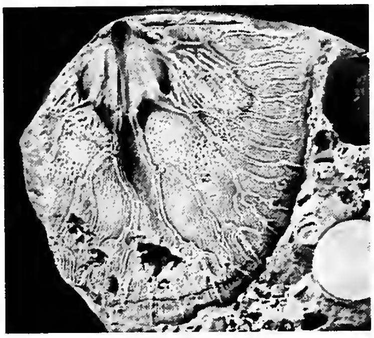


54b

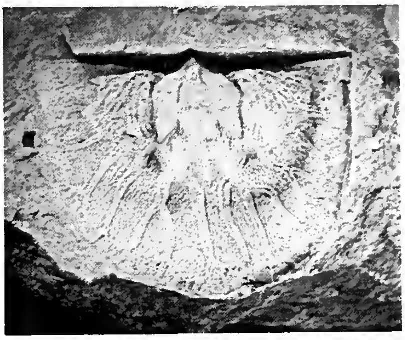


55

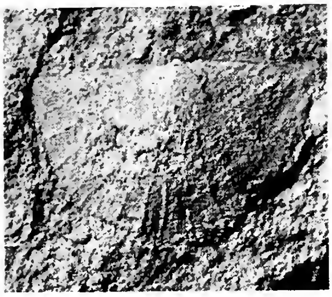
56



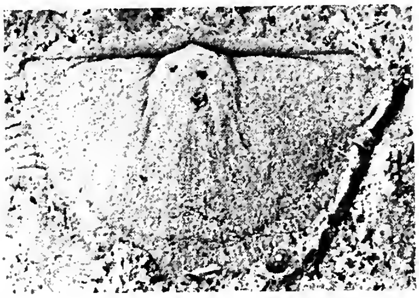
57



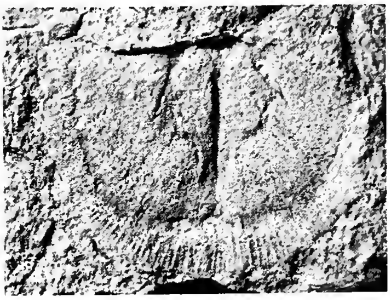
58



59



60



61

ig. 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.

igs 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.

igs 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.

igs 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.

PECIES ASSIGNED

alaeostrophomena angulata Cooper, 1956: 702; pl. 168, figs 3–10; pl. 194, figs 19–22 from the Botetourt Formation (L. Caradoc), Catawba, Virginia, USA.

alaeostrophomena canalis Lockley, 1980: 210; figs 47–52 from Gelli-grîn Formation (U. Caradoc), Gelli-grîn, Powys, Wales.

trophomena 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).

rthis 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).

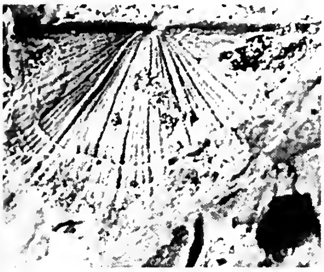
Ishimia narulgensis Nikitin, 1974: 63; pl. 6, figs 4–6 from Tselinograd Horizon (Llandeilo–L. Caradoc), Narulgen,

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

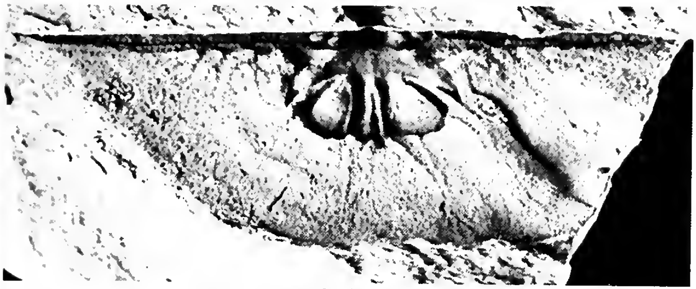
62b



63

62c

62d

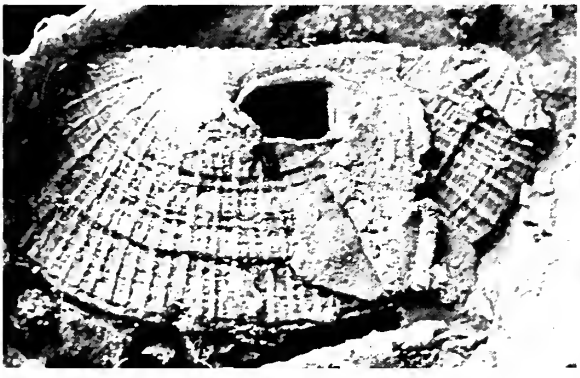


64a

64b

65a

65b



66

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 ith a swollen knob at the anterior end and interesting small emicircular bemas. Two of the three specimens (PMO 6931, Fig. 65 and PMO 66939, Fig. 64) have distinct side epta confined within the bema, the third (PMO 66940, Fig. 6) has side septa only faintly developed, but appears to epresent a younger growth stage. There is some doubt on the ature of the hinge line; Spjeldnaes describes *Grorudia* as aving a smooth hinge line (1957: 61) but *Alwynella* as possessing crenulations (1957: 86). All the specimens we have een have smooth hinge lines apart from PMO 66931 (Fig. 65) hich has some small structures on the hinge line, but these ppear too irregular to be termed denticulations.

PECIES ASSIGNED

rorudia ? glabrata Spjeldnaes, 1957: 63; pl. 1, figs 4, 8, 18 from Zone 4aβ–4bα (L. Caradoc), Blindern, Oslo, Norway.

rorudia 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

962 *Tetraodontella* Jaanusson: 1
965 *Tetraodontella* Williams: H376

YPE SPECIES. *Tetraodontella biseptata* Jaanusson, 1962.

IAGNOSIS. Like *Calyptolepta* but with double median sep- um, united posteriorly and centrally. Weak platform present.

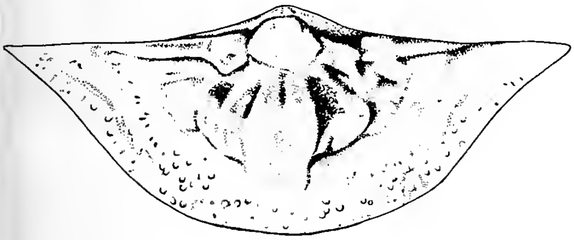


Fig. 68 *Tetraodontella biseptata* Jaanusson, 1962, from Dalby Limestone (M. Caradoc), Sweden, brachial valve interior (based on Williams 1965: fig. 240.2c), × 6·5.

EMARKS. Only two brachial valve interiors of the type ecies have been illustrated; one (Jaanusson 1962: pl. 1, figs 4–16) has a slim central shaft to the cardinal process, whilst e other (Williams 1965: fig. 240, 2c) has a large bulbous rdinal process (Fig. 68). Thus further collection, analysis nd illustration of topotype specimens is clearly desirable, nce these two illustrated specimens seem so different from ach other.

PECIES ASSIGNED

etraodontella biseptata Jaanusson, 1962: 3; pl. 1, figs 11–18 from Dalby Limestone (M. Caradoc), Böda Hamn borehole, Öland, Sweden.

PECIES QUESTIONABLY ASSIGNED

etraodontella aquiloides Fu, 1975: 109; pl. 12, fig. 19 from Xiliangsi Formation (L. Llanvirn), Liangshan, Nanzheng County, S. Shaanxi Province, China (no interiors illustrated).

etraodontella 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

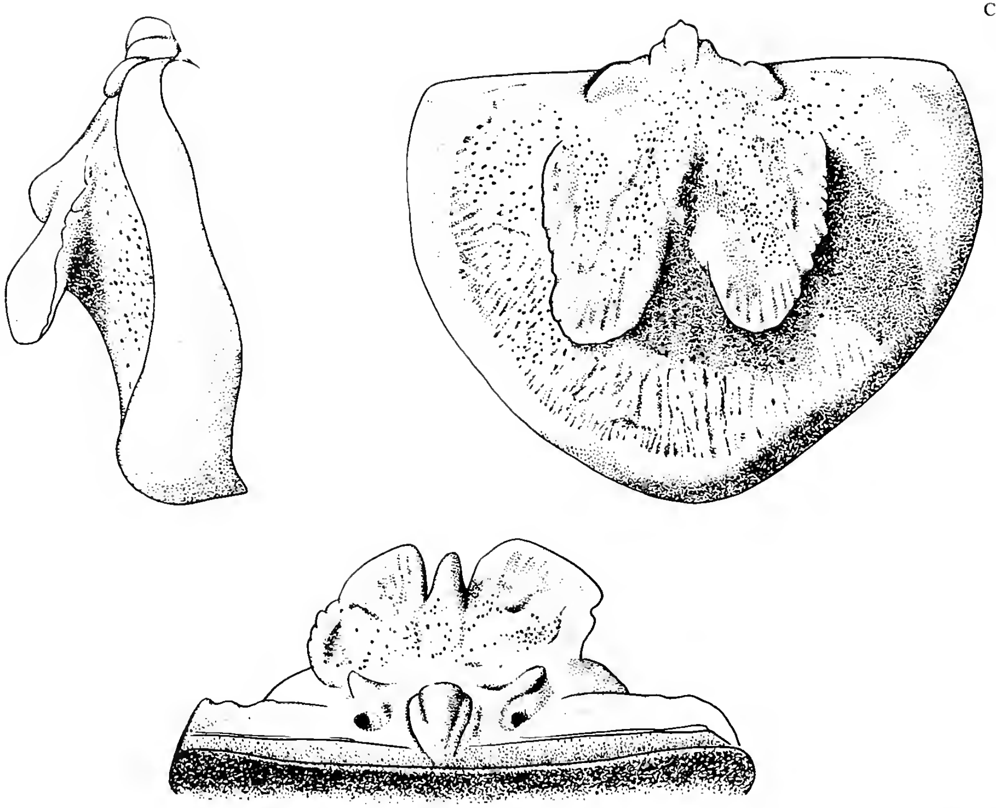


Fig. 69 *Bilobia musca* (Öpik, 1930), from Kukruse Formation (L. Caradoc), Kohtla-Järve, Estonia, USSR, interior of brachial valve showing the very elevated bema (based on BB 5202), × 12.

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

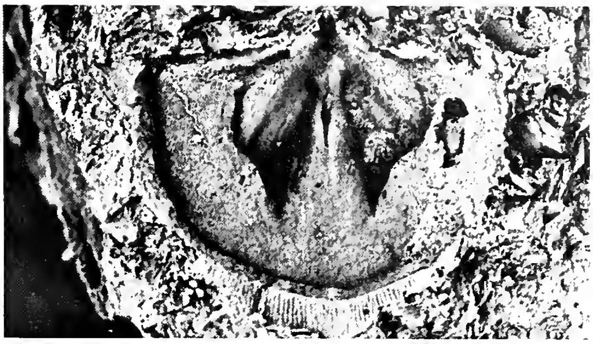
1933	*Leangella* Öpik: 42
1936	*Diambonia* Cooper & Kindle: 356
1961	*Tufoleptina* Havlíček: 447
1965	*Leangella* Williams: H378
1967	*Tufoleptina* Havlíček: 33
1968	*Leangella* (*Opikella*) Amsden: 48
1970	*Leangella* Cocks: 156

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


70a


71


70b


70c

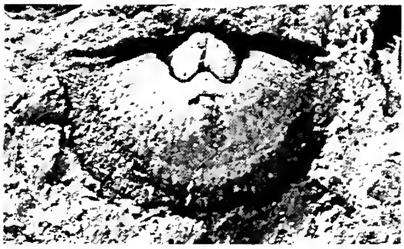

72


73a


73b


73c


74


75


76

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

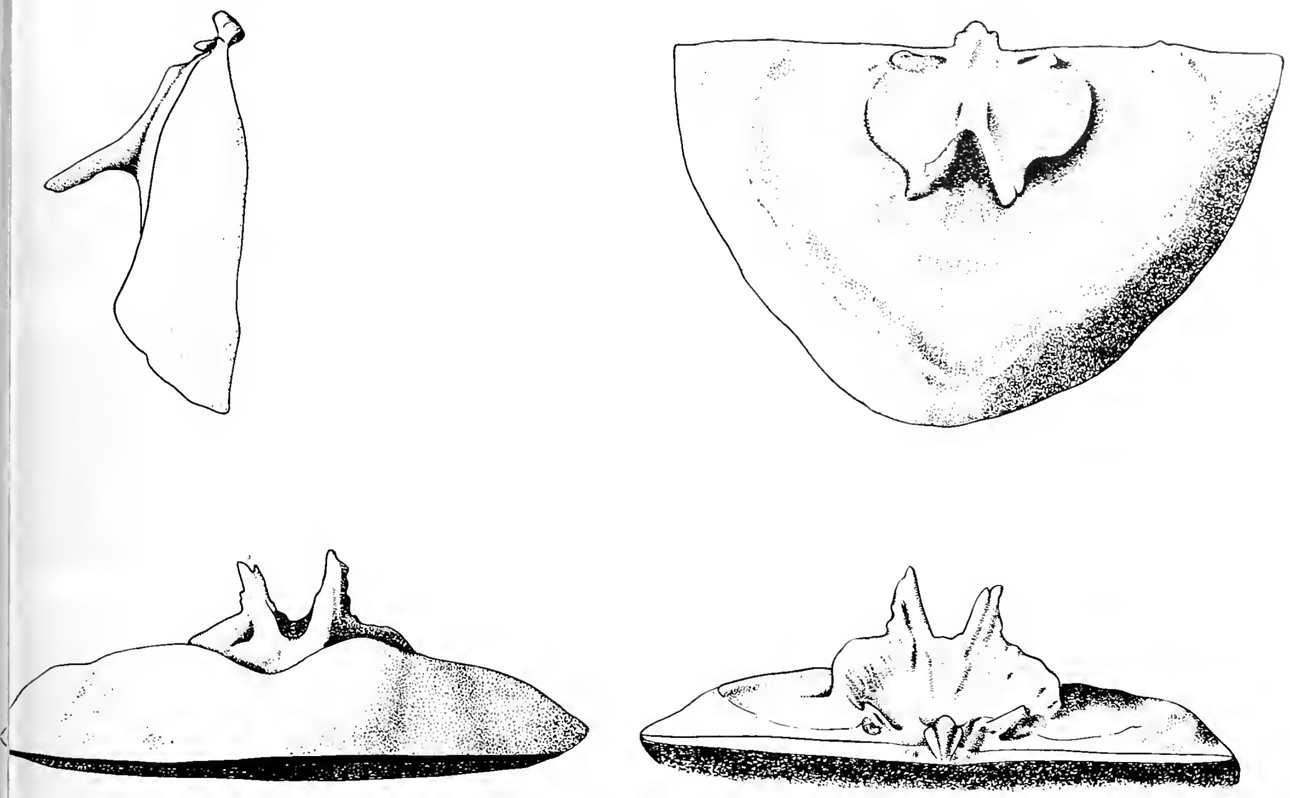


Fig. 77 *Leangella* (*Leangella*) *gibbosa* (Winchell & Schuchert, 1892), from Stewartville Formation (L. Ashgill), between Stewartville and Chatville, Minnesota, USA, lateral downward, anterior and posterior views of a brachial valve interior, based on BC 7272, × 9.

(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*).

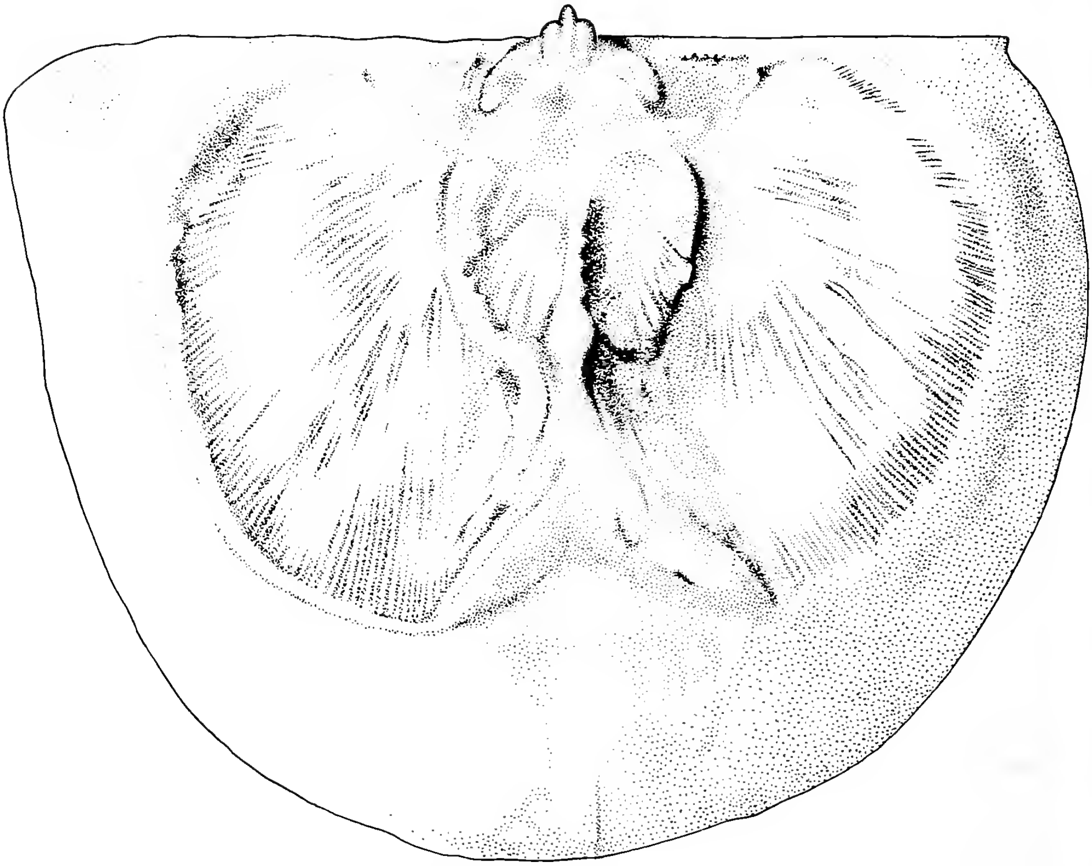


Fig. 78 *Leptestia musculosa* Bekker, 1922, from Kukruse Formation (L. Caradoc), Kohtla-Järve, Estonia, USSR, brachial valve interior, based on BB 5189, × 6.

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.

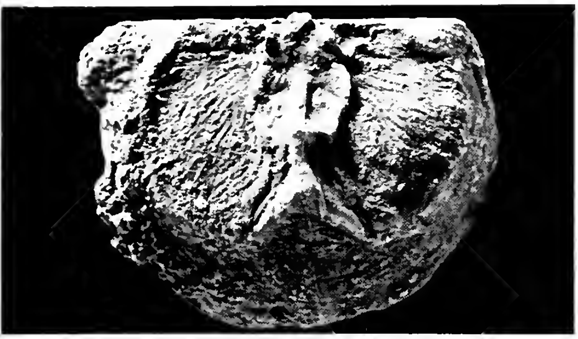
SPECIES QUESTIONABLY ASSIGNED

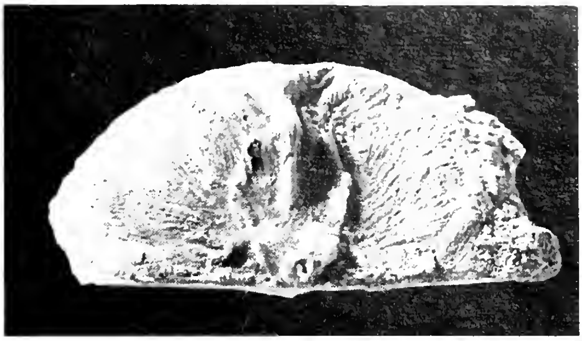
Sampo hiiuensis var. *mucronata* Öpik, 1933: 39; fig. 2E from Rakvere Formation (U. Caradoc), Pühalepa, Hiiumaa, Estonia, USSR (no interiors known).

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*).


79a


79b


79c


80

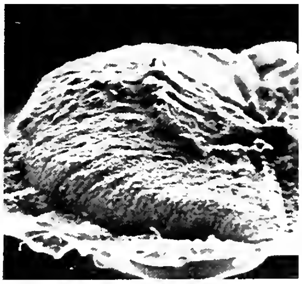

81a


81b


81c


82a


82b


81d


83a


83b


83c

ig. 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.

igs 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.

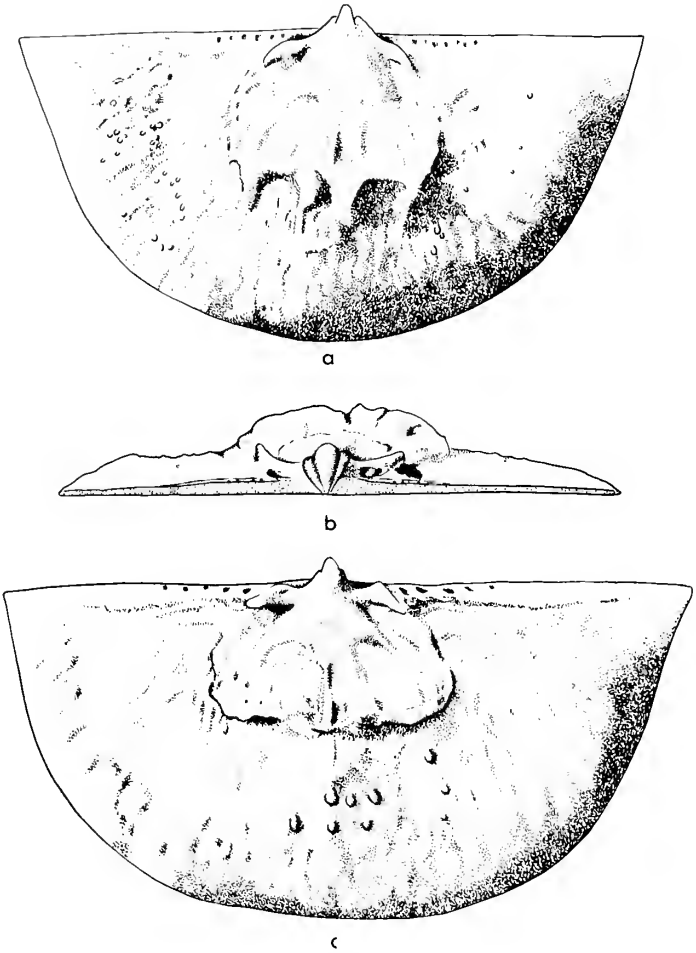


Fig. 84 *Rurambonites ruralis* (Reed, 1917) gen. nov., from Starfish Bed, South Threave Formation (Ashgill: U. Rawtheyan), Girvan, Strathclyde, Scotland, showing the bema variation in the interiors of two brachial valves (a, b after BC 7204, c after BC 7200), × 5.

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.

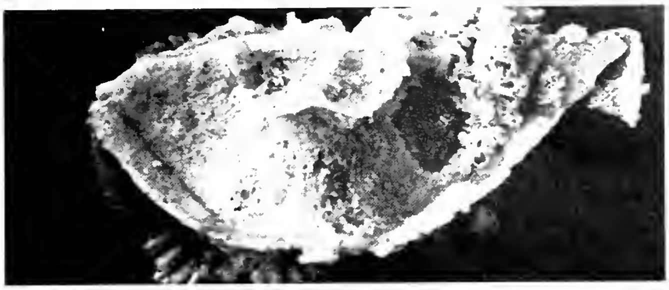
RANGE. Llandeilo–Caradoc.

XENAMBONITES Cooper, 1956
Figs 85, 86

1956 *Xenambonites* Cooper: 813
1965 *Xenambonites* Williams: H381

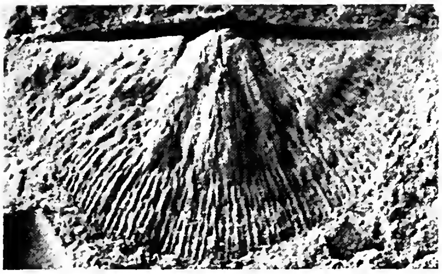
TYPE SPECIES. *Xenambonites undosus* Cooper, 1956.

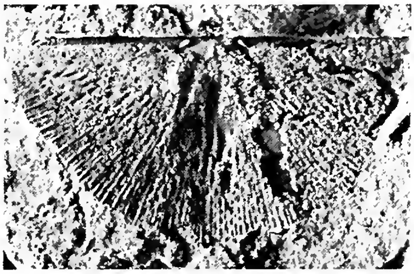

85a

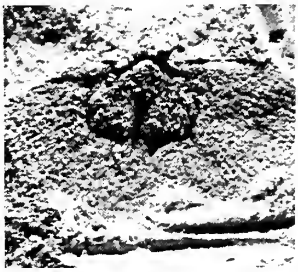

86


85b

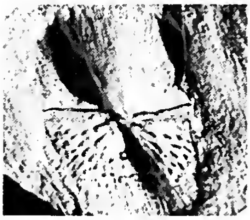

87

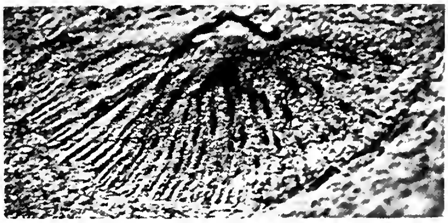

88


89


90


91


92


93

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 norilskensis 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

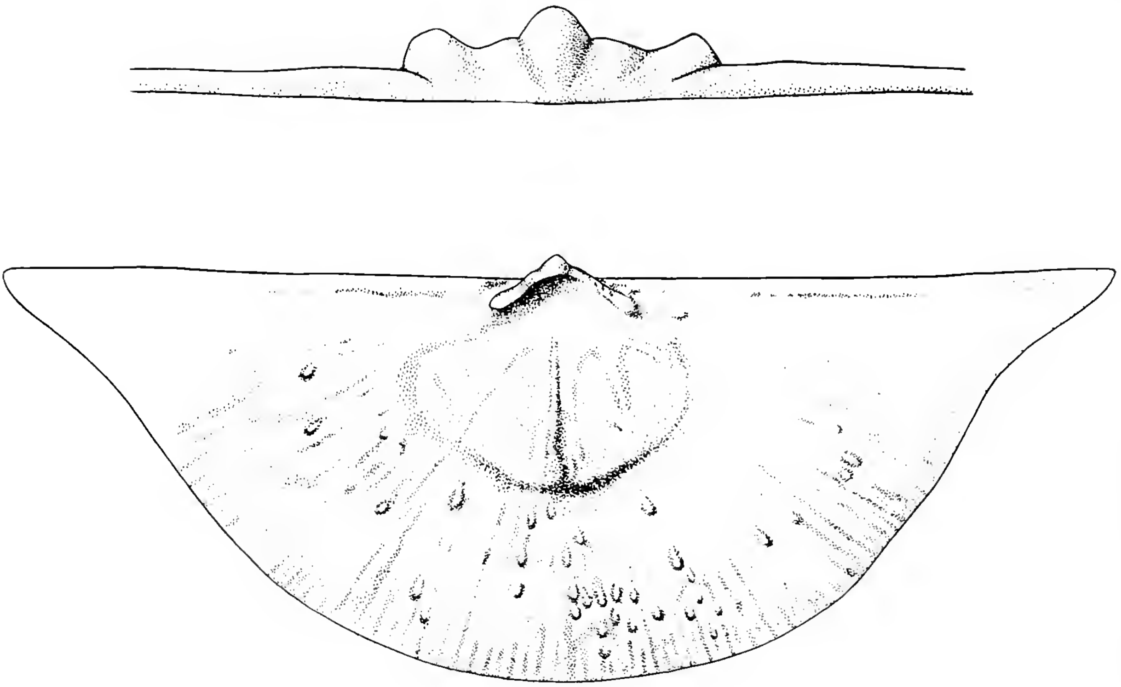


Fig. 94 *Aegiria* (*Aegiria*) *aquila aquila* (Barrande, 1848), from Zahoraný Formation (M. Caradoc), Palmovka, Praha-Libeň, Czechoslovakia; a, posterior view of cardinal process, × 25 and b, brachial valve interior, × 12 (based on BC 7212).

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).

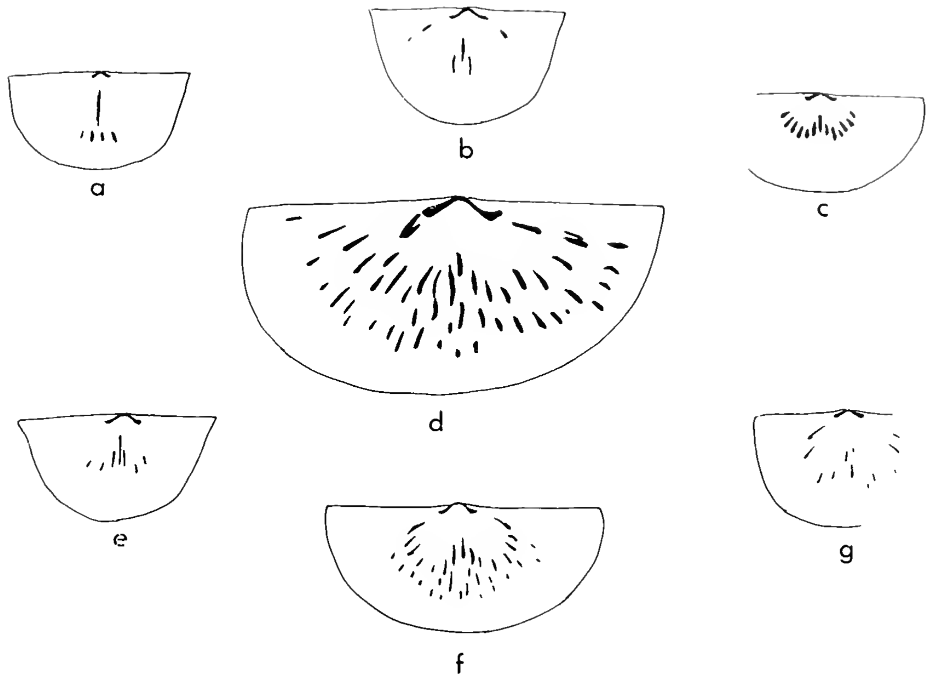


Fig. 95 Brachial valve interiors demonstrating all variants between *'Chonetoidea'* and *'Sericoidea'*. a, *'Sericoidea' minor* Percival, 1979, from Malongulli Formation (U. Caradoc), Copper Mine Creek, New South Wales, Australia (after Percival 1979: fig. 5.A12), × 5; b, *'Chonetoidea' enerrima* Havlíček, 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.

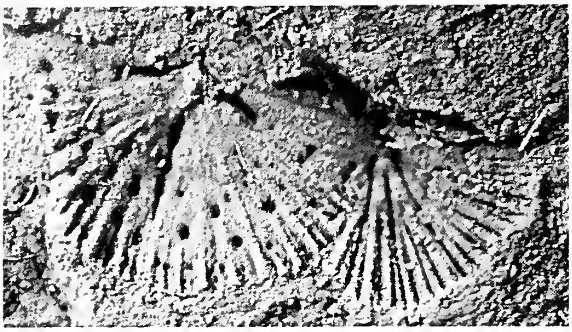
SPECIES REJECTED

Chonetoidea alpha Spjeldnaes, 1957: 107; pl. 2, figs 20–22 from Zone 4bα (U. Caradoc), Billingstad, Asker, Norway (assigned to *Aegiria*).

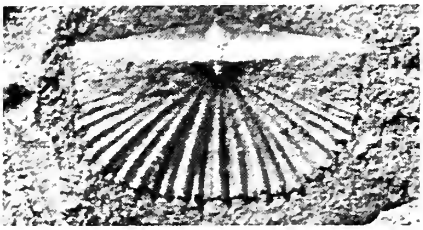
Chonetoidea (*Aegiria*) *nacta* Reed, 1952: 53; pl. 2, fig. 13 from Killey Bridge Formation (L. Ashgill), Pomeroy, Co. Tyrone, Northern Ireland (synonymized with *Sowerbyella thraivensis* Reed by Mitchell 1977: 81).

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:

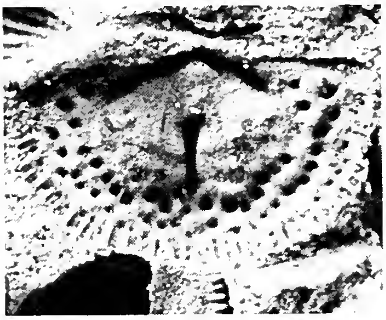

97


98


99

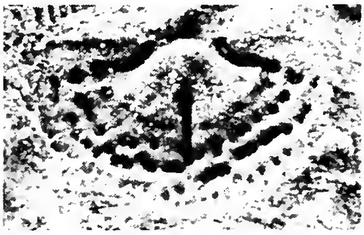

100


101

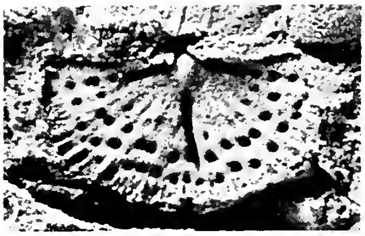

102a


102b


103


104


105


106

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*).

ericoidea 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

YPE SPECIES. *Leptaena grayi* Davidson, 1849. Named after).T. Jones.

IAGNOSIS. Like *Chonetoidea*, but with circular papillae ather than elongated. Sometimes septules with 2 prominent ibercles posterolaterally inside the pedicle valve.

EMARKS. Only *Kassinella* and *Trimurellina* within the Plecmbonitacea also possess the pair of tubercles sometimes een within the pedicle valve of *Jonesea* (e.g. Cocks 1970: pl. 7, fig. 13). The bema is usually absent, but is occasionally een. The type species was previously assigned (e.g. Cocks 970) to *Aegiria*, but the new genus differs from *Aegiria* in the irtual absence of a bema, as well as in possessing the rominent papillae and tubercles. It seems probable that ystematic reassessment would much reduce the number of eal species from the nominal list below.

PECIES ASSIGNED

honetoidea andersoni Johnson, Boucot & Murphy, 1976: 58; pl. 20, figs 3–25 from Roberts Mountain Formation (Ludlow), Birch Creek, Roberts Mountains, Nevada, USA.

egiromena durbenensis Nikitin, *in* Nikitin *et al.* 1980: 52; pl. 13, figs 16–22 from Durben Formation (U. Ashgill), Durben, Chu-Ili Mountains, Kazakhstan, USSR.

eptaena 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).

egiromena incerta Wan, 1982: 41; pl. 11, figs 19, 20 from Shihniulan Formation (U. Llandovery), Guanyinqiao, Oijiang County, Sichuan Province, SW China.

honetoidea 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.

egiria mariaformis Lenz, 1677*a*: 67; pl. 8, figs 6–9, 12–21, from L. Road River Formation (Pridoli), Royal Creek, Yukon, Canada.

egiria cf. *mariaformis* Lenz, 1977*b*: 1536; pl. 5, figs 19, 22–28 from U. Whittaker Formation (Wenlock), Avalanche Lake, Mackenzie Mountains, Canada.

egiria 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.

rthis 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).

egiromena 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.

egiria thomasi Talent, 1965: 24; pl. 6, figs 1, 3, 5–7 from Dargile Formation (Ludlow), Heathcote, Victoria, Australia.

Aegiromena ultima Marek & Havlívek, 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.

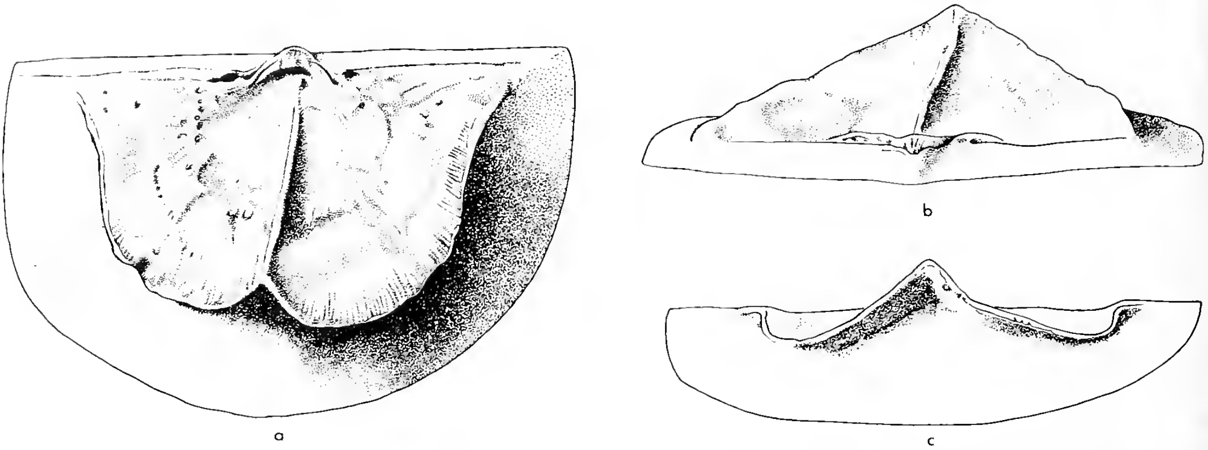


Fig. 107 *Anoptambonites grayae* (Davidson, 1883), downwards, posterior and anterior views of the brachial valve interior, from Craighead Limestone (U. Caradoc), Craighead, Girvan, Strathclyde, Scotland (based on BB 15869), × 2·5.

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

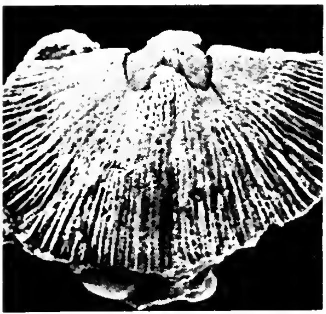
Anoptambonites aktasensis Nikitin & Popov, 1984: 147; pl. 18, figs 17–23 from Erkebinankski Horizon (Caradoc), Chinghiz Mountains, Kazakhstan, USSR (has pedicle valve platform and median septum in the brachial valve is much wider than in other *Anoptambonites*).

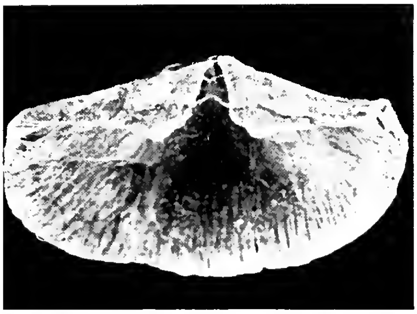
Fig. 108 *Anoptambonites* sp., natural internal mould of pedicle valve, the original of Williams 1962: pl. 16, fig. 10, from Balclatchie Conglomerate (L. Caradoc), Penwhapple Burn, Girvan, Strathclyde, Scotland, BB 25950, × 4.

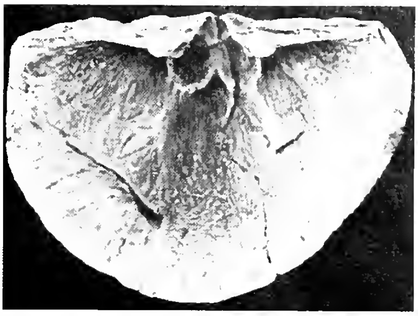
Figs 109–111 *Anoptambonites grayae* (Davidson, 1883), topotypes from Craighead Limestone (U. Caradoc), Craighead, Girvan, Strathclyde, Scotland. Fig. 109, posterior and downward views of a pedicle valve interior, the original of Williams 1962: pl. 16, figs 11, BB 15868, × 3·5; Fig. 110, brachial valve 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.


108

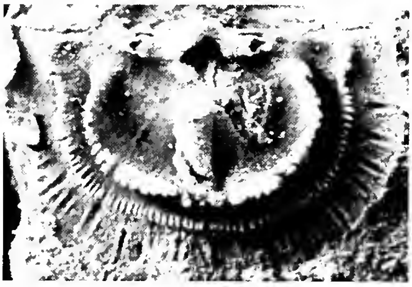

109a


109b


110

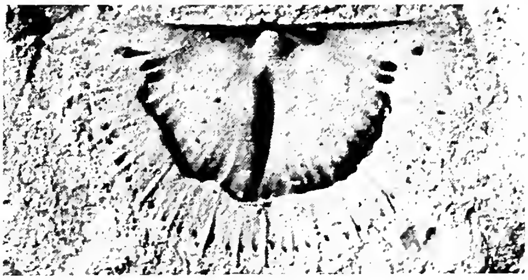

111


112


113


114


115


116


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 reinvestigation 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 fron Králův Dvůr Formation (M. Ashgill), Kosov, Bohemia, Czechoslovakia (revised by Havlíček 1967: 35; pl. 2, figs 1–6 as *Anoptambonites moneta* including junior synonyn *Orthis humillima* Barrande, 1879: pl. 69, fig. V-1 from th 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, Nev South Wales, Australia.

Durranella septata Percival 1979: 97, figs 3A: 1–9 fron Goomumbla Volcanics (U. Caradoc), Gunningbland, Nev South Wales, Australia.

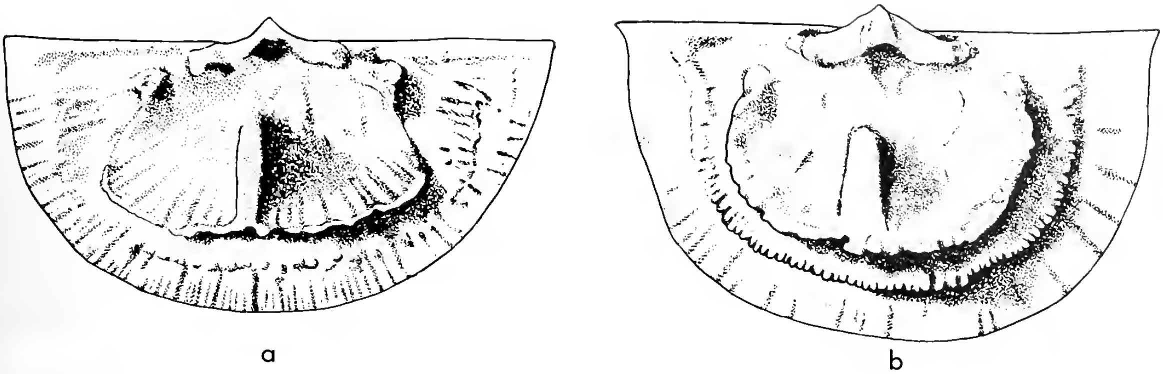


Fig. 118 *Kassinella* (*Kassinella*) sp. showing variation in the brachial valve interior from a population in the Changwu Formation (M. Ashgill), Jiangshan County, SW Zhejiang Province, China: a, after NIGP 101835, × 12; b, after NIGP 101836, × 12.

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

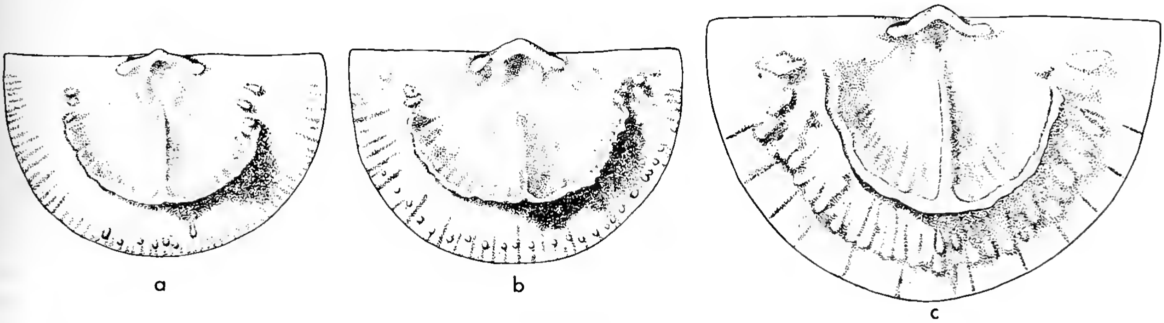
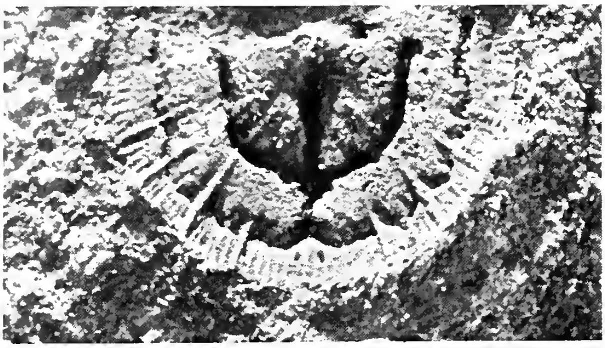
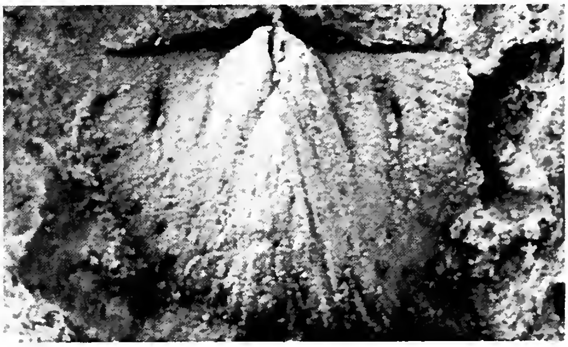


Fig. 119 *Kassinella* (*Kassinella*) *albida* (Reed, 1917), showing variation in the brachial valve interior in the topotype population from Whitehouse Beds (Caradoc–Ashgill), Whitehouse Bay, Girvan, Strathclyde, Scotland: a, after BB 92584; b, after BB 92573; c, after B 73542, the lectotype, all × 8.

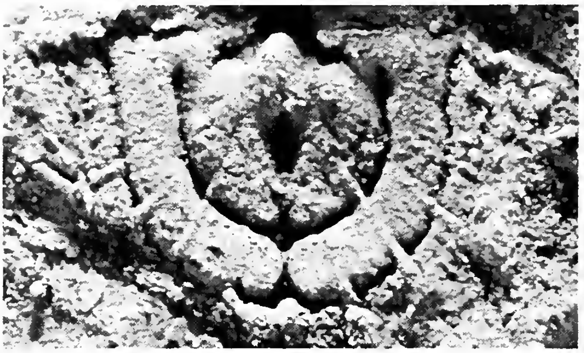


120



121

122



123

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.

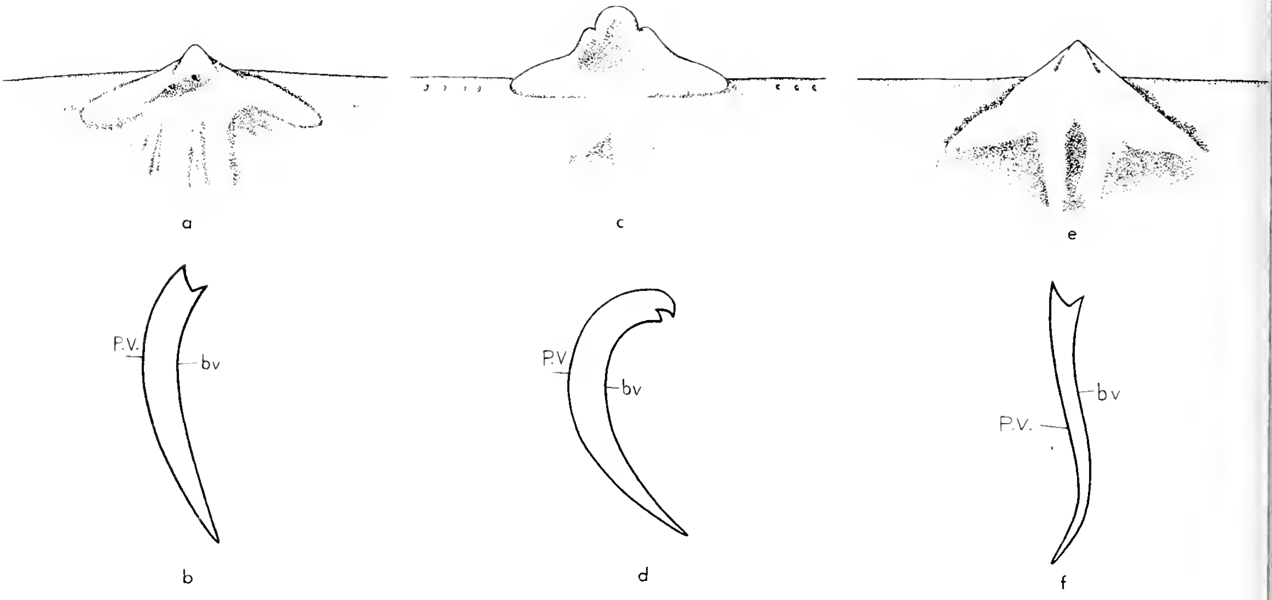


Fig. 124 Variation in the cardinal process and valve shape amongst various genera of Sowerbyellinae: a, b, *Sowerbyella eximia* Cooper, 1956 from Martinsburg Formation (L. Caradoc), Virginia, USA; c, d, *Eoplectodonta duvalii* (Davidson, 1847), from Slite Marl (Wenlock), Gotland Sweden; e, f, *Gunningblandella resupinata* Percival, 1979, from Goonumbla Volcanics (U. Caradoc), New South Wales, Australia.

an be unequivocally assigned to *Sowerbyella*. In most of the pecies of *Sowerbyella* itself, including *S. sericea* the type pecies, the bema is well developed. The family is divided nto three subfamilies on the division of the bema and hether or not the cardinal process is differentiated into separate recognizable structure, or whether, as in the raspedeliinae, it is totally fused and inseparable from the ther central structures on the brachial valve hinge line.

UBFAMILIES ASSIGNED. Sowerbyellinae Öpik, 1930; Craspe-eliinae subfam. nov.; Ptychoglyptinae Cooper, 1956.

ANGE. Llanvirn to Eifelian.

Subfamily **SOWERBYELLINAE** Öpik, 1930

965 Sowerbyellinae Williams: H378
967 Sowerbyellinae Havlíček: 54
970 Sowerbyellinae Cocks: 164

IAGNOSIS. Bema divided. Cardinal process differentiated.

ENERA ASSIGNED. *Anisopleurella* Cooper, 1956; *Dubiolepna* Havlíček, 1967; *Eoplectodonta* (*Eoplectodonta*) Kozowski, 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; *owerbyella* (*Sowerbyella*) Jones, 1928, including *Viruella* Rõõmusoks, 1959; *Sowerbyella* (*Eochonetes*) Reed 1917, ncluding *Thaerodonta* Wang, 1949; *Sowerbyella* (*Rugosowerbyella*) Mitchell, 1977.

ANGE. Llanvirn (*Sowerbyella antiqua*) to Eifelian (*Plectoonta 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 uboval bema. No denticles on hinge line. Bema usually horter than in *Eoplectodonta*. Median septum present in rachial valve. Like *Sowerbyella* but no prominent paired entral 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.

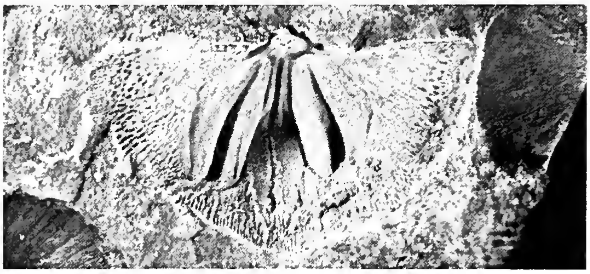
EOPLECTODONTA (EOPLECTODONTA) Kozlowski, 1929
Figs 128–137

1929 *Plectodonta* (*Eoplectodonta*) Kozlowski: 112
1956 *Eoplectodonta* Cooper: 807

125

126

127



128

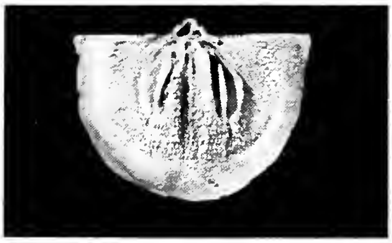
129

130a 130b 130c

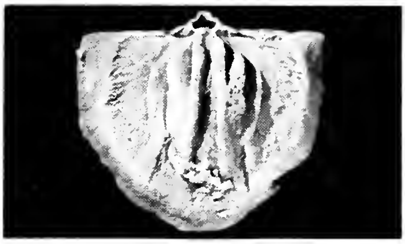
131

132

133



134



135

136

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.

961 *Ygera* Havlíček: 449
965 *Eoplectodonta* Williams: H380 *pars* (*non Thaerodonta*)
967 *Ygera* Havlíček: 58
970 *Eoplectodonta* Cocks: 166

TYPE SPECIES. *Sowerbyella precursor* Jones, 1928, a junior ubjective 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 n 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 acked a septum, and also the 'ill-defined lobes of visceral ield' (= 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 s 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 he 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^c^Coy, *in* Sedgwick & M^c^Coy 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.

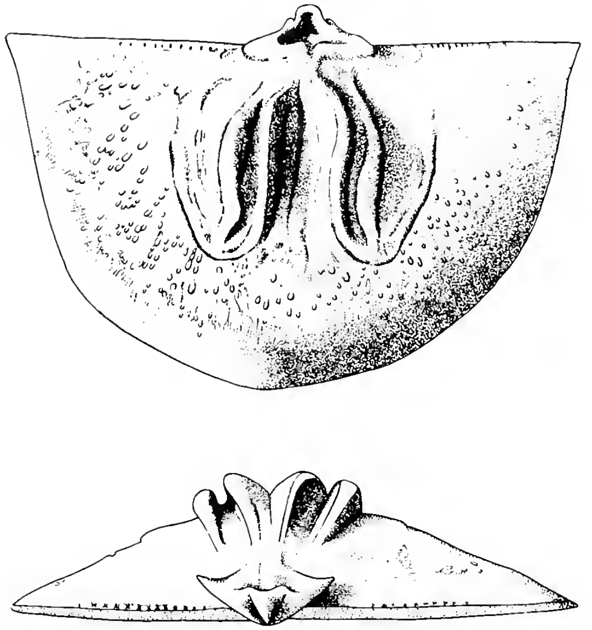


Fig. 137 *Eoplectodonta duvalii* (Davidson, 1847), from Slite Marl (Wenlock), Gotland, Sweden, posterior and downward views of a brachial valve interior (based on BB 31837), × 5.

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), Lističe, 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.

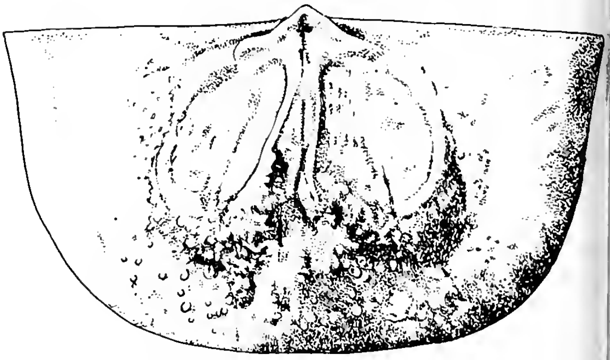


Fig. 138 *Sowerbyella* (*Sowerbyella*) *sericea* (J. de C. Sowerby, 1839), from Horderley Sandstone (L. Caradoc), Shropshire, England, brachial valve interior (based on BC 6051–3), × 6.

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.

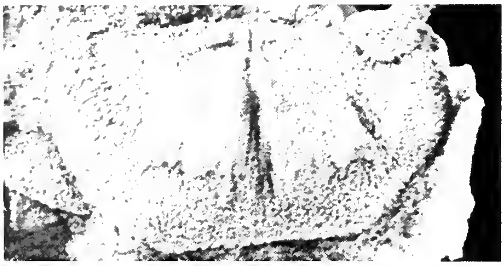
Sowerbyella (*Viruella*) *minima* Rõõmusoks, 1959: 22; pl. 3, figs 1–6 from Kukruse Horizon (L. Caradoc), Lasnamagi, Estonia, USSR.

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).

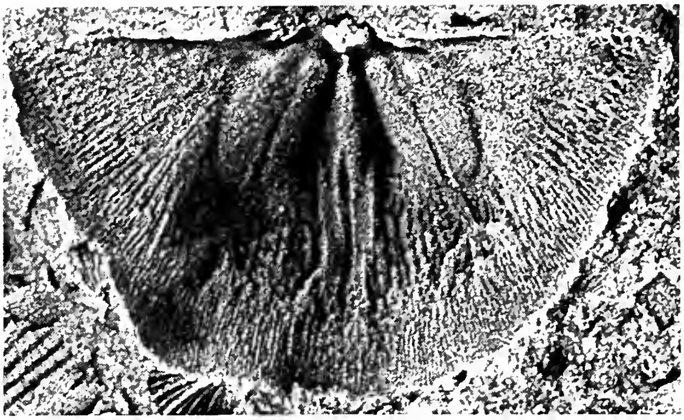
Sowerbyella monilifera Cooper, 1956: 785; pl. 199, figs 1–8; pl. 206, figs 16–28 from Decorah Formation (L.–M. Caradoc), Ellsworth, Wisconsin, USA.

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.

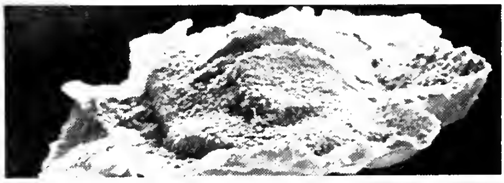
Sowerbyella musculosa Williams, 1963: 433; pl. 11, figs 18–27 from Allt Ddu Group (L. Caradoc), Bala, Gwynedd, Wales.



139a

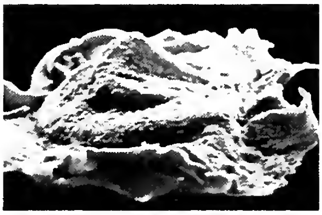


140

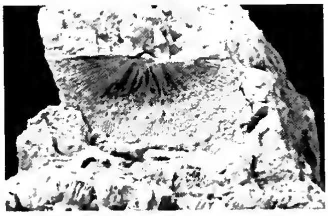


139b

141a



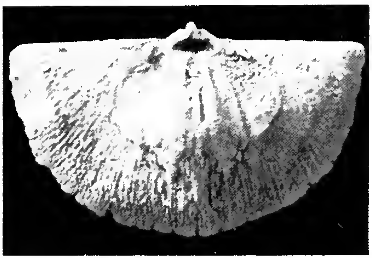
141b



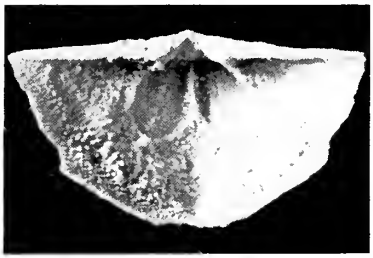
142

141c

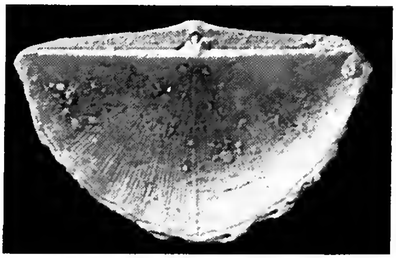
143



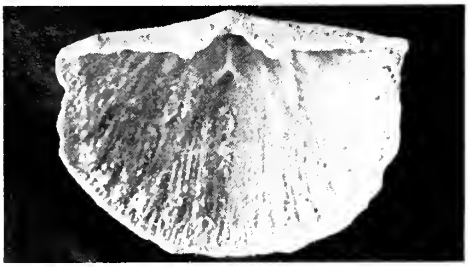
144



145



146



147

148a

148b

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-Järve, 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).

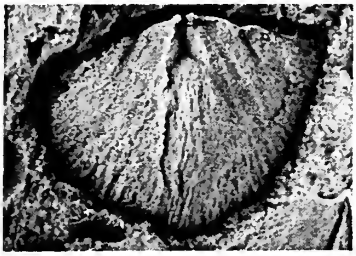
Sowerbyella subovalis Wilson, 1932: 393; pl. 4, figs 10, 11 from L. Coburg formation (U. Caradoc), Cornwall, Ontario, Canada (no interiors figured).

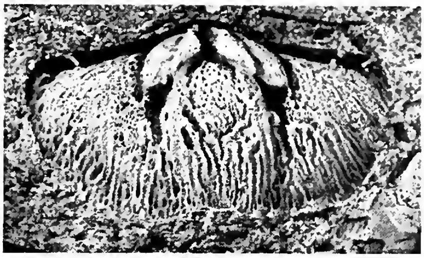
Orthis tennuissimestriata McCoy, 1846: 35; pl. 3, fig. 20 from beds of Caradoc age, Slieve Roe, Co. Wicklow, Ireland (no interiors figured).

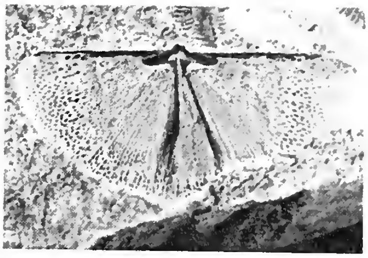
Chonetes? *thebavensis* Reed, 1906: 57; pl. 5, fig. 16 from Naungkangyi Beds (? L. Caradoc), Lebyaungbyan, Northern Shan States, Burma (no interiors known).

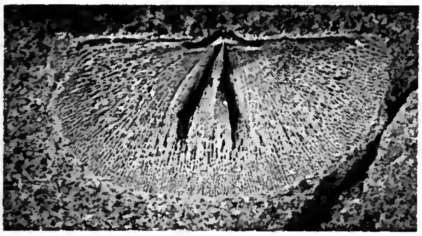
Leptaena trabeata Lindström, *in* Angelin & Lindström 1880: 30; pl. 17, figs 1–4 from Upper Ordovician Beds (?Fjäcka Shales), Västergötland, Sweden (no interiors figured).

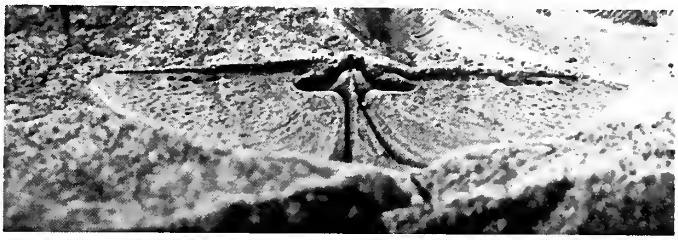
Sowerbyella undosa Öpik, 1930: 159; pl. 21, figs 265–6 from Idavere Formation (L. Caradoc), Kohtla, Estonia, USSR (no interiors figured).


149


150


151a


152


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*)).

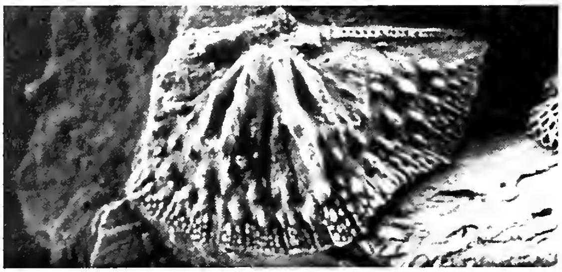
SOWERBYELLA (EOCHONETES) Reed, 1917
Figs 149–152

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

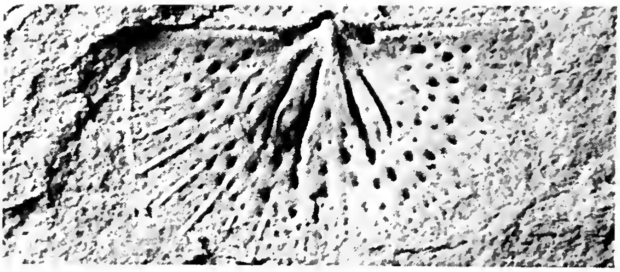
TYPE SPECIES. *Chonetes* (*Eochonetes*) *advena* Reed, 1917. Type species of *Thaerodonta* is *Thaerodonta aspera* Wang, 1949.

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.

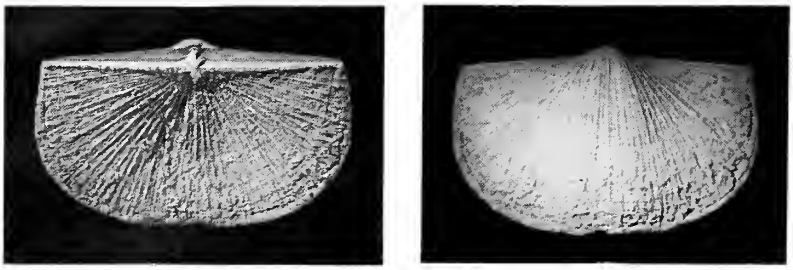
DISCUSSION. Close examination of topotype *Eochonetes advena* reveals the presence of denticles on the brachial valve hinge line (particularly laterally) and corresponding fossettes on the pedicle valve hinge line (Fig. 151). As discussed below, this is the only point of difference between *Thaerodonta* 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



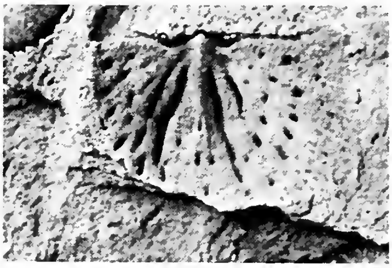
153



154



155a 155b



156

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.

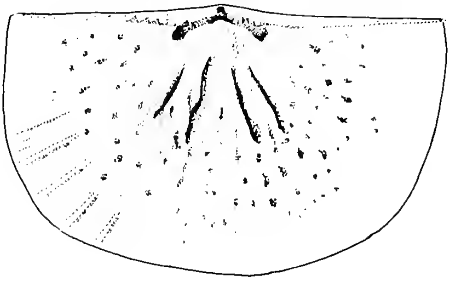


Fig. 157 *Plectodonta mariae* Kozlowski, 1929, internal mould of brachial valve, from Taina Formation (Lochkovian), Rukhotin, Podolia, Ukraine, USSR (based on BB 65810), × 12.

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).

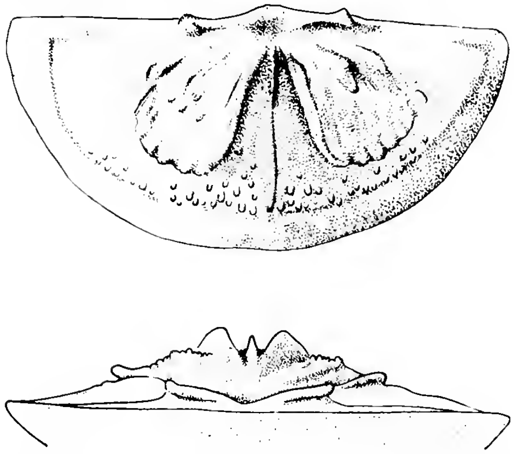


Fig. 158 *Cooperea siphonata* (Cooper, 1956), interior views of the brachial valve, from Pratt Ferry Formation (Llandeilo), Pratt Ferry, Alabama, USA (based on BC 10305), × 15.

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

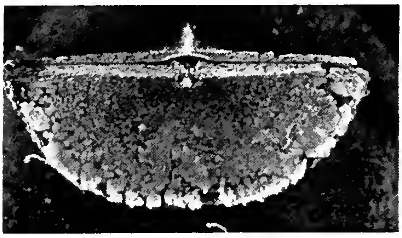
TYPE SPECIES. *Craspedelia marginata* Cooper, 1956.

DIAGNOSIS. As for subfamily. Geniculate with additional anterior deflection and with a fold and sulcus. No ornament known.

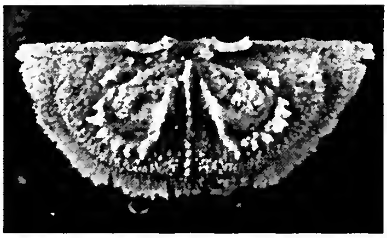
159

160

161a



162



163

161b

164a

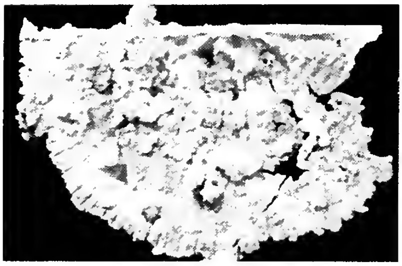
164b

165a

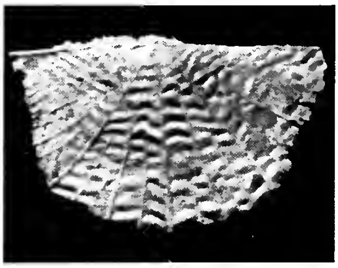
165b

165c

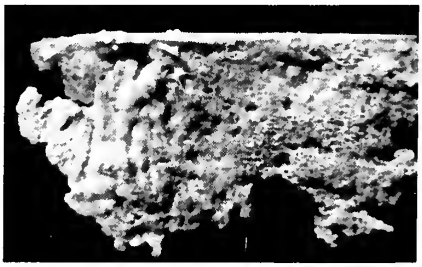
166a



167



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.

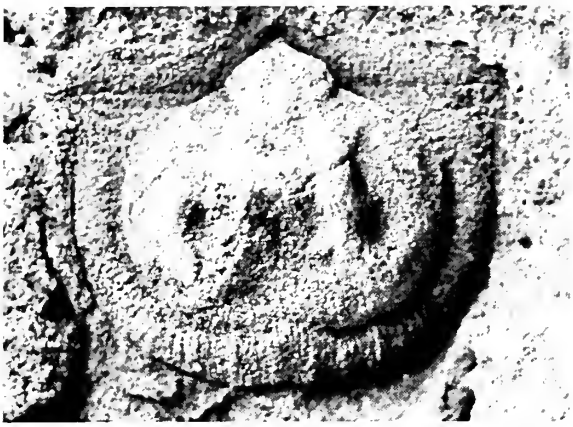
SPECIES ASSIGNED

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.

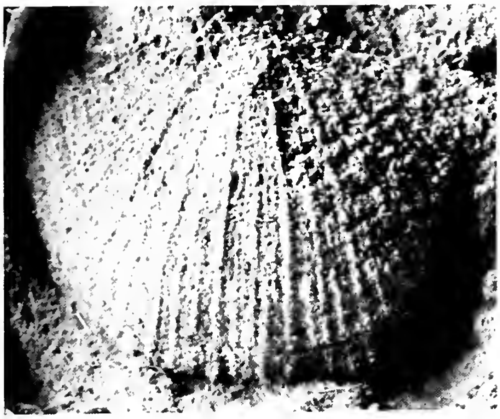


169a

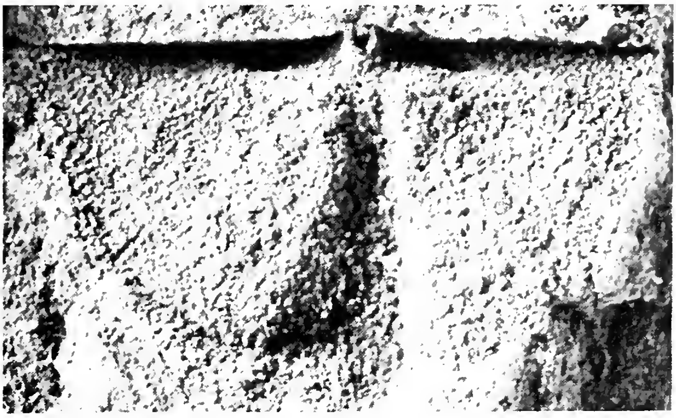
170

169b

171a



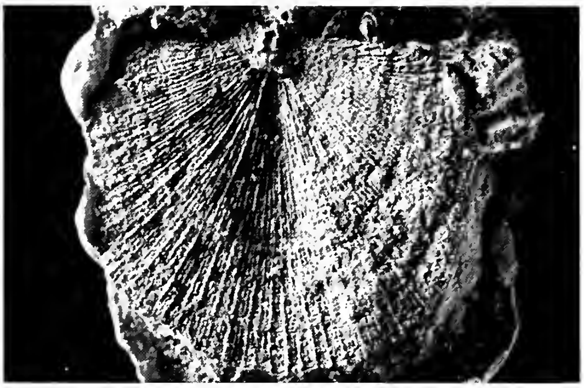
172



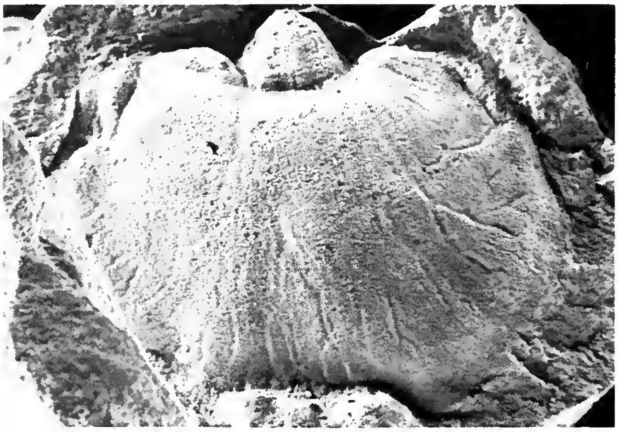
171b

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



174

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.

ACKNOWLEDGEMENTS AND SPECIMEN REPOSITORIES. We are most grateful to the Royal Society for financial support for Rong Jia-yu to come to the British Museum (Natural History) (B, BB and BC) for a seven month period during which most of this research took place. We are also grateful to Dr C. H. C. Brunton for reading the manuscript, Dr G. A. Cooper (USNM) for sending many photographs and specimens on exchange, Dr B. S. Norford for sending unpublished data on *Petroria*, Dr J. D. Lawson for collecting *Jonesea* material and Miss V. A. Harris for typing the manuscript.

The following museum curators kindly supplied type material on loan: Dr A. W. A. Rushton, British Geological Survey (GSM); Dr T. E. Bolton, Geological Survey of Canada (GSC); Dr D. L. Bruton, Paleontologisk Museum, Oslo (PMO); Dr T. L. Modzalevskaya, VSEGEI, Leningrad (VSEGEI); Dr I. Strachan, Birmingham University (BU) and Mr H. P. Powell, Oxford University Museum (OUM). Other repositories are Nanjing Institute of Geology and Palaeontology, Academia Sinica (NIGP), British Geological Survey, Edinburgh (GSE) and Sedgwick Museum, Cambridge (SMA).

REFERENCES

Alekseeva, R. E. & Erlanger, O. A. 1983. New assemblage of Silurian brachiopods from the north-west of Mongolia. *Trudȳ Sovmestnaya Sovietsko-Mongolskayaya Paleontogicheskaya Expeditsiar*, Moscow, **20**: 25–36, pls 6, 7.

Amsden, T. W. 1958. Stratigraphy and paleontology of the Hunton Group in the Arbuckle Mountain region. Part II. Haragan articulate brachiopods. *Bulletin of the Oklahoma Geological Survey*, Norman, **78**: 1–144, pls 1–10.

—— 1968. Articulate brachiopods of the St Clair Limestone (Silurian), Arkansas, and the Clarita Formation (Silurian), Oklahoma. *Journal of Paleontology*, Tulsa, **42** (3) Suppl.: 1–117, pls 1–20.

—— 1974. Late Ordovician and early Silurian articulate brachiopods from Oklahoma, southwestern Illinois, and eastern Missouri. *Bulletin of the Oklahoma Geological Survey*, Norman, **119**: 1–154, pls 1–28.

Andreeva, O. N. 1985. Middle Ordovician brachiopods and trilobites of Tuva and the Altai region. *Paleontological Zhurnal*, Moscow, **2**: 38–47.

Angelin, N. P. & Lindström, G. 1880. *Fragmenta Silurica e dono Caroli Henrici Wegelin*. 60 pp., pls 1–20. Stockholm.

Balashov, E. G., Vostokova, V. A., Eltisheva, R. S., Obut, A. M., Oradovskaya, M. M., Preobrazhenski, B. V., Rozman, K. S., Sobolevskaya, R. F. & Chugaeva, M. N. 1968. *Field Atlas of the Ordovician fauna in NE USSR*. 142 pp., 71 pls. Novosibirsk.

Barrande, J. 1848. *Über die Brachiopoden der Silurischen Schichten von Boehmen*. Part 2. 104 pp., pls 16–23. Vienna.

—— 1879. *Système silurien du centre de la Boheme. 1ère partie*. **5**. *Classe des Mollusques. Ordre des Brachiopodes*. 226 pp., 154 pls. Prague and Paris.

Bassler, R. S. 1919. The Cambrian and Ordovician deposits of Maryland. *Maryland Geological Survey Report*, Baltimore: 117–167.

Bates, D. E. B. 1968. The Lower Palaeozoic brachiopod and trilobite faunas of Anglesey. *Bulletin of the British Museum (Natural History)*, London, (Geology) **16** (4): 125–199, pls 1–14.

Bekker, H. 1922. A new brachiopod *(Leptestia)* from the Kuckers Stage in Estonia. *Geological Magazine*, London, **59**: 361–365, 4 figs.

Bendetto, J. L. & Herrera, Z. A. 1987. *Sanjuanella*, un nuevo genero de la Subfamila Ahtiellinae (Brachiopoda, Plectambonitacea) del Ordovicico de la Precordillera Argentina. *IV Congreso Latinoamericano de Paleontologia*, Bolivia, **1**: 97–109, pl. 1.

—— **& Zarela, A. M.** 1986. Braquiopodos del suborden Strophomenidina de la Formación San Juan (Ordovicico temprano), Precordillera Argentina. *IV Congresso Argentino Palaeontologia y Bioestratigrafia*, **1**: 113–123, pls 1–3.

Billings, E. 1865. *Paleozoic fossils*, **1**. 426 pp., 401 figs. Montreal.

Bondarev, V. I. 1968. Stratigraphy and characteristics of brachiopods from the Ordovician deposits in the south of Novaya Zemlya, Vaigach Isand and northern Pai-Khoi. *Trudȳ nauchno-issledovatel'skoyo Instituta Geologii Arktiki*, Leningrad, **157**: 3–144.

Borissiak, M. A. 1956. Rod *Kassinella* (Genus *Kassinella*). *Materiali vsesoyuznogo nauchno-issledovatelskii Geologicheskova Instituta*, Moscow, (NS) **12**: 50–52 [In Russian].

—— 1972. New late Ordovician strophomenoids of eastern Kazakhstan. In: *Novie Vidi Drevnik Rastenii i Bespozvonochnik SSSR*. 372 pp., 75 pls. Moscow.

Boucot, A. J., Johnson, J. G. & Ning Zhang 1988. Silurian (Wenlockian) brachiopods from southeastern California. *Palaeontographica*, Stuttgart, (A) **201**: 103–127, pls 1–9.

Brown, I. A. 1949. Occurrence of the brachiopod genus *Plectodonta* Kozlowski at Bowning, New South Wales. *Journal of the Royal Society of New South Wales*, Sydney, **82**: 196–201, pl. 14.

Brunton, C. H. C. 1972. The shell structure of chonetacean brachiopods and their ancestors. *Bulletin of the British Museum (Natural History)*, London, (Geology) **21**: 1–26, pls 1–9.

Bruton, D. L. & Harper, D. A. T. 1981. Brachiopods and trilobites of the early Ordovician serpentine Otta Conglomerate, south central Norway. *Norsk Geologisk Tidsskrift*, Oslo, **61**: 153–181.

Butts, C. 1926. Geology of Alabama. The Paleozoic rocks. *Geological Survey of Alabama Special Report*, Montgomery, **14**: 41–230, pls 3–76.

—— 1940–42. Geology of the Appalachian Valley in Virginia. *Virginia Geological Survey Bulletin*, Richmond, **52**: 119–216, pls 41–97.

Chang Mei-li 1981. *Hirnantia* fauna of the uppermost Ordovician in Yichang, Hubei. *Acta Palaeontologica Sinica*, Beijing, **20**: 557–566, pl. 1.

—— 1983. Brachiopods from the Miaopo Formation in Huanghuachang of Yichang, Hubei Province. *Acta Palaeontologica Sinica*, Beijing, **22**: 474–481, pl. 1.

Chapman, F. 1913. New or little-known Victorian fossils in the National Museum. Part 16. Some Silurian Brachiopoda. *Proceedings of the Royal Society of Victoria*, Melbourne, **26**: 99–113, pls 10, 11.

Chauvel, J., Drot, J., Pillet, J. & Tamain, G. 1970. Précisions sur l'Ordovicien moyen et supérieur de la 'serie type' du Centenillo (Sierra Morena orientale, Éspagne). *Bulletin de la Societe géologique de France*, Paris, (7) **11**: 613–626, pls 13–15.

Clark, T. H. 1924. The paleontology of the Beekmantown Series at Levis, Quebec. *Bulletin of American Paleontology*, Ithaca, **10**: 1–134, pls 1–9.

Cocks, L. R. M. 1970. Silurian brachiopods of the superfamily Plectambonitacea. *Bulletin of the British Museum (Natural History)*, London, (Geology) **19**: 139–203, pls 1–17.

—— 1978. A review of British Lower Palaeozoic Brachiopods including a synoptic revision of Davidson's monograph. *Palaeontographical Society Monograph*, London: 1–256.

—— 1982. The commoner brachiopods of the latest Ordovician of the Oslo-Asker district, Norway. *Palaeontology*, London, **25**: 755–781, pls 78–84.

—— **& Rong Jia-yu** 1988. A review of the late Ordovician *Foliomena* brachiopod fauna, with new data from China, Wales and Poland. *Palaeontology*, London, **31**: 112–117, pls 1, 2.

Cooper, G. A. 1956. Chazyan and related brachiopods. *Smithsonian miscellaneous collections*, Washington, **127**: 1–1245, pls 1–269.

—— 1988. A new genus of Plectambonitacea (Brachiopoda) from Malaysia. *Memoir New Mexico Bureau of Mines and Mineral Resources*, **44**: 185–187.

—— **& Kindle, C. H.** 1936. New brachiopods and trilobites from the Upper Ordovician of Percé, Quebec. *Journal of Paleontology*, Menasha, **10**: 348–372, pls 51–53.

—— **& Williams, A.** 1952. Significance of the stratigraphic distribution of brachiopods. *Journal of Paleontology*, Menasha, **26**: 326–337.

Cowen, R. 1975. 'Flapping valves' in brachiopods. *Lethaia*, Oslo, **8**: 23–29.

Davidson, T. 1847. Observations on some of the Wenlock-Limestone Brachiopoda, with descriptions of several new species . *London Geological Journal*, **1**: 52–65, pls 12,13.

—— 1849. Observations sur quelques brachiopodes siluriens. *Bulletin de la Societé géologique de France*, Paris, (2) **6**: 271–275.

—— 1869–71. A Monograph of the British Fossil Brachiopoda. Part VII. The Silurian Brachiopoda. **3**: 169–248, pls 23–37 (1869). **4**: 249–397, pls 38–50 (1871). *Palaeontographical Society Monograph*, London.

—— 1883. Monograph of the British Fossil Brachiopoda. Volume V. Part II. Silurian Supplement. *Palaeontographical Society Monograph*, London: 135–242, pls 8–17.

Eichwald, E. de 1855. *Lethaea Rossica ou Paléontologie de la Russe. Atlas*. 9 pp., 59 pls. Stuttgart.

—— 1860. *Lethaea Rossica ou Paléontologie de la Russe*. Premier volume. *Première et second sections de l'ancienne Période*. **1**. 1657 pp. Stuttgart.

Endo, R. 1932. The Canadian and Ordovician Formation and fossils of south Manchuria. *Bulletin United States National Museum*, Washington, **164**: 1–115, pls 33–35.

Foerste, A. F. 1890. Notes on Clinton Group fossils, with special reference to collections from Indiana, Tennessee and Georgia. *Proceedings of the Boston Society for Natural History*, **24**: 263–355, pls 5–9.

—— 1903. Silurian and Devonian Limestones of Western Tennessee. *Journal of Geology*, Chicago, **11**: 679–715.

—— 1912. *Strophomena* and other fossils. *Denison University Science Laboratory Bulletin*, **17**: 17–173.

Fu Li-pu 1975. Brachiopods. *In*: Li Yao-xi, Song Li-sheng, Zhou Zhi-qiang, Yang Jing-yao and others (eds), *Stratigraphy of the Early Palaeozoic in the West part of Dabashan Mountain*: 103–119, pls 1–70. Beijing.

—— 1982. Phylum Brachiopoda. *In*: Xi'an Institute of Geology and Mineral Resources (ed.), *Palaeontological Atlas of northwest China. Shaanxi, Gansu and Ningxia*, **1**, Precambrian to Early Palaeozoic: 95–178, pls 30–45. Beijing.

Gagel, C. 1890. Die Brachiopoden der cambrischen und silurischen Geschiebe im Diluvium der Provinzen Ost- und Westpreussen. *Beiträge zur Naturkunde Preussens*, Berlin, **6**: 1–79, pls 1–5.

Gratsianova, R. T. 1967. *Brachiopods and Stratigraphy of the Lower Devonian of the Gornoi Altai*. 177 pp., 14 pls. Moscow.

Grubbs, D. M. 1939. Fauna of the Niagaran nodules of the Chicago area. *Journal of Paleontology*, Tulsa, **13**: 543–560, pls 61, 62.

Hadding, A. 1913. Undre Dicellograptusskiffern i Skåne jämte några därmed ekvivalenta bildningar. *Lund Universitets Årsskrift*, (NF) **9** (2) No.15: 1–90, pls 1–8.

Hall, J. 1843. *Geology of New York. Part IV. Comprising the Survey of the Fourth Geological District*. 684 pp., 19 pls. Albany.

—— **& Clarke, J. M.** 1892–94. An introduction to the study of the genera of Palaeozoic Brachiopoda. *New York State Geological Survey, Palaeontology of New York*, Albany, **8** (1): 1–367, pls 1–41; (2): 1–394, pls 42–84.

Hamada, T. 1969. Devonian brachiopods from Kroh, Upper Perak in Malaysia (Malaya). *In*: Kobayashi, T. & Toriyama, R. (eds), *Geology and palaeontology of southeast Asia*, Tokyo, **7**: 1–13, pls 1, 2.

Harper, C. W. 1973. Brachiopods of the Arisaig Group (Silurian–Lower Devonian) of Nova Scotia. *Geological Survey of Canada Bulletin*, Ottawa, **215**: 1–63, pls 1–28.

arper, D. A. T. & Owen, A. W. 1984. The Caradoc brachiopod and trilobite fauna of the upper Kirkerud Group, Hadeland, Norway. *Geologica et Palaontologica*, Marburg, **18**: 21–51.

avlíček, V. 1952. [On the Ordovician representatives of the family Plectambonitidae (Brachiopoda)]. *Ústředního Ústavu Geologického Sbornik*, Prague, **19**: 397–428. [In Czech].

—— 1953. O několika nových ramenonožcich českého a moravského stredniho devonu. *Věstnik Ústředniho ústavu geologického*, Prague, **28**: 4–9, pls 1, 2.

—— 1961. Plectambonitacea im böhmischen Palaözoikum (Brachiopoda). *Věstnik Ústředniho ústavu geologického*, Prague, **36** (6): 447–451.

—— 1967. Brachiopoda of the Suborder Strophomenidina in Czechoslovakia. *Rozpravy Ústředního ústavu geologického*, Prague, **33**: 1–235, pls 1–52.

—— 1971. Brachiopodes de l'Ordovicien du Maroc. *Notes et Memoires du Service Géologique du Maroc*, Rabat, **230**: 1–135, pls 1–26.

—— 1976. Systematic position of four Ordovician brachiopod species. *Věstnik Ústředního ústavu geologického*, Prague, **51**: 367–370, pls 1, 2.

—— 1977. The Paleozoic (Cambrian–Devonian) in the Rozmitál area. *Věstnik Ústředniho ústavu geologického*, Prague, **52**: 81–94, pls 1, 2.

—— 1981. Upper Ordovician brachiopods from the Montagne Noire. *Palaeontographica*, Stuttgart, (A) **176**: 1–34, pls 1–9.

—— **& Branisa, L.** 1980. Ordovician brachiopods of Bolivia. *Rozpravy Ceskoslovenské Akademie Ved*, Prague, **90**: 1–54.

——, **Kříž, J. & Serpagli, E.** 1987. Upper Ordovician brachiopod assemblages of the Carnic Alps, Middle Carinthia and Sardinia. *Bolletino della Societa Paleontologico Italiana*, Modena, **25**: 277–311, pls 1–9.

Henningsmoen, G. 1948. Deep boring through Ordovician and Silurian strata at Kinnekulle, Vestergötland 4. The Tretaspis Series of the Kullatorp Core. *Bulletin of the Geological Institution of the University of Uppsala*, **32**: 374–432, pls 24, 25.

Herrera, Z. A. & Benedetto, J. L. 1987. El genero *Reinversella* (Brachiopoda) en el Ordovicico temprano de la Precordillera Argentina y su significado paleobiogeografico. *Decimo Congreso Geologico Argentino Actas*, **3**: 77–80.

Hessland, I. 1949. Investigations of the Lower Ordovician of the Siljan District, Sweden. V. Notes on Swedish *Ahtiella* species. *Bulletin of the Geological Institution of the University of Uppsala*, **33**: 511–527, pls 1, 2.

Holtedahl, O. 1916. The Strophomenidae of the Kristiania Region. *Videnskapsselskapets Skrifter. I. Matur-Naturv. Klasse 1915*, Oslo, **12**: 1–118, pls 1–16.

Howe, H. J. 1965. Plectambonitacea, Strophomenacea and Atrypacea from the Montoya Group (Ordovician) of Trans-Pecos, Texas. *Journal of Paleontology*, Menasha, **39**: 647–656, pls 81, 82.

—— 1972. Morphology of the brachiopod genus *Thaerodonta*. *Journal of Paleontology*, Menasha, **46**: 440–446, pls 1–3.

—— 1979. Middle and Late Ordovician plectambonitacean, rhynchonellacean, syntrophiacean, trimerellacean and atrypacean brachiopods. *Professional Paper United States Geological Survey*, Washington, **1066C**: 1–18.

—— 1988. Articulate brachiopods from the Richmondian of Tennessee. *Journal of Paleontology*, Menasha, **62**: 204–218.

Howell, B. F. 1949. New hydrozoan and brachiopod and new genus of worms from the Ordovician Schenectady Formation of New York. *Bulletin of the Wagner Free Institute of Science*, Philadelphia, **24** (1): 1–8, pls 1, 2.

Hurst, J. M. 1975. The function of the brachial valve septa in plectambonitacean brachiopods. *Lethaia*, Oslo, **8**: 63–67.

—— 1979. The stratigraphy and brachiopods of the upper part of the type Caradoc of south Salop. *Bulletin of the British Museum (Natural History)*, London, (Geology) **32**: 183–204, 557 figs.

Hussey, R. C. 1926. The Richmond Formation of Michigan. *Contributions of the Museum of Geology of the University of Michigan*, Ann Arbor, **2**: 113–187, pls 1–11.

Jaanusson, V. 1962. Two Plectambonitacean brachiopods from the Dalby Limestone (Ordovician) of Sweden. *Bulletin of the Geological Institution of the University of Uppsala*, **39**: 1–8, pl. 1.

Jahnke, H. 1971. Fauna und Alter der Erbslochgrauwacke (Brachiopoden und Trilobiten, Unter-Devon, Rheinisches Schiefergebirge und Harz). *Göttinger Arbeiten zur Geologie und Paläontologie*, **9**: 1–105, pls 1–11.

James, U. P. 1874. Descriptions of one new species of *Leptaena*, and two species of *Cyclonema* from the Lower Silurian Rocks. Cincinnati Group. *The Cincinnati Quarterly Journal of Science*, **1**: 151–153.

Johnson, J. G., Boucot, A. J. & Murphy, M. A. 1976. Wenlockian and Ludlovian age branhiopods from the Roberts Mountains Formation of Central Nevada. *University of California Geological Science Publications*, Berkeley, **115**: 1–102, pls 1–55.

Jones, O. T. 1928. *Plectambonites* and some allied genera. *Memoirs of the Geological Survey of Great Britain, Palaeontology*, London, **1**: 367–527, pls 21–25.

Klenina, L. N., Nikitin, I. F. & Popov, L. E. 1984. *Brachiopods and biostratigraphy of the Middle and Upper Ordovician of the Chinghiz ranges*. 196 pp., pls 1–20. Alma-Ata.

Kozlowski, R. 1929. Les Brachiopodes gothlandiens de la Podolie Polonaise. *Palaeontologia polonica*, Warsaw, **1**: 1–254, pls 1–12.

Kulkov, N. P. 1967. *Brachiopods and Stratigraphy of the Silurian of Gornoi Altai*. 151 pp., 21 pls. Moscow.

——, **Vladimirskaya, E. V. & Rybkina, N. L.** 1985. The brachiopods and biostratigraphy of the Upper Ordovician and Silurian of Tuva. *Trudў Akademya Nauk SSSR, Sibirskoe Otdeleniye, Institute of Geology and Geophysics*, Moscow, **635**: 1–208, pls 1–32.

Kutorga, S. 1846. Dritter Beitrag zur Paläontologie Russlands. *Verhandlungen der Mineralogischen Gesellschaft zu St Petersberg*, **1845**: 1–64, pls 3–8.

Lamansky, V. V. 1905. Die ältesten silurischen Schichten Russlands. *Comité Géologique Mémoires*, St Petersberg, (NS) **20**: 1–203, pls 1, 2.

Lamont, A. 1935. The Drummuck Group, Girvan: a stratigraphical revision, with descriptions of new fossils from the lower part of the Group. *Transactions of the Geological Society of Glasgow*, **19**: 288–332, pls 7–9.

—— **& Gilbert, D. L. F.** 1945. Upper Llandovery Brachiopoda from Coneygore Coppice and Old Storridge Common, near Alfrick, Worcestershire. *Annals and Magazine of Natural History*, London, (11) **12**: 641–682, pls 3–7.

Laurie, J. R. 1987. A re-assessment of the brachiopod genus *Spanodonta* Prendergast from the Lower Ordovician of Western Australia. *Alcheringa*, Sydney, **11**: 43–49.

Lenz, A. C. 1977*a*. Upper Silurian and Lower Devonian brachiopods of Royal Creek, Yukon, Canada. *Palaeontographica*, Stuttgart, (A) **159**: 37–109, pls 1–22.

—— 1977*b*. Llandoverian and Wenlockian brachiopods from the Canadian Cordillera. *Canadian Journal of Earth Sciences*, Ottawa, **14**: 1521–1554, pls 1–14.

Levy, R. & Nullo, F. 1975. Braquiopodos Ordovicicos de Ponon-Trehue, Bloque de San Rafael (Provincia de Mendoza, Argentina). *Actas i Congreso Argentino de Paleontologia y Bioestratigrafia 1, Tucuman*, Buenos Aires: 23–32.

Lindström, G. 1861. Bidrag till Kännedomen om Gotlands Brachiopoden. *Ofversigt af Konglingun Vetenskaps-Akademiens Förhandlingar*, Stockholm, **1860**: 337–382, pls 12, 13.

Lindström, M. 1953. On the Lower Chasmops Beds in the Fagelsang District (Scania). *Geologiska Föreningens i Stockholm Förhandlingar*, **75** (2): 125–148, 1 pl.

Liu Di-yong 1976. Ordovician brachiopods from the Mount Jolmo Lungma region. *In: A report of Scientific expeditions in the Mount Jolmo Lungma region (1966–1968). Palaeontology. Fascicule 2*: 139–158, pls 1, 2. Beijing.

——, **Xu Han-kui & Liang Wen-ping** 1983. Phylum Brachiopoda. *In*: Nanjing Institute of Geology and Mineral Resources (eds), *Palaeontological Atlas of Eastern China. Early Palaeozoic Volume*: 1–657, pls 1–176. Beijing.

Lockley, M. G. 1980. The Caradoc fanual associations of the area between Bala and Dinas Mawddwy, north Wales. *Bulletin of the British Museum (Natural History)*, London, (Geology) **33**: 165–235, 105 figs.

—— **& Williams, A.** 1981. Lower Ordovician Brachiopoda from mid and southwest Wales. *Bulletin of the British Museum (Natural History)*, London, (Geology) **35**: 1–78, 263 figs.

Lopushinskaya, T. V. 1976. Brachiopods and stratigraphy of Silurian sediments in the Northern Siberian platform. *Trudў Sibirskogo Nauchno-Issledovatel'skogo Instituta Geologii, Geofiziki i Mineral'nogo Syr'ya*, Novosibirsk, **199**: 1–96, pls 1–16.

M^c^Coy, F. 1846. *A synopsis of the Silurian fossils of Ireland collected from the several districts by Richard Griffith, F.G.S.* 72 pp., 5 pls. Dublin.

Macomber, R. W. 1970. Articulate brachiopods from the Upper Bighorn Formation (Late Ordovician) of Wyoming. *Journal of Paleontology*, Menasha, **44**: 416–450, pls 75–80.

Mansuy, H. 1916. Étude complémentaire des faunes paléozoïques et triasiques dans l'est du Tonkin. *Mémoires du Service géologique de l'Indochine*, Hanoi-Haiphong, **5** (4): 39–71, pls 7, 8.

Marek, L. & Havlíček, V. 1967. The articulate brachiopods of the Kosov Formation (Upper Ashgillian). *Věstník Ústředního ústavu geologického*, Prague, **42**: 275–284, pls 1–4.

Mather, K. F. 1917. The Trenton fauna of Wolfe Island, Ontario. *Ottawa Naturalist*, **31**: 33–40, pl. 1.

Meek, F. B. 1873. Descriptions of invertebrate fossils of the Silurian and Devonian Systems. *Geological Survey of Ohio*, Columbus, **1** (2): 1–246, pls 1–23.

Melou, M. 1971. Nouvelle espèce de *Leptestiina* dans l'Ordovicien supérieur de l'Aulne (Finistère). *Mémoires du Bureau de Recherches Géologiques et Minières*, Paris, **73**: 93–105, pls 1, 2.

—— 1973. Le genre *Aegiromena* (Brachiopode–Strophomenida) dans l'Ordovicien du Massif armoricain (France). *Annales de la Societé Géologique du Nord*, Lille, **93**: 253–264, pls 33–36.

Mikulás, R. 1983. Two new brachiopod species of the suborder Strophomenidina from the Podolí iron ore horizon (Kralovdvorian). *Casopis narodního Musea v Praze*, Prague, **152**: 4–8, pls 1, 2.

Misius, P. P. 1986. *Ordovician brachiopods of northern Kirgizia*. 254 pp., 26 pls. Frunze.

—— **& Ushatinskaya, G. T.** 1977. New Ordovician and Silurian strophomenids from Kazakhstan and Northern Khirgiz. *In*: Stukalina, G. G. (ed.), *Novye Vidy Drevnikh Rastenii Bespozvonochnykh SSSR*, Moscow, 4: 113–116.

Mitchell, J. 1923. The Strophomenidae from the fossiliferous beds of Bowning, New South Wales. Part 1, *Stropheodonta. Proceedings of the Linnean Society of New South Wales*, Sydney, **48**: 465–474.

Mitchell, W. I. 1977. The Ordovician Brachiopoda from Pomeroy, County Tyrone. *Palaeontographical Society (Monograph)*, London: 1–138, pls 1–28.

Muir-Wood, H. M. 1962. On the morphology and classification of the brachiopod suborder Chonetoidea. *British Museum (Natural History) Monograph*, London: 1–132, pls 1–16.

Neuman, R. B. 1971. An Early Middle Ordovician brachiopod assemblage from Maine, New Brunswick and Northern Newfoundland. *Smithsonian Contributions to Paleobiology*, Washington, **3**: 113–124, pls 1, 2.

—— 1977. Early Ordovician (Late Arenig) brachiopods from Virgin Arm, New World Island, Newfoundland. *Canadian Geological Survey Bulletin*, Ottawa, **261**: 11–61, pls 1–8.

—— **& Bruton, D. L.** 1974. Early middle Ordovician fossils from the Hølonda area, Trondheim region, Norway. *Norsk Geologisk Tidsskrift*, Oslo, **54**: 69–115.

Nikanorova, Y. Y. 1976. New species of *Sowerbyella* (Brachiopoda) from the Middle Ordovician of the Moscow syneclise. *Paleontological Zhurnal*, Moscow, **1976** (4): 115–118.

Nikiforova, O. I. 1954. *[Stratigraphy and brachiopods of the Silurian deposits of Podolia.]* 218 pp., 18 pls. Moscow (Trudy̆ Vsesoyuznogo Nauchno-Issdelovatelskogo Geologicheskova Instituta, VSEGEI) [In Russian].

—— 1978. Brachiopods of the Tchashmankalon, Archalyk and Minkuchar Beds. *In: Beds across the Ordovician–Silurian boundary in the Altae-Sayan and Tian-Shan regions*: 102–125, pls 18–23. Moscow.

—— **& Andreeva, O. N.** 1961. Stratigraphy of the Ordovician and Silurian of the Siberian Platform and its palaeontological significance. *Trudy̆ Vsesoyuznogo Nauchno-Issledovatelskogo Geologicheskova Instituta (VSEGEI)*, Leningrad, (NS) **56**: 1–412, pls 1–56.

——, **Modzalevskaya, T. L. & Bassett, M. G.** 1985. Review of the Upper Silurian and Lower Devonian articulate brachiopods of Podolia. *Special Papers in Palaeontology*, London, **34**: 1–66, pls 1–16.

Nikitin, I. F. 1974. [New Middle Ordovician Plectambonitacea (Brachiopoda) from Kazakhstan]. *Paleontologicheskii Zhurnal*, Moscow, **1974** (3): 55–66, 2 pls [In Russian].

—— **& Popov, L. E.** 1983. Sredneordovikskie Ortatsei i Plektambonitatsei severnogo Priishim'ia i Basseina Reki Akzhar u Tsentralnom Kazakstane (Brakhiopody). *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva*, Leningrad, **26**: 228–247, 3 pls.

——, —— **& Rukavishnikova, T. B.** 1980. Class Articulata. *In*: Apollonov, M. K., Bandaletov, S. M. & Nikitin, I. F. (eds), *The Ordovician–Silurian boundary in Kazakhstan*: 37–74, pls 10–21. Alma-Ata.

Nikitina, O. I. 1985. A new brachiopod association from the Middle Ordovician of southern Kazakhstan. *Paleontologicheskii Zhurnal*, Moscow, **1985** (4): 21–29, pls 1, 2.

Norford, B. S. 1969. Ordovivian and Silurian stratigraphy of the southern Rocky Mountains. *Bulletin Geological Survey of Canada*, Ottawa, **176**: 1–90.

Northrop, S. A. 1939. Paleontology and stratigraphy of the Silurian rocks of the Port Daniel–Black Cape region, Gaspé. *Special Paper of the Geological Society of America*, New York, **21**: 1–302, pls 1–28.

Öpik, A. A. 1930. Brachiopoda Protremata der Estländischen Ordovischen Kukruse-Stufe. *Acta et Commentationes Universitatis Tartuensis*, Tartu, **A17** (1): 1–262, pls 1–22.

—— 1932. Über die Plectellinen. *Acta et Commentationes Universitatis Tartuensis*, Tartu, **23** (3): 1–85, pls 1–12.

—— 1933. Über Plectamboniten. *Acta et Commentationes Universitatis Tartuensis*, Tartu, **24** (7): 1–79, pls 1–12.

—— 1939. Brachiopoden und Ostrakoden aus dem Expansusschiefer norwegens. *Norsk Geologisk Tidsskrift*, Oslo, **19**: 117–142, pls 1–6.

—— 1953. Lower Silurian fossils from the 'Illaenus Band', Heathcote, Victoria. *Memoirs of the Geological Survey of Victoria*, Melbourne, **19**: 1–42, pls 1–13.

Pander, C. H. 1830. *Beiträge zur Geognosie des Russischen Reiches*. 165 pp., 31 pls. St Petersburg.

Percival, I. G. 1979. Ordovician plectambonitacean brachiopods from New South Wales. *Alcheringa*, Sydney, **3**: 91–116.

Petrunina, Z. E. & Severgina, L. G. 1962. On the stratigraphy of the Ordovician of the north-west Altai Mountains. *Materiali po Geologii zapadnoi sibiri Kraya*, Tomsk, **63**: 81–93, pls 1–4.

Phillips, J. & Salter, J. W. 1848. Palaeontological appendix to Professor John Phillips' Memoir on the Malvern Hills compared with the Palaeozoic districts of Abberley etc. *Memoirs of the Geological Survey of Great Britain*, London, **2** (1): 331–386, pls 4–30.

Phleger, F. B. 1933. Notes on certain Ordovician faunas of the Inyo Mountains, California. *Bulletin of the South California Academy of Sciences*, Los Angeles, **32**: 1–21, pls 1, 2.

Popov, L. E. 1980*a*. New strophomenoids from the Middle Ordovician of northern Kazakhstan. *Novie Vidi drevnich rastenii i bespozbonochnich SSSR*, **5**: 54–57, pl. 17.

—— 1980*b*. New brachiopod species from the Middle Ordovician of Chu-Ili Mountains. *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva*, Leningrad, **23**: 139–158.

Poulsen, C. 1943. The Silurian faunas of North Greenland. *Meddelelser om Grønland*, Copenhagen, **72** (3): 1–60, pls 1–6.

Prendergast, K. L. 1935. Some Western Australian Upper Palaeozoic fossils. *Journal of the Royal Society of Western Australia*, Perth, **21**: 9–35, 3 pls.

Raymond, P. E. 1921. A contribution to the description of the fauna of the Trenton Group. *Museum Bulletin of the Geological Survey of Canada*, Ottawa, **31**: 1–64.

—— 1928. The brachiopods of the Lenoir and Athens Formations of Tennessee and Virginia. *Bulletin of the Museum of Comparative Zoology*, Harvard, **68**: 293–309, pls 1–3.

Reed, F. R. C. 1906. The Lower Palaeozoic fossils of the northern Shan States, Burma. *Palaeontologia Indica*, Calcutta, (NS) **2** (3): 1–154, pls 1–8.

—— 1912. Ordovician and Silurian fossils from the central Himalayas. *Palaeontologia Indica*, Calcutta, (NS) **7** (2): 1–168, pls 1–20.

—— 1917. The Ordovician and Silurian Brachiopoda of the Girvan District. *Transactions of the Royal Society of Edinburgh*, **51**: 795–998, pls 1–24.

—— 1932*a*. Report on the brachiopods from the Trondheim area. *Skrifter utgitt av det Norske Videnskaps-Akademi i Oslo I. Mat.-Naturv. Klasse*, Oslo, **4**: 115–146, pls 1–5.

—— 1932*b*. Notes on some Lower Palaeozoic fossil from the Southern Shan States. *Record of the Geological Survey of India*, Calcutta, **66**: 181–211, pl. 3.

—— 1935. Some new brachiopods from Girvan. *Annals and Magazine of Natural History*, London, (10) **16**: 1–12, pl. 1.

—— 1936. The Lower Palaeozoic faunas of the southern Shan States. *Palaeontologia Indica*, Calcutta, (NS) **21** (3): 1–130, pls 1–7.

—— 1941. A new genus of trilobites and other fossils from Girvan. *Geological Magazine*, London, **78**: 268–278, pl. 5.

—— 1944. Notes on some new Ordovician brachiopods from Girvan. *Annals and Magazine of Natural History*, London, (11) **11**: 215–222, pl. 3.

—— 1945. Notes on some Ordovician Brachiopods and a Trilobite from the Balclatchie Beds of Girvan. *Annals and Magazine of Natural History*, London, (11) **12**: 309–316, pl. 1.

—— 1952. Revision of certain Ordovician fossils from County Tyrone. *Proceedings of the Irish Academy*, Dublin, **55** (B): 29–136, pls 1–5.

Rice, W. F. 1987. The systematics and biostratigraphy of the Brachiopoda of the Decorah Shale at St Paul, Minnesota. *Minnesota Geological Survey Report of Investigations*, **35**: 136–166, pls 1–4.

Roemer, F. A. 1850. Beiträge zur geologischen Kenntnis des nortwestlichen Harzgebirges. *Palaeontographica*, Cassel, **3**: 1–67, pls 1–8.

Rong Jia-yu 1984. Brachiopods of latest Ordovician in the Yichang District, Western Hubei, Central China. *In: Stratigraphy and Palaeontology of Systemic boundaries in China. Ordovician–Silurian boundary* **1**: 111–176, pls 1–14. Anhui.

——, **Xu Han-kui & Yang Xue-chang** 1974. Silurian brachiopods. *In*: Nanjing Institute of Geology and Palaeontology, Academia Sinica (ed.), *Handbook of Stratigraphy and Palaeontology in southwest China*: 195–208, pls 92–96. Beijing.

—— **& Yang Xue-chang** 1981. Middle and late early Silurian brachiopod faunas in southwest China. *Memoirs of Nanjing Institute of Geology and Palaeontology, Academia Sinica*, Beijing, **13**: 163–270, pls 1–26.

Rõõmusoks, A. 1959. Strophomenoidea of the Ordovician and Silurian of Estonia I. The genus *Sowerbyella* Jones. *Tartu Riikliku Ulikod Toimetised*, Tartu, **75**: 11–50, pls 1–8.

—— 1963. Strophomenoidea of the Ordovician and Silurian from Estonia 2. New genera from the Harju Series. *Eesti NSV Teaduste Akadeemia Toimetised*, Tallinn, **3**: 231–241, pls 1, 2.

—— 1981. Strophomenida of the Ordovician and Silurian of Estonia III. Genus *Thaerodonta* Wang. *Eesti NSV Teaduste Akadeemia Toimetised 30. Koide Geoloogia*, Tallinn, **1981** (2): 61–71, pls 1, 2.

Ross, R. J. 1970. Ordovician brachiopods, trilobites and stratigraphy in Eastern and Central Nevada. *Professional Paper United States Geological Survey*, Washington, **639**: 1–103, pls 1–19.

—— 1972. Fossils from the Ordovician bioherm at Meiklejohn Peak, Nevada. *Professional Paper United States Geological Survey*, Washington, **685**: 1–47, pls 1–26.

—— **& Dutro, J. T.** 1966. Silicified Ordovician brachiopods from east-central Alaska. *Smithsonian Miscellaneous Collections*, Washington, **149** (7): 1–22, pls 1–3.

—— **& James, N. P.** 1987. Brachiopod biostratigraphy of the Middle Ordovician Cow Head and Table Head group, western Newfoundland. *Canadian Journal of Earth Sciences*, Ottawa, **24**: 70–95.

Rozman, K. S. 1964. Brachiopods of the Middle and late Ordovician of Selenniakh mountain range. *Trudy̆ Akademiya Nauk SSSR, Geologicheskii Institut*, Moscow, **106**: 109–193, pls 7–23.

—— 1977. New orthids and strophomenids from the Upper Ordovician of Mongolia. *Paleontologicheskii Zhurnal*, Moscow, **1977** (3): 83–97, pls 5, 6.

—— 1978. Brachiopods of the Obikalon Beds. *In: Beds across the Ordovician–Silurian boundary in the Altae-Sayan and Tian-Shan regions*: 75–101, pls 12–17. Moscow.

—— 1981. Middle and Upper Ordovician brachiopods of Mongolia. *Trudȳ Akademia Nauk SSSR, Geologicheskii Institut*, Moscow, **354**: 117–176, pls 24–45.

Ruedemann, R. 1901. Trenton Conglomerate of Rysedorph Hill, Rensselaer Co., N.Y. and its fauna. *Bulletin of the New York State Museum*, Albany, **49**: 1–114, pls 1–7.

—— 1912. The Lower Siluric shales of the Mohawk valley. *Albany Education Department New York State Museum Bulletin*, Albany, **162**: 1–151, pls 1–10.

Rukavishnikova, T. B. 1956. Ordovician brachiopods from Kazakhstan. *Trudȳ Akademia Nauk SSSR, Geologicheskii Institut*, Moscow, **1**: 105–168, 5 pls [In Russian].

Rybnikova, M. V. 1967. Brachiopods. *In: Stratigraphy, fauna and conditions of deposition of the Silurian rocks of the central pre-Baltic*: 169–221, pls 14–25. Riga.

Salter, J. W. & Blanford, H. F. 1865. *Palaeontology of Niti in the Northern Himalaya: being descriptions and figures of the Palaeozoic and Secondary Fossils*. 112 pp., 23 pls. Calcutta.

Sardeson, F. W. 1892. The range and distribution of the Lower Silurian fauna of Minnesota with descriptions of some new species. *Minnesota Academy of Natural Sciences Bulletin*, Minneapolis, **3**: 326–343, pls 4–6.

Savage, N. M. 1974. The brachiopods of the Lower Devonian Maradana Shale, New South Wales. *Palaeontographica*, Stuttgart, (A) **146**: 1–51, pls 1–11.

Schmidt, F. 1858. Untersuchungen über die silurische Formation von Ehstland, Nord-Livland und Oesel. *Archiv für die Naturkunde Liv-, Ehst und Kurlands*, Dorpat: 1–247, pl. 1.

Schmidt, H. W. 1939. Die Grenzschichten Silur-Devon in Thüringen. *Abhandlungen der Preussischen Geologischen Landesanstalt*, Berlin, **195**: 1–100, pls 1–4.

Schuchert, C. & Cooper, G. A. 1930. Upper Ordovician and Lower Devonian stratigraphy and paleontology of Percé, Quebec. Part II. *American Journal of Science*, New Haven, **118**: 265–288, pls 1, 2.

—— —— 1931. Synopsis of the brachiopod genera of the suborders Orthoidea and Pentameroidea, with notes on the Telotremata. *American Journal of Science*, New Haven, (5) **22**: 241–251.

Sedgwick, A. & McCoy, F. 1851–55. *A synopsis of the classification of the British Palaeozoic rocks, with a systematic description of the British Palaeozoic fossils in the Geological Musuem of the University of Cambridge*. 661 pp., 25 pls. London and Cambridge.

Severgina, L. G. 1960. Brachiopods. *In*: Khalfina, L. L. (ed.), Biostratigraphy of the Palaeozoic of the Sayano-Altai Mountains. Lower Palaeozoic. *Trudȳ Sibirskogo Nauchno-issledovatel'skogo Instituta Geologii, Geofiziki i mineral'nogo Sȳr'ya (SNIIGIMS)*, Leningrad, **19**: 1–498, pls 1–53.

—— 1967. New species and genera of Ordovician brachiopods from the Sayano-Altai hill district. *Tomsk Universati Ychenky Zapadni*, **63**: 120–140, pls 1–5.

—— 1984*a*. Lower Ordovician brachiopods of the Gornoi Altai, Kuznetz Alatai, Shori hill and Salair. *Trudȳ Akademia Nauk SSSR, Sibirskoe Otdelenie*, Novosibirsk, **565**: 34–53, pls 1–5.

—— 1984*b*. Some Upper Ordovician (Ashgill) brachiopods of the Gornoi Altai. *Trudȳ Instituta Geologii i Geofiziki Akademia Nauk SSSR, Sibirskoe Otdelenie*, Moscow, **584**: 39–48, pls 3, 4.

Shaler, N. S. 1865. List of the Brachiopoda from the Island of Anticosti sent by the Museum of Comparative Zoology to different institutions in exchange for other specimens, with annotations. *Bulletin of the Museum of Comparative Zoology*, Harvard, **1**: 61–70.

Sheehan, P. M. 1973. Brachiopods from the Jerrestad Mudstone (Early Ashgillian, Ordovician) from a boring in southern Sweden. *Geologica et Palaeontologica*, Marburg, **7**: 59–76, pls 1–3.

—— 1976. Late Silurian brachiopods from northwestern Utah. *Journal of Paleontology*, Menasha, **50**: 710–733, pls 1–5.

Sokolskaya, A. N. 1960. Order Strophomenida. *In: Osnovy Paleontologii. Mshanki, Brakhiopodi*: 206–220, pls 27–32. Moscow.

Solle, G. 1938. Sowerbyellinae im Unter- und Mitteldevon (Brachiopoda, Plectambonitidae). *Senckenbergiana*, Frankfurt, **20**: 264–279.

Sowerby, J. de C. 1839. Shells. *In*: Murchison, R. I., *The Silurian System. Part II. Organic Remains*: 579–712, pls 1–27. London.

Spjeldnaes, N. 1957. The Middle Ordovician of the Oslo Region, Norway 8. Brachiopoda of the suborder Strophomenoidea. *Norsk Geologisk Tidsskrift*, Oslo, **37**: 1–214, pls 1–14.

Strusz, D. L. 1982. Wenlock brachiopods from Canberra, Australia. *Alcheringa*, Sydney, **6**: 105–142.

Su Yang-zheng 1980. Cambrian to Devonian brachiopods. In: Shenyang Institute of Geology and Mineral Resources (ed.), *Paleontological Atlas of Northeast China. Paleozoic volume*: 254–327, pls 1–261. Beijing.

Tachibana, K. 1976. Silurian brachiopods from the Kesen District of the Kitakami Mountainland, Northeast Japan. *Annual Reports of the Faculty of Education, Iwate University*, **36** (3): 31–51, pls 1–7.

Talent, J. A. 1965. The Silurian and early Devonian faunas of the Heathcote District, Victoria. *Geological Survey of Victoria Memoir*, Melbourne, **26**: 1–55, pls 1–27.

Teichert, C. 1928. Stratigraphische und paläontologische Untersuchungun im unteren Gotlandium (Tamsal-Stufe) des westlichen Estland und der Insel Dagö. *Neues Jahrbuch für Mineralogie und Geologie*, Stuttgart, **60** (B): 1–112, pls 1–5.

—— 1937. Ordovician and Silurian faunas from Arctic Canada. *In: Report of the 5th Thule Expedition 1921–1924*, **1** (5): 1–169, 24 pls. Copenhagen.

Temple, J. T. 1970. The Lower Llandovery brachiopods and trilobites from Ffridd Mathrafal, near Meifod, Mongomeryshire. *Palaeontographical Society Monograph*, London: 1–76, pls 1–19.

—— 1987. Early Llandovery brachiopods of Wales. *Palaeontographical Society Monograph*, London: 1–137, pls 1–15.

Tsegelnyk, P. D. 1976. *Brachiopods and stratigraphy of the Lower Palaeozoic of Bolino-Podolii*. 156 pp., 12 pls. Kiev.

Twenhofel, W. H. 1928. Geology of Anticosti Island. *Geological Survey of Canada Memoir*, Ottawa, **154**: 1–481, pls 1–60.

Ulrich, E. O. 1879. Descriptions of new genera and species of fossils from the Lower Silurian about Cincinnati. *The Journal of the Cincinnati Society of Natural History*, **2**: 8–30, pl. 7.

—— **& Cooper, G. A.** 1936. New genera and species of Ozarkian and Canadian brachiopods. *Journal of Paleontology*, Tulsa, **10**: 616–631.

—— —— 1938. Ozarkian and Canadian Brachiopoda. *Geological Society of America Special Paper*, New York, **13**: 1–323, pls 1–58.

—— —— 1942. New genera of Ordovician brachiopods. *Journal of Paleontology*, Tulsa, **16**: 620–626, pl. 90.

Villas, E. 1985. Braquiopodos del Ordovicico medio y superior de las Cadenas ibericas orientales. *Memorias del Museo Paleontologico de la Universidad de Zaragoza*, **1**: 1–223, pls 1–34.

Vinassa, P. de R. 1927. Fossili Ordoviciani sardi. *Memoria Royale Accademia Lincei*, Rome, (6) **2** (16): 437–496.

Volk, M. 1939. *Sowerbyella* im Mitteldevon Thüringens. *Senckenbergiana*, Frankfurt, **21**: 386–389.

Wahlenberg, G. 1818. Petrificata Telluris Suecanae examinata. *Nova Acta Regiae Societatis Scientiarum Upsaliensis*, (for 1821) **8**: 1–116, pls 1–7.

Wang Zhen-quan 1982. Brachiopods. *In: The Silurian Stratigraphy and Paleontology in Guanyinqiao, Qijiang, Sichuan*: 41–43, pls 10–13. Chengdu.

Wang Shu-min & Yan Guo-shun 1978. Ordovician brachiopods. *In: Sinian to Permian stratigraphy and palaeontology in the eastern Yangtze Gorges*: 210–228, pls 52–62. Beijing.

Wang Yu 1949. Maquoketa Brachiopoda of Iowa. *Geological Society of America Memoir*, New York, **42**: 1–55, pls 1–12.

Whittington, H. B. 1938. New Caradocian brachiopods from the Berwyn Hills, North Wales. *Annals and Magazine of Natural History*, London, (11) **2**: 241–259, pls 10, 11.

—— **& Williams, A.** 1955. The fauna of the Derfel Limestone of the Arenig District, North Wales. *Philosophical Transactions of the Royal Society*, London, (B) **238**: 397–430, pls 38–40.

Willard, B. 1928. The brachiopods of the Ottosee and Holston Formations of Tennessee and Virginia. *Bulletin of the Museum of Comparative Zoology*, Harvard, **68**: 255–292, pls 1–3.

Williams, A. 1949. New Lower Ordovician brachiopods from the Llandeilo–Llangadock District. Part II. *Geological Magazine*, London, **86**: 226–238, pl. 11.

—— 1953. The classification of the strophomenoid brachiopods. *Journal of the Washington Academy of Sciences*, **43**: 1–13.

—— 1962. The Barr and Lower Ardmillan Series (Caradoc) of the Girvan District, south-west Ayrshire, with descriptions of the Brachiopoda. *Geological Society of London Memoir*, **3**: 1–267, pls 1–25.

—— 1963. The Caradocian brachiopod faunas of the Bala District, Merionethshire. *Bulletin of the British Museum (Natural History)*, London, (Geology) **8**: 327–471, pls 1–16.

—— 1965. Plectambonitacea. *In*: Williams, A. *et al.*, *Treatise on Invertebrate Paleontology*, **H.** Brachiopoda. 927 pp. Lawrence.

—— 1974. Ordovician Brachiopoda from the Shelve District, Shropshire. *Bulletin of the British Museum (Natural History)*, London, (Geology) Supplement **11**: 1–163, pls 1–28.

—— **& Curry, G. B.** 1985. Lower Ordovician Brachiopoda from the Tourmakeady Limestone, County Mayo, Ireland. *Bulletin of the British Museum (Natural History)*, London, (Geology) **38**: 183–269.

Wilson, A. E. 1926. An Upper Ordovician fauna from the Rocky Mountains, British Columbia. *Geological Survey of Canada Department of Mines and Resources Bulletin*, Ottawa, **44**: 1–34, pls 1–5.

—— 1932. Ordovician fossils from the region of Cornwall, Ontario. *Transactions of the Royal Society of Canada*, Ottawa, **26**: 373–404, pls 1–6.

—— 1946. Brachiopoda of the Ottawa Formation of the Ottawa–St Lawrence Lowland. *Canadian Department of Mines Geological Survey Bulletin*, Ottawa, **8**: 1–149, pls 1–11.

Winchell, N. H. & Schuchert, C. 1892. Preliminary descriptions of new Brachiopoda from Trenton and Hudson River Groups of Minnesota. *American Geologist*, Minneapolis, **9**: 284–294.

Wolburg, J. 1933. Das Devon im Gebiet der oberen Lenne. *Abhandlungen der Preussischen Geologischen Landesantalt*, Berlin, **151**: 1–70, pls 1–3.

Xia Dong-diqu Zendan Ji Zhierdie Ji Diceng Xue-li[1] 1978. *Sinian to Permian stratigraphy and Palaeontology in the Yangste Gorge area*: 1–381, pls 1–116. Beijing.

Xian Si-yuan & Jiang Zong-long 1978. Phylum Brachiopoda. *In: Palaeontological Atlas of southwest China, Guizhou Volume 1. Cambrian to Devonian*: 251–337, pls 94–128. Beijing.

Xu Han-kui 1979. Brachiopods from the Tangxiang Formation (Devonian) in Nandan of Guangxi. *Acta Palaeontologica Sinica*, Beijing, **18**: 362–382, pls 1–4.

—— **& Liu Di-yong** 1984. Late early Ordovician brachiopods of southwestern China. *Bulletin Nanjing Institute of Geology and Palaeontology, Academia Sinica*, **8**: 147–235, pls 1–18.

——, **Rong Jia-yu & Liu Di-yong** 1974. Ordovician Brachiopods. *In:* Nanjing Institute of Geology and Palaeontology, Academia Sinica (ed.), *Handbook of Stratigraphy and Palaeontology in southwest China*: 144–154, pls 64–66. Beijing.

—— **& Su Yi-bao** 1979. Middle Ordovician brachiopods from Yaxian, Hainan Island. *In: Conference on iron mine geology in China. Selected papers on stratigraphy and paleontology*: 101–116. Beijing.

Yadrenkina, A. C. 1965. New species of brachiopods from Upper Cambrian and Ordovician deposits of north west Siberian platform. *Trudy̆ Sibirskogo Nauchno-issledovatel'skogo Instituta Geologii, Geofiziki i mineral'nogo Sy̆r'ya*, Leningrad, **34**: 6–21, pls 1, 2.

Yang Xue-chang & Rong Jia-yu 1982. Brachiopods from the Upper Xiushan Formation (Silurian) in the Sichuan–Guizhou–Hunan–Hubei border region. *Acta Palaeontologia Sinica*, Beijing, **21**: 417–434, pls 1–3.

Yin, T. H. (Yin Zan-Xun) 1937. Brief description of the Ordovician and Silurian fossils from Shihtien. *Bulletin of the Geological Society of China*, Peking, **16**: 281–302, pls 1, 2.

Young, T. P. & Gibbons, M. 1983. *Chonetoidea* (Brachiopoda) from the Pusgillian (Upper Ordovician) of Cautley. *The Sheffield University Geological Society Journal*, **8** (2): 95–104, pl. 1.

Zeng Qing-luan 1977. Phylum Brachiopoda. *In:* Hubei Institute of Geological Sciences and others (ed.), *Palaeontological Atlas of Central-South Region. Early Palaeozoic section*: 27–69, pls 10–23. Beijing.

Zhang Zi-xin 1981. Brachiopods. *In: Atlas of fossils of Xinjiang Province 1. Upper Proterozoic–Lower Palaeozoic*: 75–106, pls 38–45. Beijing.

[1] This title means 'Geological Bureau of Hubei Province' – no authors were named in it.

INDEX

Names in Roman type are current, those in italics are obsolete. Qualifications, such as aff., cf. and var. are omitted.

Bulletin of the British Museum (Natural History)

Geology Series

Most earlier Geology *Bulletins* are still in print. A full list of available titles can be obtained from Publication Sales (address inside front cover).

Vol. 36 No. 1 Middle Cambrian trilobites from the Sosink Formation, Derik–Mardin district, south-eastern Turkey. W. T. Dean. 1982. Pp. 1–41, 68 figs. £5.80

Vol. 36 No. 2 Miscellanea: Dinantian terebratulids—New microfossils—*Neseuretus*—*Archaeocidaris whatleyensis*—Carboniferous dasyclad—*Nanjinoporella*—Toarcian bryozoans—Drybrook Sandstone plants—British fossil bintoniellids—*Uraloporella*. 1982. Pp. 43–155. £19.80

Vol. 36 No. 3 The Ordovician Graptolites of Spitsbergen. R. A. Cooper & R. A. Fortey. 1982. Pp. 157–302, 6 plates, 83 figs, 2 tables. £20.50

Vol. 36 No. 4 Campanian and Maastrichtian sphenodiscid ammonites from southern Nigeria. P. M. P. Zaborski. 1982. Pp. 303–332, 36 figs. £4.00

Vol. 37 No. 1 Taxonomy of the arthrodire *Phlyctaenius* from the Lower or Middle Devonian of Campbellton, New Brunswick, Canada. V. T. Young. 1983. Pp. 1–35, 18 figs. £5.00

Vol. 37 No. 2 *Ailsacrinus* gen. nov., an aberrant millericrinid from the Middle Jurassic of Britain. P. D. Taylor. 1983. Pp. 37–77, 48 figs, 1 table. £5.90

Vol. 37 No. 3 Miscellanea: Permian *Glossopteris* in Turkey—Wealden *Theriosuchus*—Wealden conifer—Permian plants of Saudi Arabia—Carboniferous Edrioasteroidea—British cicadas—Dittonian cephalaspids. 1983. Pp. 79–171. £13.50

Vol. 37 No. 4 The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. B. G. Gardiner. 1984. Pp. 173–428, 145 figs, 4 plates. 0 565 00967 2. £39.00

Vol. 38 No. 1 New tertiary pycnodonts from the Tilemsi valley, Republic of Mali. A. E. Longbottom. 1984. Pp. 1–26, 29 figs, 3 tables. 0 565 07000 2. £3.90

Vol. 38 No. 2 Silicified brachiopods from the Viséan of County Fermanagh, Ireland. (III) Rhynchonellids, Spiriferids and Terebratulids. C. H. C. Brunton. 1984. Pp 27–130, 213 figs. 0 565 07001 0. £16.20

Vol. 38 No. 3 The Llandovery Series of the Type Area. L. R. M. Cocks, N. H. Woodcock, R. B. Rickards, J. T. Temple & P. D. Lane. 1984. Pp. 131–182, 70 figs. 0 565 07004 5. £7.80

Vol. 38 No. 4 Lower Ordovician Brachiopoda from the Tourmakeady Limestone, Co. Mayo, Ireland. A. Williams & G. B. Curry. 1985. Pp. 183–269, 214 figs. 0 565 07003 7. £14.50

Vol. 38 No. 5 Miscellanea: Productacean growth and shell shape—Jurassic alga *Palaeosiphonium*—Upper Ordovician brachiopods and trilobites—Lower Devonian Osteostraci from Podolia—*Hipparion* from Diavata—Preparation and study of Singa skull—Carboniferous and Permian bryozoa—Lower Eocene trionychid—Montsech fossil insects. 1985. Pp. 271–412. 0 565 07004 5. £24.00

Vol. 39 No. 1 Upper Cretaceous ammonites from the Calabar region, south-east Nigeria. P. M. P. Zaborski. 1985. Pp. 1–72, 66 figs. 0 565 07006 1. £11.00

Vol. 39 No. 2 Cenomanian and Turonian ammonites from the Novo Redondo area, Angola. M. K. Howarth. 1985. Pp. 73–105. 33 figs. 0 565 07006 1. £5.60

Vol. 39 No. 3 The systematics and palaeogeography of the Lower Jurassic insects of Dorset, England. P. E. S. Whalley. 1985. Pp. 107–189, 87 figs, 2 tables. 0 565 07008 8. £14.00

Vol. 39 No. 4 Mammals from the Bartonian (middle/late Eocene) of the Hampshire Basin, southern England. J. J. Hooker, 1986. Pp. 191–478, 71 figs, 39 tables. 0 565 07009 6. £49.50

Vol. 40 No. 1 The Ordovician graptolites of the Shelve District, Shropshire. I. Strachan. 1986. Pp. 1–58, 38 figs. 0 565 07010 X. £9.00

Vol. 40 No. 2 The Cretaceous echinoid *Boletechinus*, with notes on the phylogeny of the Glyphocyphidae and Temnopleuridae. D. N. Lewis. 1986. Pp. 59–90, 11 figs, 7 tables. 0 565 07011 8. £5.60

Vol. 40 No. 3 The trilobite fauna of the Raheen Formation (upper Caradoc), Co. Waterford, Ireland. A. W. Owen, R. P. Tripp & S. F. Morris. 1986. Pp. 91–122, 88 figs. 0 565 07012 6. £5.60

Vol. 40 No. 4 Miscellanea I: Lower Turonian cirripede—Indian coleoid *Naefia*—Cretaceous–Recent Craniidae—Lectotypes of Girvan trilobites—Brachiopods from Provence—Lower Cretaceous cheilostomes. 1986. Pp. 125–222. 0 565 07013 4. £19.00

Vol. 40 No. 5 Miscellanea II: New material of *Kimmerosaurus*—Edgehills Sandstone plants—Lithogeochemistry of Mendip rocks—Specimens previously recorded as teuthids—Carboniferous lycopsid *Anabathra*—*Meyenodendron*, new Alaskian lepidodendrid. 1986. Pp. 225–297. 0 565 07014 2. £13.00

Vol. 41 No. 1 The Downtonian ostracoderm *Sclerodus* Agassiz (Osteostraci: Tremataspididae), P. L. Forey. 1987. Pp. 1–30. 11 figs. 0 565 07015 0. £5.50

Vol. 41 No. 2 Lower Turonian (Cretaceous) ammonites from south-east Nigeria. P. M. P. Zaborski. 1987. Pp. 31–66. 46 figs. 0 565 07016 9. £6.50

Vol. 41 No. 3 The Arenig Series in South Wales: Stratigraphy and Palaeontology. I. The Arenig Series in South Wales. R. A. Fortey & R. M. Owens. II. Appendix. Acritarchs and Chitinozoa from the Arenig Series of South-west Wales. S. G. Molyneux. 1987. Pp. 67–364. 289 figs. 0 565 07017 7. £59.00

Vol. 41 No. 4 Miocene geology and palaeontology of Ad Dabtiyah, Saudi Arabia. Compiled by P. J. Whybrow. 1987. Pp. 365–457, 54 figs. 0 565 07019 3. £18.00

Vol. 42 Cenomanian and Lower Turonian Echinoderms from Wilmington, south-east Devon. A. B. Smith, C. R. C. Paul, A. S. Gale & S. K. Donovan. 1988. 244 pp., 80 figs, 50 pls. 0 565 07018 5. £46.50

Vol. 43 A Global Analysis of the Ordovician–Silurian boundary. Edited by L. R. M. Cocks & R. B. Rickards. 1988. 394 pp., figs. 0565 07020 7. £70.00

Vol. 44 No. 1 Miscellanea: Palaeocene wood from Mali—Chapelcorner fish bed—*Heterotheca* coprolites—Mesozoic Neuroptera and Raphidioptera. 1988. Pp. 1–63. 0 565 07021 5. £12.00

Vol. 44 No. 2 Cenomanian brachiopods from the Lower Chalk of Britain and northern Europe. E. F. Owen. 1988. Pp. 65–175. 0 565 07022 3. £21.00

Vol. 44 No. 3 The ammonite zonal sequence and ammonite taxonomy in the *Douvilleiceras mammillatum* Superzone (Lower Albian) in Europe. H. G. Owen. 1988. Pp. 177–231. 0 565 07023 1. £10.30

Vol. 44 No. 4 Cassiopidae (Cretaceous Mesogastropoda): taxonomy and ecology. R. J. Cleevely & N. J. Morris. 1988. Pp. 233–291. 0 565 07024 X. £11.00

CONTENTS

Bulletin British Museum (Natural History)
GEOLOGY SERIES
Vol. 45, No. 1, July 1989

Bulletin British Museum (Natural History)

Geology Series

A review of the Tertiary non-marine molluscan faunas of the Pebasian and other inland basins of north-western South America

VOLUME 45 NUMBER 2 29 MARCH 1990

The *Bulletin of the British Museum (Natural History)*, instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

Papers in the *Bulletin* are primarily the results of research carried out on the unique and ever-growing collections of the Museum, both by the scientific staff and by specialists from elsewhere who make use of the Museum's resources. Many of the papers are works of reference that will remain indispensable for years to come.

A volume contains about 400 pages, made up by two numbers: published Spring and Autumn. Subscriptions may be placed for one or more of the series on an Annual basis. Individual numbers and back numbers can be purchased and a Bulletin catalogue, by series, is available. Orders and enquiries should be sent to:

Sales Department,
Natural History Museum Publications,
British Museum (Natural History),
Cromwell Road,
London SW7 5BD

Telephone: 01-938 9386
Telex: 929437 NH PUBS G
Fax: 01-938 8709

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Geol.)

ISBN 0 565 07026 6
ISSN 0007–1471

Geology Series
Vol 45 No 2 pp 165–372

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 29 March 1990

Bull. Br. Mus. nat. Hist. (Geol.) **45** (2) 165–371

Issued 29 March 1990

A review of the Tertiary non-marine molluscan faunas of the Pebasian and other inland basins of north-western South America

C. P. NUTTALL

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

CONTENTS

Synopsis. Non-marine Tertiary molluscan faunas of Colombia, Ecuador and the 'Pebasian' of the Upper Amazon Basin of eastern Peru and adjoining parts of Brazil are reviewed, and compared with the living fauna of South America. New Colombian fossil faunas from La Tagua, on Rio Caqueta, and Puerto Nariño, on Rio Marañón, are described: the latter is Pebasian. The new La Tagua fauna provides a valuable link, permitting correlation between the Santa Teresa (San Juan de Rio Seco of Anderson, 1928), La Cira (both Magdalena Valley) and Pebasian faunas.

All are thought to be Miocene: the Pebasian, the only one in which living species (of Hemisininae and *Mytilopsis*) occur, may be the youngest. Some faunas, mainly from the Rio Jurua region of Brazil, strongly resemble those of the present day and are considered to be post-Pebasian. The Mugrosa fauna (Magdalena Valley), now reduced to two species one of which occurs in the La Cira, is, if not Miocene, unlikely to be much older. The earliest Magdalena Valley fauna is the Los Corros, which may be late Eocene or early Oligocene and has very little in common with the overlying Mugrosa and La Cira. Faunas from the intermontane basins of Ecuador, including the rich Loyola and Mangán of Cuenca Basin, are accepted as Miocene, following Bristow & Parodiz (1982).

Modifications are proposed to the hypothesis of Kätzer (1903), who suggested that during the Tertiary the Upper Amazon area was occupied by an inland sedimentary basin connected to the sea by the Marañón Portal lying to the south of the Bay of Guayaquil. Evidence is presented that during the mid-Tertiary a brackish water connection existed between the Upper Amazon Valley and the Caribbean by a north–south trough, lying parallel to the still rising Andes and occupied by a continually shifting pattern of streams, swamps and lakes of varying salinity. Similarities between the La Cira and Santa Teresa faunas of the Magdalena Valley and those of La Tagua demonstrate that they were all deposited before the Andean orogeny at the close of the Miocene raised the Cordillera Oriental to form a mountain barrier impenetrable to aquatic molluscs between the Magdalena and Upper Amazon Valleys. There is also some palaeontological evidence for fresh (not brackish) water connections from the Pebasian Basin, running eastwards down the present Amazon Valley between the Guiana and Brazilian Shields and southwards towards the estuary of Rio de la Plata.

Taxonomic conclusions include the following. *Eubora, Tropidobora* and *Toxosoma* are now assigned to the Lithoglyphinae (Rissoacea, Hydrobiidae). *Nanivitrea* is the first representative of the Cochliopinae (Hydrobiidae) to be recognized fossil in South America. Vitrinellidae (Rissoacea) are recognized in the Pebasian, the first known non-marine occurrence of the family. At least one species is thought to be lecithotrophic, the first record of this mode of development in the family. The Mutelacea are distinguished from the Unionacea by their coarser prismatic shell layer. *Ostomya*, which may share common ancestry with *Guianadesma*, is redescribed and transferred from the Lyonsiidae to the Corbulidae.

The following new taxa are described. Gastropoda: Rissoacea, Hydrobiidae, *Dyris hauxwelli, D. semituberculata, Liris acicularis* (Littoridininae); *Nanivitrea colombiana* (Cochliopinae); Vitrinellidae, *Vitrinella (Vitrinellops) hauxwelli, V. (V.) degrevei*; Cerithiacea, Thiaridae, *Sheppardiconcha lataguensis, Longiverena colombiana* and *Verena lataguensis*. Bivalvia, Corbulidae, *Pachydon ovalis, P. trigonalis* and the genus *Pebasia* (type species *Pachydon dispar* Conrad), which probably shares common ancestry with *Pachydon*.

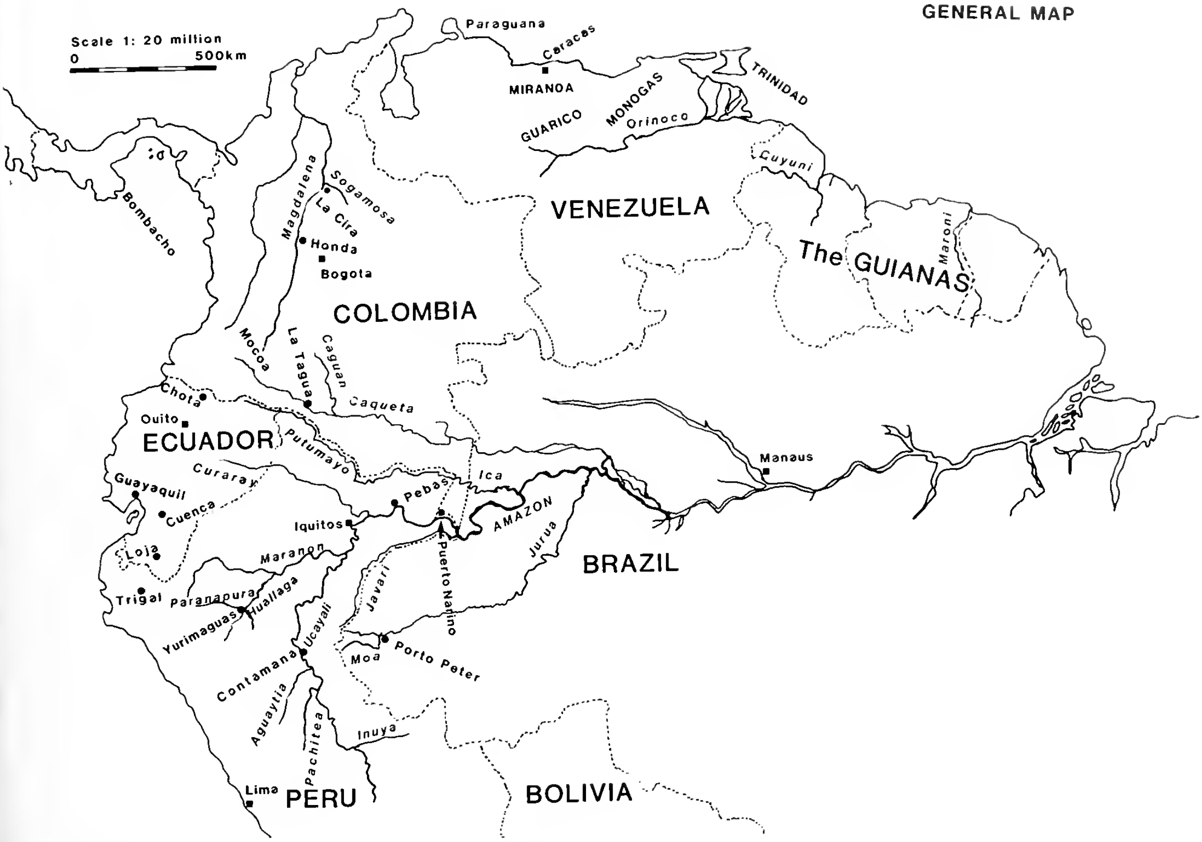
Lectotypes of the following nominal species are selected. Gastropods: *Aylacostoma tuberculata* Spix, 1827; *Cerithium coronatum* Etheridge, 1879; *Dyris gracilis* Conrad, 1871; *Hemisinus behni* Reeve, 1860; *H. eucosmius* Pilsbry & Olsson, 1935; *H. hopkinsi* P. & O., 1935; *H. lapazanus* P. & O., 1935; *H. obesus* Reeve, 1860; *H. olivaceus* Reeve, 1860; *H. pulcher* Reeve, 1860; *H. punctatus* Reeve, 1860; *H. tenellus* Reeve, 1860; *H. tenuilabris* Reeve, 1860; *H. zebra* Reeve, 1860; *H. (Verena) avus* Pilsbry & Olsson 1935; *H. (V.) laevicarinata* P. & O., 1935; *Liris laqueata* Conrad, 1871; *Melania bicarinata* Etheridge, 1879; *M. nicotiana* Reeve, 1860; *M. scalarioiodes* Etheridge, 1879; *M. venezuelensis* Reeve, 1859; *Neretina puncta* Etheridge, 1879; *N. ziczac* Etheridge, 1879; *Strombus lineolatus* Wood, 1828; *Turbonilla minuscula* Gabb, 1869. Bivalves: *Anisothyris (Pachydon) tumida* Etheridge, 1879; *Corbula abundans* Pilsbry & Olsson, 1935; *C. canamaensis* Etheridge, 1879; *C. hettneri* Anderson, 1928; *C. magdalensis* Pilsbry & Olsson, 1935; *Dreissensia dalli* Clerc, *in* Joukowsky & Clerc 1906; *Pachydon cuneatus* Conrad, 1871; *P. dispar* Conrad, 1874.

INTRODUCTION

This work is a partial revision of the Tertiary non-marine molluscan faunas of the north-western quadrant of South America, bounded approximately by 10° S and 60° W. It is concerned with their systematic descriptions, and also their stratigraphical and palaeogeographical implications. When considering these latter aspects, it must be borne in mind that these non-marine fossiliferous horizons seldom exceed ten metres in thickness, but occur in basins where as much as 10,000 m of sediment have accumulated during the Tertiary (Campbell & Bürgl 1965: 581). Much of this thickness may have been deposited very rapidly following uplift during mountain-building phases, whilst the fossiliferous bands may represent comparatively quiet periods, with slow deposition of lake and other fresh-water sediments. Nevertheless, it is more than likely that the non-marine molluscan fossil record accounts for only a tiny percentage of Tertiary time. In addition, the various periods of mountain-building will have greatly changed the geography of the region since the fossiliferous sequences were deposited. At the present day, in the Amazon Valley such beds lie at well under 300 m above sea level, whilst at the other extreme, the not necessarily contemporaneous deposits of the intermontane basins of Ecuador (Cuenca etc.) lie at altitudes of between 2,500 and 3,500 m. Furthermore, uplift has caused relative vertical movements of approximately 8,000 m in the base of the Tertiary in the Eastern Cordillera of the Colombian Andes (Campbell & Bürgl 1965: 567).

The study was primarily concerned with newly collected faunas from La Tagua on the Rio Caqueta, Colombia, and their relationship with similar, but by no means identical, faunas from some 500 km further south in the Pebasian Basin of the Upper Amazon in Peru. It does not deal in any detail with taxa which are unimportant in these faunas: thus the Corbiculacea are omitted and the Naiades (Unionacea and Mutelacea) are treated comparatively briefly. The other faunas upon which the work concentrates are from the Magdalena Valley in Colombia and those from the intermontane basins of Ecuador. In addition, a search has been made of both Tertiary and Recent faunas, in particular of Central America and the Caribbean as well as the remainder of South America, for comparable taxa.

Some of the allegedly Palaeogene faunas, described



ig. 1 General Map of northern South America to show principal rivers and most places referred to in the text. See also Figs 4 (p. 172), 443 and 444 (p. 323).

Anderson 1928, Pilsbry & Olsson 1935) from the Magdalena Valley of Colombia, have proved younger than originally hought, and have species in common with the new faunas rom about 500 km further south in the La Tagua region of Colombia, which is now part of the present-day Amazon Valley system. The implication is that these faunas must redate the late Miocene Andean orogeny which raised the Cordillera Oriental now separating the Magdalena Valley rom the Upper Amazon Valley of eastern Peru as well as rom the Oriente of Ecuador.

The first work dealing with the Amazon Basin Tertiary molluscan faunas was that of Gabb (1869), who described a mall fresh- or brackish-water fauna from Pebas on Rio Marañón in eastern Peru. Now known as Pebasian faunas, hese proved to be both rich and unusual and were the subject f several papers, mostly written in the 1870s. They have also n the past been termed Iquitosian (Steinmann 1930, unseen; ee p. 357), after the particularly rich fauna of Iquitos. In the resent work, the term **Pebasian** is used to describe the faunas f the Pebas district, as well as the age of the deposits in which they occur and the basin in which these deposits are ound. The fauna of Pebas itself is comparatively poorly nown and the exposures there were apparently last examined y Bassler, *c.*1925; his collection was discussed briefly by Villard (1966). Measurements of the sections at Pebas were iven by Hartt (1872); details in later papers by other authors re always based on his figures. In these circumstances, the resent paper hardly seems to be an appropriate place in which to propose the use of the term 'Pebasian' in a formal sense. It is not, therefore, here recognized as being an established Stage. Costa (1980: 870) introduced the term 'Formação Pebas' informally, followed (1981: 635) by a formal description of the Formation.

Brazilian geologists responsible for the *Projeto Radambrasil* volumes (e.g. del'Arco 1977) have referred the Pebasian faunas to the Solimões Formation. However, their maps show large tracts of Tertiary deposits, stretching as far east as Manaus, as belonging to this formation, and they have also referred to it other faunas, both of vertebrates and of molluscs, more resembling those of the present-day Amazon Valley but having almost nothing in common with those of the Pebasian. The differing opinions held by various authors as to the age of the Pebasian are summarized in the well-illustrated monograph of de Greve (1938: 123), and range from Palaeogene to Pliocene. In recent years, they are generally accepted as probably Pliocene, but in the present study it is recognized that they could well be Miocene. The non-marine molluscan faunas of the Pebasian have been described in several other papers (Woodward 1871, Conrad 1871*b*, 1874a, *b*, Boettger 1878, Etheridge 1879, Roxo 1924). More recent works (Santos & Castro 1967, Costa 1980, 1981, Kadolsky 1980) have been mainly of a revisory nature.

The Pebasian faunas are markedly different from those of the present day (Baker 1914, Haas 1949*a*, *b*, 1950, 1952, 1955), suggesting very different facies. The 'fresh-water mussels', Unionacea and Mutelacea, and river snails of the

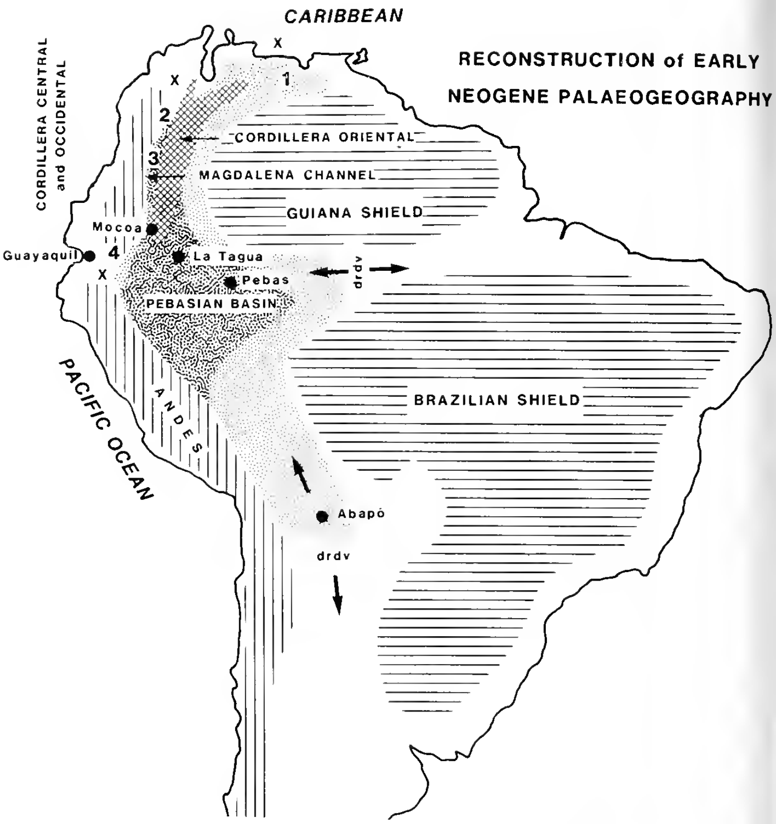


Fig. 2 Reconstruction of early Neogene palaeogeography (See also Fig. 453, p. 351). Key: horizontal lines, ancient massifs; vertical lines, Andes mountains (except for cross-hatched, Cordillera Oriental of Colombian Andes); light stipple, maximum extent of possible brackish water basin; heavy stipple, areas where there is some fossil evidence for the existence of a brackish-water basin; drdv, drainage divides; arrows, direction of river flow; X, possible connections between brackish water basin and sea.
Numbers indicate general areas from which other non-marine faunas have been described. 1, northern Venezuela (Palmer 1945; Rutsch 1952; Macsotay 1968); 2, Middle Magdalena Valley (Pilsbry & Olsson 1935); 3, Upper Magdalena Valley (Porta 1966); 4, Cuenca and other intermontane basins of Ecuador (Bristow & Parodiz 1982). *Pachydon* possibly occurred as far south as the Abapó region of Bolivia (p. 344).
South America is shown as an island, predating the formation of the Panama land bridge in the late Neogene. The Cordillera Oriental was raised during Middle and Late Miocene orogenies, and prior to this there would have been no barrier between the Magdalena and Amazon Valleys. During the rise of the Cordillera Oriental, the Magdalena is presumed to have formed a north–south channel whose southern end was eventually closed in the Mocoa region.

Thiaridae are often surprisingly uncommon, whilst all records of the Pleuroceridae appear to be based on misidentifications of Thiaridae. As expected, Hydrobiidae are common, but the genera present in the Pebasian are largely endemic. Among the most striking features of the Pebasian is the presence of the families Neritidae, Corbulidae and Dreissenidae which are now absent from the region and tend to be indicative of at least brackish if not marginal marine conditions. Perhaps the most surprising occurrence is that of Vitrinellidae (Rissoacea), a family with an otherwise entirely marine distribution. The presence of this Pebasian molluscan assemblage in the Upper Amazon Basin has important implications when the palaeogeography of the continent is considered.

One of the features of the present-day topography is the broad strip of comparatively low-lying terrain stretching from the Caribbean to the estuary of the Rio de la Plata, with the Andes lying along its western margin and the Guiana and Brazilian shields to the east. The evidence from both the fossil and Recent distribution patterns of the molluscs points to a connection northward from the Amazon region to the Caribbean during the Tertiary; the presence of identical species in the La Tagua and Magdalena Valley fossil faunas suggest a direct connection between the two areas. From this it follows that they predate the Late Miocene orogeny that raised the Cordillera Oriental of the Colombian Andes, creating a barrier to aquatic molluscs. The fossil faunas of Argentina do not suggest a similar marine to brackish connection from the Upper Amazon to Rio de la Plata. However, some fresh-water Hydrobiidae (Subfamily Lithoglyphinae) now living in the La Plata region appear to be the closest relatives, either fossil or Recent, of the more unusual Pebasian members of the family. No acceptable evidence has been found of a marine east/west migration route during the Tertiary along the course of the present-day Amazon, even though this idea has been recently resurrected by Sheppard & Bate (1980), who described ostracod faunas from the Pebasian and the La Tagua Beds. The possibility of a connection with the Pacific through the so-called Marañón Portal, lying in the Ecuadorian–Peruvian boundary region, was first postulated by Kätzer (1903) and has been espoused by several subsequent authors. Its existence is accepted herein as being likely, but none of the available evidence invalidates the argument in favour of an additional connection northward to the Caribbean.

The present study stemmed from an enquiry for the identification of Tertiary non-marine molluscan fossils found at the completely new Colombian localities at La Tagua, on Rio Caqueta, where it crosses the Equator. The material was collected by the Colombian Amazonas Expedition (CAE), and submitted in 1978 by Michael J. Eden, a geographer of London University. In 1979, Eden forwarded more material collected by Mr Nout Weeda (also CAE), from a different locality near La Tagua which yielded better-preserved material, and from another entirely new locality, Puerto Nariño on the Colombian Amazon, which contained a slightly unusual Pebasian fauna. See p. 172.

The Palaeontology Department of the British Museum (Natural History) (BMPD) already possessed two collections of Pebasian fossils from the Upper Amazon region of Peru. That from Canamá was collected by Brown, who gave an account of the geology (1879). The small fauna was described by Etheridge (1879): unfortunately, much of the material is lost, having apparently never reached the Museum. The other

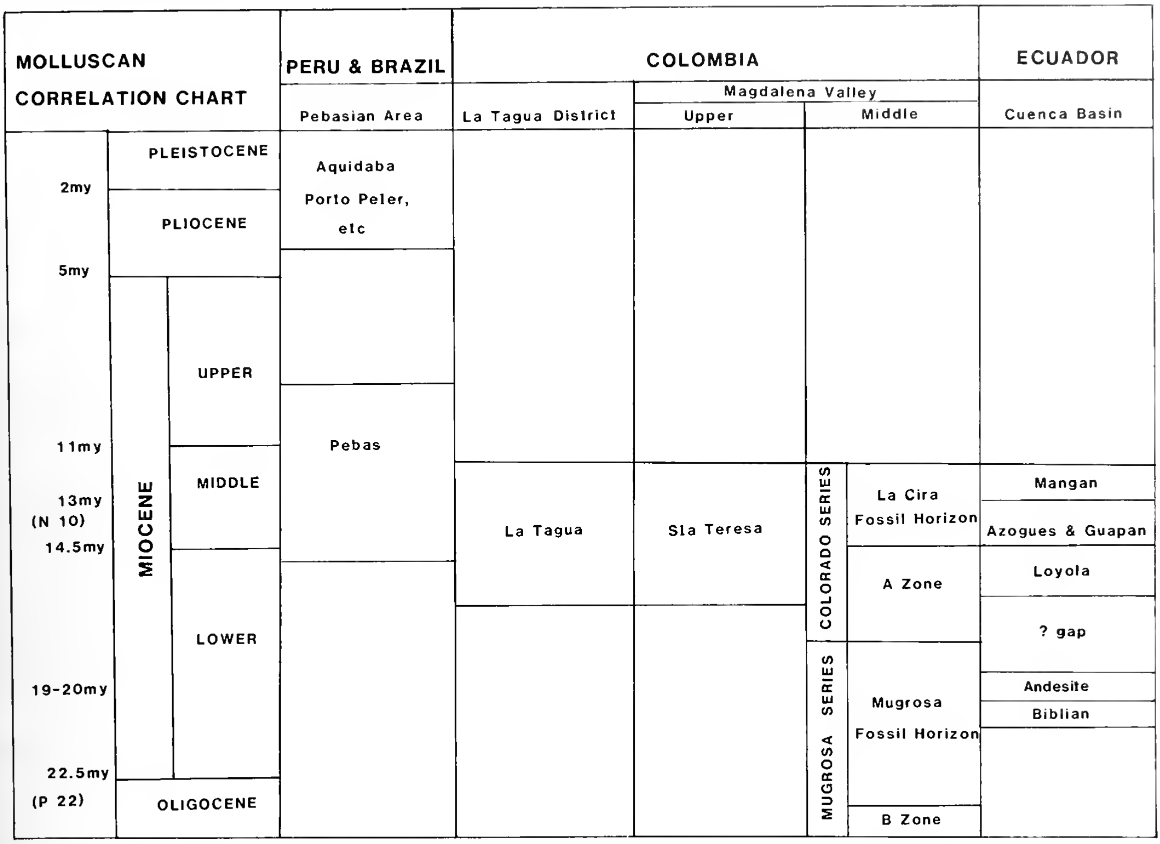


Fig. 3 Stratigraphical table, summarizing the molluscan evidence for the ages of the principal faunas discussed in this paper. It attempts to equate them with evidence from other sources (other macrofossils and microfossils, and radioactive dating of the andesite underlying the Loyola Formation of the Cuenca Basin). The principal molluscan faunas are also shown as being older than the Andean orogeny at the close of the Miocene. Note that the Mugrosa faunas of the Middle Magdalena Valley, Colombia, are shown as Lower Miocene, whilst rather indirect palynological evidence (Fig. 443, p. 323) suggests they might be Oligocene.

collection is much larger, consisting of well over a thousand specimens. It has been considerably enhanced in the course of the present study by the extraction of numerous small specimens from its rock matrix. It was made in about 1870, mainly from Pichana, but partly from Pebas itself, by a naturalist, Juan Hauxwell, who was said to have spent some thirty years exploring in the Amazon area. This collection was the subject of a paper by Woodward (1871) whilst Conrad, working in Philadelphia, was almost simultaneously (1871*a*, *b*) describing another large sample of Hauxwell's material. Most of the new species were described in Conrad's second paper: his nomenclature was followed by Woodward, who was clearly aware of Conrad's work.

In 1969 Parodiz reviewed the Tertiary non-marine faunas of South America: from the entire continent, a total of 137 species were dealt with. Parodiz never claimed that this work was comprehensive, and among several omissions are most of the brackish-water genera which occur in the Pebasian. More recently, Bristow & Parodiz (1982) have provided an account of the stratigraphy and a revision of the molluscan palaeontology of the Tertiary intermontane basins of Ecuador. Their material is divided between the Carnegie Museum, Pittsburgh and the BMNH (BMPD). Further revision herein shows that the faunal links suggested by Parodiz between these Ecuadorian faunas and those of the Pebasian are largely illusory.

The majority of the genera present in all these fossil faunas have living type species. The living South American freshwater molluscan fauna is, not surprisingly, comparatively unknown. The collections in the Zoology Department of the British Museum (Natural History) (BMZD) consist mainly of samples of type and figured specimens, dating from the nineteenth century. The general collection of comparative material is also somewhat inadequate, being both small and with, for the most part, imprecise locality data. In consequence, it has been difficult to investigate either variation within species or possible synonymies. Information on both the geographical ranges and habitats of species has had to be gleaned mostly from the literature, which is largely far from modern.

COLLECTIONS STUDIED AND ABBREVIATIONS

Collections studied

The list below gives the abbreviations used throughout the text for the institutions housing the collections studied.

ANSP Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A.;

BMPD	Palaeontology Department, British Museum (Natural History);
BMZD	Zoology Department, British Museum (Natural History);
CAS	California Academy of Sciences, San Francisco, California, U.S.A.
NYSM	New York State Museum, Albany, New York State, U.S.A.;
PRI	Paleontological Research Institute, Ithaca, New York State, U.S.A.;
PIMUZ	Paläontologische Institut und Muzeum der Universität Zurich, CH-8006, Switzerland;
USNM	United States National Museum, Washington, DC, U.S.A.

Other material has been borrowed from: Naturhistorisches Museum, Basel, Switzerland; Muséum d'Histoire Naturelle, Genève, Switzerland; Zoologisches Staatsammlung, München, West Germany; and The Zoological Museum, University of Michigan, Ann Arbour, Michigan, U.S.A.

Abbreviations, etc.

The following abbreviations for dimensions are used:

br,	breadth
brap,	breadth of aperture
d,	diameter (instead of br for planorbiform gastropods)
diag,	diagonal
e,	estimated
h,	height
hap,	height of aperture
hbw,	height of body whorl
l,	length
lv,	left valve
rv,	right valve
sv,	single valve
vbr,	valve breadth (for single, disassociated valves of bivalves)
w,	width.

The spire angle (sa) of gastropods is measured across the periphery of the last whorl unless stated to the contrary.

Synonymies are constructed along the lines suggested by Matthews (1973). In all faunal lists, new taxa described therein are indicated by capital letters, and original material of other authors' which has been seen by me is indicated by 'v' Thus:

Pachydon OVALIS (sp. nov.)
v *PEBASIA dispar* (Conrad) (specimen seen) (gen. nov.)
v *LONGIVERENA EUCOSMIA* (Pilsbry & Olsson, 1935) (specimen seen) (gen. et. sp. nov.)

DESCRIPTIONS OF NEW LOCALITIES AND FAUNAS

La Tagua, Colombia (Eden and Weeda collections) 0° 05′ N, 74° 40′ W

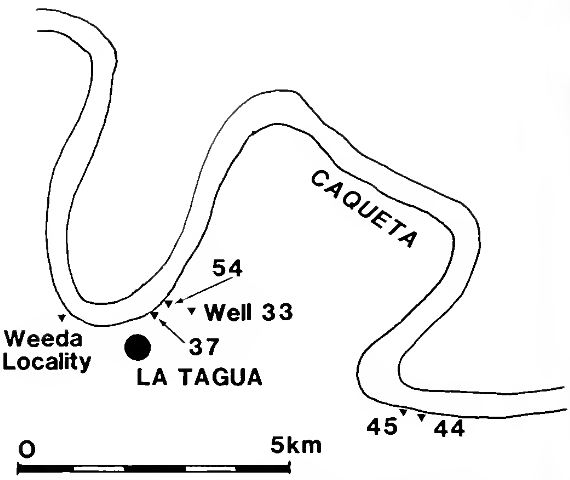


Fig. 4 La Tagua District. Map showing the relationships between the fossil localities in the La Tagua region, Colombia, based on a sketch map by M. J. Eden. Loc. 37 is at landing stage for La Tagua.

M. J. Eden and D. F. M. McGregor, both of Bedford College, London, and J. A. Morelo V of Istituto Geografico 'Agustin Codazzi', Bogotá, three geographers of the Colombian Amazonas Expedition (CAE), collected several samples of matrix rich in fossil molluscs from the La Tagua district of the Caqueta Valley, at *c.* 240 m above sea level (Eden, personal communication) during 1978, whilst primarily engaged in a geomorphological survey. Part of their work has appeared in Eden *et al.* (1982), in which a type section at Loc. CAE33 of the newly named La Tagua Beds was described (1982: 350–351). Nout Weeda, a Dutchman, then also working with CAE, independently discovered a different locality 1.5 km upstream from La Tagua. His material from this locality was passed to me in 1979 by Eden, at the same time as his collection from Puerto Nariño (p. 176). Unfortunately, there are no field notes with Weeda's collection, which has yielded many of the best-preserved fossils. However, it is fairly similar in both lithology and fauna to CAE33/570–670, but the rock is rather softer, so that the fossils are more easily extracted. Sheppard & Bate (1980) described a new ostracod fauna obtained from the only two La Tagua samples which they examined. That which they listed as CAE/GEO/33 was, in fact, from level 480–560 of the type section. The other was CAE/GEO/54. Details are given below; in many cases GEO is omitted for the sake of brevity.

My preliminary opinion that the La Tagua Beds might be correlated with the Pebas Beds of Brazil and Peru was quoted in Eden *et al.* (1982). Similar views were also quoted in Bristow & Parodiz (1982: 16, 19, 20). In the latter work my provisional identifications were given. Since then, I have studied both Weeda's collection and type material held in other museums, and a revised list of determinations is given below to avoid any further possible confusion.

determinations, Nuttall *in* Bristow & Parodiz (1982: 20)	**revised determinations**
Dyris gracilis	*Dyris* sp. indet.
Doryssa sp.	*Longiverena colombiana* sp. nov.
Cochliopina sp.	*Nanivitrea colombiana* sp. nov.
Aylacostoma browni	*Verena lataguensis* sp. nov.
Hydrobia cf. *ortoni*	*Dyris* sp. indet.
Anisothyris erectus	*Pachydon erectus* Conrad
Anisothyris sp.	*Pachydon hettneri* (Anderson)
unidentified unionids	*Diplodon (Ecuadorea)* aff. *bristowi* Parodiz and shell fragments

The only other known records of fossils from the region are those by Stirton (1953: 610), who stated that Axel Olsson and Donald Macgregor had found a possible caiman (Crocodilia) scapula in Tertiary clays and ferrugineous sandstone with *Unio* and other fresh-water fossils in the banks of Rio Guaybero five miles (8 km) below the mouth of Rio Heroru (*c.*1° 30′S, 73° 55′W). He also recorded a possible Oligocene *Eostoeiromys* sp. (Rodentia) from about 30 km east of La Tagua, at the confluence of Rio Peneyita and Rio Caqueta (*c.* 0° 07′S, 74° 22′W).

Type section of La Tagua Beds

Eden *et al.* (1982) designated the youngest Tertiary deposit of reddish surface sediments, often with a high silty component, as the Trinidad Bed. This shares the same type section as the La Tagua Beds in a recently dug water well, which is wide enough for a man to be lowered down with a rope to collect fossils and measure the section. This well is in La Tagua, 600 m from the river (Loc. CAE33). Here (1982: 351–352), 3.3 m thickness of Trinidad Bed overlies 3.4 m of La Tagua Beds exposed before the bottom of the well is reached. At other localities a much greater thickness of La Tagua Beds is reported, for instance over 14.2 m at CAE15 (1982: 354). The section at CAE33 is described fully in Eden *et al.* (1982); the following details are sufficient for this account.

Trinidad Bed	(0–330 cm)	
La Tagua Beds	(330–420 cm)	90 cm of light grey silty loam to silty clay, with yellowish brown to strong brown mottling. No fossils.
	(420–480 cm)	60 cm of light greyish brown to grey loam to sandy clay loam. Few fine unidentifiable shell fragments.
	(480–560 cm)	80 cm very dark grey shelly siltstone. Molluscs abundant, crowded together, mostly crushed.
	(560–570 cm)	10 cm described by Eden *et al.* as hardened lignite, with associated pyrites. It includes part of a fossilized branch, against which shells have drifted. Fossils abundant, mostly crushed, often partly pyritized.
	(570–670 cm)	100 cm light grey, rather hard siltstone. Fossils scattered throughout not arranged on bedding planes, and not as common as at two preceding horizons. Shells pale creamy coloured, shell material soft, easily damaged.
		[bottom of well]

CAE/GEO/33/480–560 cm

The sample of about 700 g (before processing) of partly carbonaceous grey clay, crowded with broken shell material most of which is fragmentary, yielded however some specimens good enough to identify and describe. The molluscs had to be extracted manually, using a needle sharpened to a chisel point, and needed hardening as development proceeded. Wetting the clay almost invariably resulted in the fossils disintegrating, and treatment with hydrogen peroxide, the method used to extract the ostracod fauna, proved useless for the molluscs. The following Mollusca were recovered:

Pachydon hettneri (Anderson)
Pachydon OVALIS sp. nov.
Pachydon erectus Conrad
Dyris tricarinata (Boettger)
Dyris SEMITUBERCULATA sp. nov.
Nanivitrea COLOMBIANA sp. nov.
Longiverena COLOMBIANA sp. nov.
Verena LATAGUENSIS sp. nov.

Eight of the eleven named fossil molluscan species known from La Tagua occur in this sample. The absentees are *Mytilopsis scripta* Conrad, from Sample 33/570–670, *Sheppardiconcha lataguensis* sp. nov. from Weeda's locality and CAE37, and *Diplodon (Ecuadorea)* aff. *bristowi* Parodiz from CAE54. In addition, unidentifiable *Dyris*, which do not belong to the two named species, occur in several samples. Shell fragments of naiades are also present. The age of the fauna is discussed at the end of the section. Extinct *Pachydon* may be indicative of brackish conditions whilst the living genera of Thiaridae, *Longiverena* and *Verena*, are river snails known only from fresh water. *Dyris*, which is common in the Pebasian, was presumably tolerant of brackish conditions. Living Littoridininae include the rather similar *Heleobia*, some species of which may be found in either fresh or brackish water (Marcus & Marcus 1963*a*, *b*, as *Littoridina*). This is the first fossil record of Cochliopinae, of which *Nanivitrea* is a member. The subfamily is generally fresh-water, but its distribution, which includes the Pearl Islands off the Pacific coast of Panama and also islands of the Caribbean, suggests that some of its members have an ability to cope with salt water at some stage in their life cycle. All the species occur in profusion with the exception of *L. colombiana* and *V. lataguensis*. There are no traces of either pulmonate gastropods (fresh-water or terrestrial) or of the Corbiculacea, an almost exclusively fresh-water superfamily of bivalves, in any of the La Tagua samples. The naiades (Unionacea and Mutelacea) do occur elsewhere at La Tagua but not in sample 33/480–560.

Sheppard & Bate (1980) record the following ostracods:

(1) *Cytheridella POSTORNATA* Sheppard & Bate
(2) *Pelocypris zilchi* Triebel
(3) *Darwinula* sp.
(4) *Cypria AQUALICA* Sheppard & Bate
(5) *Perissocytheridea FORMOSA* Sheppard & Bate
(6) *RHADINOCYTHERURA AMAZONENSIS* Sheppard & Bate
(7) *Ambocythere CAMPANA* Sheppard & Bate
(8) *Cyprideis PURPERI COLOMBIAENSIS* Sheppard & Bate

The only other known occurrence of (1) is at La Tagua CAE54. Similarly, (2) is known only from its type occurrence in the ?Pleistocene of San Salvador. Species (3) to (7) were also described from the Pebasian, probably of Pichana (Woodward's sample of the Hauxwell Collection). *Cyprideis purperi purperi* Sheppard & Bate was described from the same Pichana sample and also occurs at CPCAN 111, San Paulo da Olivença (Purper 1977) and at Canamá (herein, p. 328), both of which are Pebasian. Its subspecies *colombiaensis* is known only from 33/480–560.

Species (1) to (4) are indicative of fresh water, (5) and (8) of brackish conditions, whilst (6) and (7) belong to genera considered by Sheppard & Bate to be marine, *Rhadinocytherura* being newly described by them.

CAE/GEO/33/560–570 cm

This sample consisted of about 1 kg of shelly grey clay and carbonized wood. It appeared to be a shell drift which had accumulated against a tree-branch: part of the clay adjacent to the branch is pyritized. The fossils were even more difficult to extract and clean than those from the overlying level (480–560). The following molluscan fauna was recorded:

Pachydon hettneri (Anderson)
Pachydon OVALIS sp. nov.
Dyris sp. (or spp.) indet.
Longiverena cf. *COLOMBIANA* sp. nov.
Verena LATAGUENSIS sp. nov.

The fauna is very similar to that of the overlying sample (33/480–560): apparent absences of species are almost certainly because much of the fragmentary shell material was unidentifiable. The fauna could be indicative of brackish conditions, but fresh-water Thiaridae are also present.

CAE/GEO/33/570–670 cm

A sample of about 700 g of hard, pale grey, almost chalky marl, with fossils scattered randomly. Molluscan fauna:

Pachydon hettneri (Anderson)
Pachydon erectus Conrad
Mytilopsis scripta Conrad
Dyris sp. (or spp.) indet.
Longiverena cf. *COLOMBIANA* sp. nov.
(fragments only)

Only the rare and fragmentary *L. colombiana* is indicative of fresh water; all the other taxa are also tolerant of brackish water. The occurrence of rare specimens of *M. scripta*, resembling in its very triangular shape that figured by Pilsbry & Olsson (1935) from the La Cira fossil horizon of the Middle Magdalena Valley, is of particular interest.

CAE/GEO/37

From the southern (right) bank of Rio Caqueta, about 800 m downstream of La Tagua, the sample of about 350 g of dark, iron-stained, sandstone 'rotten-stone' is crowded with moulds of molluscs. Only three species can be recognized:

Pachydon hettneri (Anderson)
Pachydon OVALIS sp. nov.
Sheppardiconcha cf. *LATAGUENSIS* sp. nov.

Sheppardiconcha, an extinct genus of Thiaridae, probably lived in fresh water. *S. lataguensis* is better preserved at its type locality (1.5 km upstream from La Tagua; Weeda collection). *Pachydon*, indicative of brackish water, is very common at this locality. As in the other La Tagua samples, the brackish elements in the fauna dominate those of fresh water.

CAE/GEO/54

Immediately adjacent to, and downstream of, CAE37. The sample consisted of about 500 g of medium grey clay with bedding planes covered in shells, mainly small *Pachydon* with some *Dyris*. The other taxa are uncommon. Molluscan fauna:

Diplodon (Ecuadorea) aff. *bristowi* (Parodiz)
Pachydon hettneri (Anderson)
Pachydon erectus Conrad
Pachydon OVALIS sp. nov.
Dyris tricarinata (Boettger)
Dyris SEMITUBERCULATA sp. nov.
Nanivitrea COLOMBIANA sp. nov.
Longiverena COLOMBIANA sp. nov.

This is the type locality for the ostracod *Cythiridella postornata* Sheppard & Bate 1980, which also occurs in sample CAE33/480–560. It was described as a fresh-water species. The molluscs are the usual mixture of taxa with wide salinity tolerance accompanied by some of definite fresh-water origin. The single valve of the unionacean *D. (E.)* aff. *bristowi* is the only named naiad from La Tagua.

CAE/GEO/44

About 15 km downstream (6 km SE by E as the crow flies) from La Tagua, on right (south) bank of Rio Caqueta. Sample of 600 g of pale yellow to buff decalcified mudstone, with comparatively few, dark, rust-coloured moulds of shells scattered randomly throughout. It has been possible to make good latex casts showing sculptural details clearly from these moulds, which are not crowded together in an indeterminate mass as at CAE37. Only four species can be recognized:

Pachydon erectus Conrad
Pachydon hettneri (Anderson)
Pachydon cf. *OVALIS* sp. nov.
Longiverena COLOMBIANA sp. nov.

CAE/GEO/45

About 500 m upstream from CAE44. About 500 g of crumbly, dirty pale buff to grey limestone containing fossil shells with poorly preserved and extremely fragile surface sculpture. Fauna:

Pachydon erectus Conrad
Pachydon hettneri (Anderson)
Dyris cf. *SEMITUBERCULATA* sp. nov.
Nanivitrea cf. *COLOMBIANA* sp. nov.

A single turriculate shell which could be either *Sheppardiconcha* or *Longiverena* is also present. One specimen of each of the *Pachydon* species are well preserved.

Weeda Collection locality, 1.5 km upstream from La Tagua

About 300 g of pale grey, soft marl with fragile fossil shells which have well-preserved sculpture. Fossils were extracted by washing down the sediment with water. The process may be speeded up by the use of hydrogen peroxide. Fauna:

naiad shell fragments (probably Mutelacea)
Pachydon OVALIS sp. nov.
Dyris tricarinata (Boettger)
Dyris SEMITUBERCULATA sp. nov.
Nanivitrea COLOMBIANA sp. nov.
Sheppardiconcha LATAGUENSIS sp. nov.

This is the type locality of the four new species listed above. *Pachydon* is rare. This, in combination with the abundance of naiad shell fragments and the presence of *Sheppardiconcha*, suggests that the water at this locality might have been less brackish than usual during the deposition of the La Tagua Beds.

Age of the La Tagua Beds

The names of the eleven determinable molluscan species (six of which are new) of the La Tagua fauna are given above, pp. 173–4; the full ostracod fauna is also listed there. The ostracod fauna indicates a strong correlation between the La Tagua and the Pebas Beds. Sheppard & Bate (1980: 122, text-fig. 6) showed that of the 14 taxa (13 of which were new) in the combined fauna from the two regions, 8 occurred in the

La Tagua Beds, 11 in the Pebasian, 5 being common to both. In addition, different subspecies of *Cyprideis purperi* were found in the two regions. The only comparison that they make between these faunas and any other is their record of the probably Pleistocene species *Pelocypris zilchi* Triebel (1953) from San Salvador.

Diplodon (Ecuadorea) aff. *bristowi* Parodiz is the only naiad from the La Tagua Beds well enough preserved to be named. Parodiz' holotype (the only known specimen; see p. 273) is from the basal Loyola Formation of the Cuenca Basin.

Nanivitrea colombiana sp. nov. is the first fossil record of the genus from South America. Only one living species, *N. kugleri* (Forcart), which was described from Venezuela (as *Valvata*), is recognized from the continent.

No living species are known from the La Tagua fauna. The genera *Pachydon, Dyris* and *Sheppardiconcha* are extinct. None of the genera which are endemic (or almost so) to the Pebasian have been found at La Tagua: *Pebasia, Eubora, Toxosoma* and *Tropidobora* are all absent. It should be remembered that such a list is subject to alteration: until very recently it would have contained *Pachydon, Liris* and *Dyris* now all known to occur outside the Pebasian Basin, whilst *Pebasia* is described as new herein (p. 315). *Neritina* is important at many Pebasian localities but has not been found at La Tagua.

The La Cira fauna may represent a rather more fresh-water facies than that of La Tagua. Although *Pachydon* and *Mytilopsis* are present, the La Cira fauna contains four genera of naiades, *Triplodon* and *Diplodon (Rhipidodonta)* of the Unionacea and *Monocondylaea* and *Anodontites* of the Mutelacea, as well as the river snails *Verena* and *Longiverena.*

As shown above, the similarities between the La Tagua molluscan fauna and those of the inter-Andean basins of Ecuador are not particularly strong. Faunal lists in Bristow & Parodiz (1982) have been revised herein: see p. 172. They demonstrate that the Ecuadorean bivalve faunas are rich in fresh-water Unionacea, Mutelacea and Corbiculacea, whilst both *Pachydon* and *Mytilopsis* are lacking. In contrast, at La Tagua *Pachydon* and *Mytilopsis* are the only bivalves present except for *Diplodon (Ecuadorea)* aff. *bristowi* Parodiz and indeterminate naiad shell fragments. The Ecuadorian gastropod faunas are very different from those of La Tagua, being dominated by *Sheppardiconcha.* Both *Verena* and *Dyris* are present but uncommon. The presence of several other genera is more indicative of fresh than brackish water. Surprisingly, *Neritina,* though uncommon, occurs at several of the Ecuadorean localities. It is absent from La Tagua.

Sheppardiconcha, an extinct genus of Thiaridae perhaps most closely allied to *Basistoma*, was first described from the Cuenca Basin and also occurs in several Pebasian localities and at La Tagua (Weeda's locality only). *Verena lataguensis* has a rather aciculate spire and most resembles *V. browni* (Etheridge) which has a similar distribution to *Sheppardiconcha* in the Pebasian of the Amazon Basin. It also bears a strong resemblance to *V. barloventoensis* (Macsotay 1968), originally described as *Hemisinus*, from the Siquire Formation (?late Oligocene to early or middle Miocene) of Venezuela. A similar, high-spired, but unnamed *Verena* occurs in the Cuenca Basin. The species of *Verena* known from the Magdalena Valley Tertiary *(Hemisinus avus* and *H. laevicarina*, both of Pilsbry & Olsson, and *Ampullaria guaduasensis* (Anderson)) have low obtuse spires like the living type species, *V. crenocarina* (Moricand), and do not resemble *V. lataguensis* closely.

Dyris is represented by several fairly common species in the Pebasian, from which it was described, but its only known representative in the Magdalena Basin is the poorly preserved *D. lacirana* (Pilsbry & Olsson). At La Tagua it is an important element of the fauna, as both named species and numerous specifically indeterminate specimens, possibly representing more than one species. *D. tricarinata* (Boettger) is apparently a highly variable species. Perhaps more than one species is grouped under this name: already the rather similar *D. hauxwelli* sp. nov. has been separated from this 'group', and in the circumstances it would seem unwise to claim a close correlation between the Pebasian, the La Tagua Beds and also the San Cayetano Formation of the Loja Basin, Ecuador on the basis that all three contain *D. tricarinata. D. semituberculata* sp. nov. is easily distinguished from the other described species of the genus by its collabral wrinkling. Its variable spiral sculpture is reminiscent of that found in two Pebasian species, *D. lintea* (Conrad) and *D. tricarinata.*

The La Tagua specimens (CAE33/570–670) identified herein as *Pachydon erectus* have some resemblance to its subspecies *elongatus* (Boettger) from the Pebasian; *P. erectus* (s.s.) Conrad, also Pebasian, is in contrast the largest known species of *Pachydon. P. ovalis* sp. nov. has some resemblance to *P. amazonensis* from the Pebasian.

The molluscan fauna of the La Tagua Beds provides links between the Pebasian of the Amazon Basin and the non-marine Tertiary of the Magdalena Valley, lying to the west of the Eastern Cordillera. It also shows a slight resemblance to the several faunas of the inter-Andean Tertiary basins of Ecuador.

Pachydon hettneri was first described by Anderson (1928) from near San Juan de Rio Seco in the Upper Magdalena Valley. This species is very distinctive because of its strong posterior diagonal angulation and prominent corselet. It was the dominant member, occurring in great profusion, of a small brackish-water fauna which he thought came from the Eocene Guaduas Series. This fauna, which is now referred to the Santa Teresa Formation, is discussed herein (p. 335) and is now thought to be, at the earliest, late Oligocene, but is almost certainly Miocene. At La Tagua, this species is among the most common, occurring in the majority of samples.

Longiverena colombiana, although described herein as a new species, is nevertheless very similar to *L. eucosmia* (Pilsbry & Olsson 1935) which was described from the Mugrosa fossil horizon of the Middle Magdalena Valley. It is now thought that several other nominal species these authors described, both from this horizon and from the overlying La Cira fossil horizon of probable Miocene age, are referable to this species. In addition, both *Semisinus peyeri* de Greve, from the Pebasian of Iquitos, and its subspecies *dickersoni* Palmer, from the Loyola formation of the Cuenca basin, Ecuador, are here regarded as synonyms of *L. eucosmia.* It may be suggested that there is no great difference in the ages of all the deposits in which this species and the similar *L. colombiana* have been found. This, too, points to a Miocene age.

Specimens of the Pebasian species *Mytilopsis scripta* Conrad, with very triangular shells and characterized by straight hinge lines and markedly angular diagonal umbonal ridges, occur at CAE33/570–670. They are very similar to those described from Canamá on Rio Javari as *M. acuta* (Etheridge) and from the La Cira horizon as *M. cira* (Pilsbry & Olsson 1935). *Mytilopsis* is byssally attached, and if, as frequently happens, individuals grow crowded together, they may show wide variation in shape. The other species of *Mytilopsis* occurring in the Pebasian (but not found at either La Tagua or La Cira) is the living *M. sallei* (Recluz), which is characterized by a curved hinge line. As *M. sallei* is now recognized as occurring in the late Oligocene, it is clear that no precise stratigraphical conclusions should be based on occurrences of this genus.

The above analysis establishes that the facies in these different basins are not strictly comparable. It is difficult to pursue this point much further because it is known that many of the other faunas under consideration are 'mixed' in the sense that they come from more than one locality, and the accurate data necessary to disentangle them is not always available. If it is accepted that the La Tagua facies is not exactly similar to that pertaining in any of the other basins, then it must follow that the generic composition of the faunas is not necessarily going to be identical. The greater the number of genera in common, the greater the possible number of species in common: the converse is obviously true.

In these circumstances the presence of *Pachydon hettneri* (Anderson), *Mytilopsis scripta* Conrad and *Longiverena colombiana* sp. nov. in the La Tagua fauna suggests that its age may well be similar to that of the *Pachydon hettneri* horizon (Santa Teresa Formation) of the Upper Magdalena Valley and to its supposed correlative, the La Cira fauna of the Middle Magdalena Valley. At the same time, the presence of *Pachydon erectus* Conrad and *Dyris tricarinata* (Boettger) suggests that the La Tagua fauna is of more or less similar age to the Pebasian, which being the only one to contain living species is likely to be younger than the other fossil faunas under consideration.

An age within the Miocene is therefore favoured for the La Tagua fauna.

Puerto Nariño, Colombia (Weeda collection)
3° 38′ S, 70° 33′ W

Puerto Nariño lies some 60 km west of Leticia on the northern (left, Colombian) side of Rio Solimões, at about the above position. It is reasonably close to two classic Pebasian localities, Canamá (Etheridge 1879) and Três Unidos (Roxo 1924), both of which lie to the south, on Rio Javari. The collection was made by Mr Nout Weeda, and was handed to me for study, along with his collection from La Tagua, by M. J. Eden in 1979. No further details about the locality are known.

The single sample consisted of about 700 g of friable, rather silty, pale grey to dark grey, carbonaceous clay, which had disintegarated into small lumps about 15 mm in diameter. The sample contains well over a thousand fossil shells, many of which were already virtually free of matrix. Almost undamaged shells and badly broken specimens are about equally common. Bivalves with the two valves together are extremely rare. Further cleaning of half the sample was accomplished by treating it with dilute hydrogen peroxide. The residue is dominated by *Verena browni* (Etheridge) and *Liris scalarioides* (Etheridge), and to a lesser extent by *Toxosoma eborea* Conrad and the two species of *Dyris* present. Only three species of *Pachydon* have been found here: *P. trigonalis* sp. nov. is reasonably common, but both *P. cuneatus* Conrad and *P. tenuis* Gabb are rare. All the *Ostomya* specimens consist only of broken pieces showing the hinge characters of the genus. Both *Pebasia* and *Mytilopsis* are represented by one valve each. Nacreous shell fragments of naiades – usually about 10 mm across – are extremely common. Their prismatic layer, on which the sculpture occurs, has invariably been worn away, so that it is not possible to assign them even to their correct superfamily. One gastropod shell fragment, about 3 cm across, is identified as *Ampullaria*. The following Mollusca are recorded:

Pachydon tenuis Gabb
Pachydon cuneatus Conrad
Pachydon TRIGONALIS sp. nov.
Pebasia dispar (Conrad)
Ostomya sp. indet.
Mytilopsis sallei (Recluz)
Dyris ortoni (Conrad)
Dyris lintea (Conrad)
Liris scalarioides (Etheridge)
Toxosoma eborea Conrad
Verena browni (Etheridge)
Ampullaria (s.l.) sp. indet.

Although undoubtedly Pebasian, this fauna differs from those of the classic faunas of Pichana and Iquitos in several ways. It is highly fossiliferous, yet only twelve taxa have been found. However, it is not known whether the fossils came from only one level or whether several different layers were sampled; it is thus idle to speculate on how complete the collection is. The present fauna contains only three species of *Pachydon*, instead of the seven or eight which might be expected. Moreover, *P. trigonalis* is new, though also known to occur at Canamá, having been extracted from matrix in the course of the present study. The Puerto Nariño shells of one of the other species, *P. cuneatus*, are slightly atypical. It is one of the rarest at Iquitos and Pichana: at both these localities the most common species of *Pachydon* are *P. tenuis* Gabb, *P. erectus* Conrad, and the type species *P. obliquus* Gabb. Both *Ostomya* and *Mytilopsis* are always uncommon, if present. The specimens assigned to both of the *Dyris* species listed above appear to be slightly unusual and perhaps local variants. Other species of *Dyris*, including the normally common *D. tricarinata* (Boettger), are absent.

Liris scalarioides appears from de Greve's illustrations (1938), misidentified as *Liris minuscula* (Gabb), to be common at Iquitos. It was orginally described from Canamá. Its full geographical distribution is not known: its presence at other localities under different specific names can only be assessed when good figures are available. The Puerto Nariño specimens assigned to *Toxosoma eborea* are also slightly atypical of the species, being rather larger and having a more rounded profile to the body whorl than is usual in specimens from Pichana and Canamá. It is the only species of the genus, which is endemic to the Pebasian. The specimens identified as *Verena browni* (Etheridge) are certainly conspecific with shells wrongly determined as *Aylacostoma sulcata* (Conrad) from Três Unidos (Parodiz 1969), as Parodiz himself acknowledged (personal communication). They are also similar to Etheridge's type illustration of the species from Canamá, but some slight doubt must remain about this determination as the type material is lost. Notable absentees from the Puerto Nariño fauna include *Eubora* and *Tropidobora*, both endemic to the Pebasian, and *Neritina*, which is common in most Pebasian faunas including Pichana, Iquitos, Canamá and Três Unidos.

The presence – assuming correct identification – of *Verena browni* also at Canamá and Três Unidos and the occurrence of *Pachydon trigonalis* at Canamá suggests that these two faunas are more similar than others to the Puerto Nariño

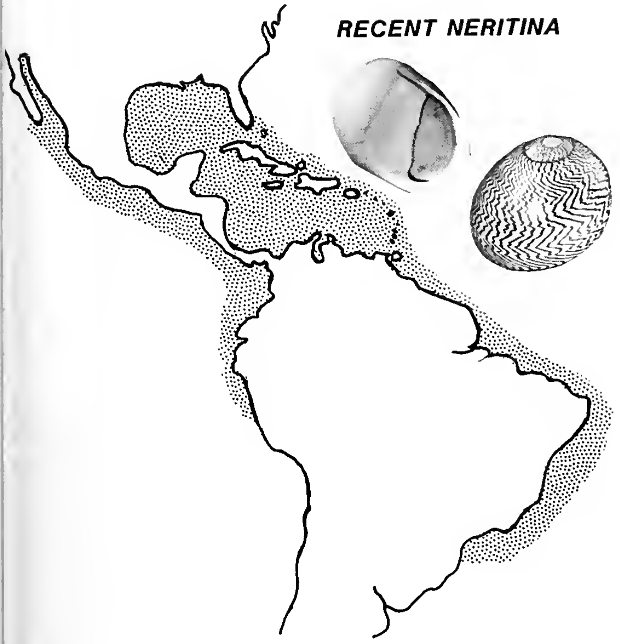


Fig. 5 Recent distribution of *Neritina*. Insets: top, front view of *N. lineolata* (Lamarck), Para, Brazil; bottom, rear view of *N. zebra* (Bruguière), Surinam; both about × 1.

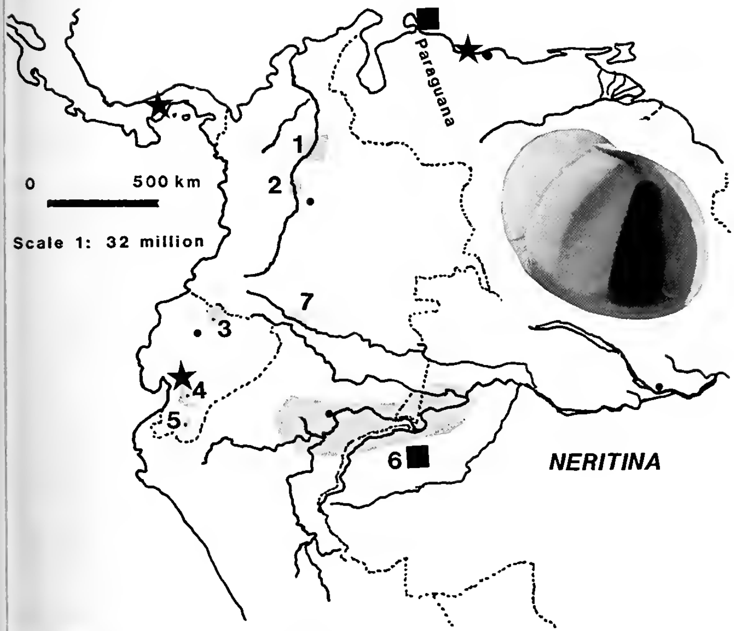
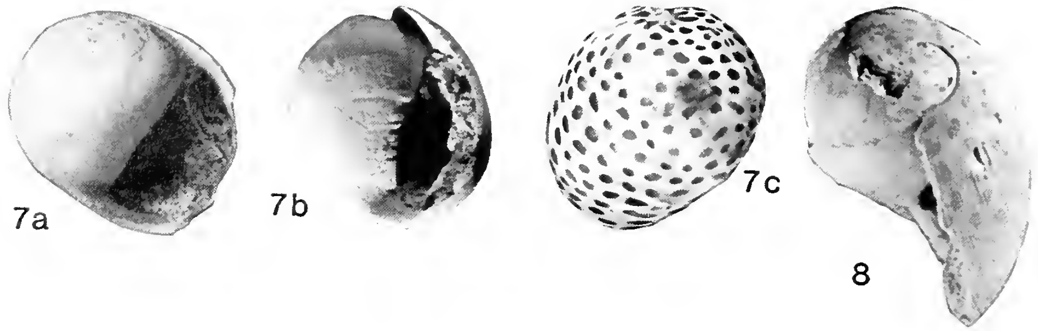


Fig. 6 Neogene distribution of *Neritina*. ■ = *N. ortoni* Conrad; ★ = other species. The genus is uncommon during the Neogene in the Caribbean region but has been recorded from Jamaica and the Dominican Republic.
Key: 1, Middle Magdalena deposits (Pilsbry & Olsson 1935); 2, Upper Magdalena Valley (Anderson 1928, Butler 1942, Porta 1966); 3, Chota Basin, 4, Cuenca Basin and 5, Loja and Malacatos Basins (all Bristow & Parodiz 1982); 6, Pebasian Basin (numerous authors and herein); 7, La Tagua (herein).

auna. These three geographically close localities appear o form a natural group within the Pebasian. It should e pointed out, however, that the sediments of Puerto ariño and Canamá preserved in BMPD are very different.

The Puerto Nariño fauna may represent a rather less rackish facies than is usual in the Pebasian, but the positive vidence for this is not great. *V. browni* is the only member f the fresh-water Thiaridae present, but it is extremely common. *Ostomya*, *Dyris*, *Liris* and *Toxosoma* are typical of the Pebasian and therefore are assumed to tolerate brackish conditions. The negative evidence consists of the comparative rarity of *Pachydon*, the great rarity of *Mytilopsis* and the absence of *Neritina*. In addition, naiad shell fragments are extremely abundant and certainly much more common than in the single Hauxwell Collection concretion from Pichana. This suggests that some fresh-water habitat existed not far away.



Figs 7–8 *Neritina ortoni* Conrad. Pebasian, Canamá, Peru; Brown Colln. **7**a-c, GG19993, **lectotype** (herein selected) of *Neritina puncta* Etheridge, 1879; front view, oblique view into aperture, rear view. **8**, GG21777, a paralectotype of the same, showing apical region. All × 5.

SYSTEMATIC PALAEONTOLOGY

Class **GASTROPODA** Cuvier
Subclass **PROSOBRANCHIA** Milne Edwards
Order **ARCHAEOGASTROPODA** Thiele

Superfamily **NERITACEA** Lamarck, 1809

[*nom. transl.* Thiele (1929: 71), *ex* neritacées Lamarck (1809: 319); Neritacea Rafinesque (1815: 144) (family); Neritadae Fleming (1828: 318) (family)].

Family **NERITIDAE** Lamarck, 1809

[*nom. correct.* Gray (1840: 147)]

Subfamily **NERITINAE** Lamarck, 1809

[*nom. transl.* Swainson (1840: 239, 346)]

Neritacea and Neritidae are here attributed to Lamarck (1809). This predates the usually accepted authorship of Rafinesque (1815) quoted by Keen *in* Moore (1960: 1275).

Genus ? ***NERITINA*** Lamarck, 1816

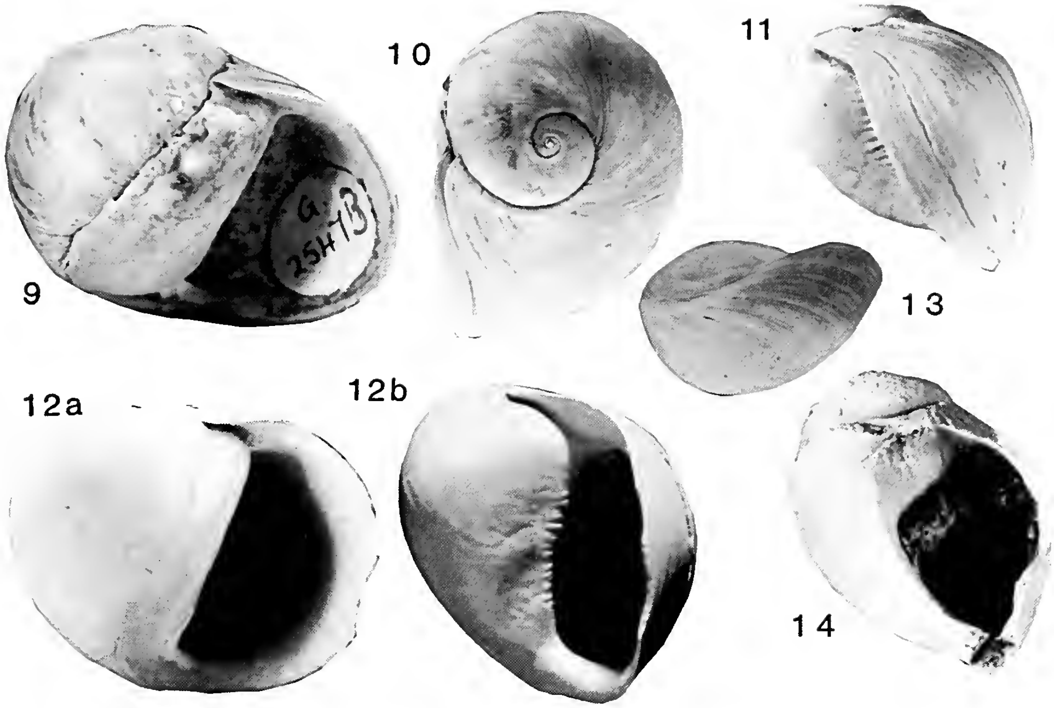
Type species. *Nerita pulligera* Linné, 1766 (ICZN Opinion 119, 1931). Recent, Indo-Pacific.

Remarks. The Pebasian Neritininae are here all placed within one species, *Neritina ortoni* Conrad, 1871. This is close to, and possibly conspecific with, a shell from the Miocene of Venezuela identified by Jung (1965) as *Neritina* aff. *woodwardi* Guppy (1866) originally described from the Neogene of Jamaica.

Some doubt must be expressed about the generic assignment of *ortoni*. Firstly, it has been impossible to find any other reasonably similar species, either fossil or Recent, from either the western Pacific or the Caribbean (Flores & Cáceras 1973, Keen 1971, Russell 1941). Secondly, the apertural features are reminiscent of, but by no means identical to, two marine genera with extremely widespread distribution: the large patelliform *Velates* (Cretaceous–Eocene) and the much smaller (*c.* 5 mm diameter) *Smaragdia* (Neogene–Recent), which is placed in its own Subfamily Smaragdiinae. Thirdly, the only operculum extracted from the matrix from Pichana, although broken, cannot be matched with that of either *Neritina*, *Theodoxus* or *Smaragdia*. The operculum of *Velates* has not been seen. In the present specimen, the peg which branches off the apophysis is missing, and this appears to be an original feature rather than as a result of damage to the specimen. The operculum of *Fluvinerita* (Recent, Jamaica) also lacks the peg, but the shell is different, and the genus seems to have been correctly placed by its original author (Pilsbry 1932) as a subgenus of *Nerita*. The operculum of *Smaragdia*, although similar to that of *N. ortoni* in general shape, does have a peg. These points are discussed below in further detail.

? ***Neritina ortoni*** Conrad, 1871 Figs 7–28

. 1869 *Neritina pupa* (Linné); Gabb: 197; pl. 16, fig. 2.
*. 1871*b* *Neritina ortoni* Conrad: 195; pl. 10, figs 5, 11.
v. 1871 *Neritina ortoni* Conrad; Woodward: 103; pl. 5, figs 2a, b.
. 1878 *Neritina ortoni* Conrad; Boettger: 428.
v. 1879 *Neritina ziczac* Etheridge: 85; pl. 7, figs 10, 10a.
v. 1879 *Neritina puncta* Etheridge: 85; pl. 7, fig. 9.
. 1906 *Neritina ortoni* Conrad; Clarke: 132.
. 1924 *Neritina ortoni* Conrad; Roxo: 47.
. 1924 *Neritina puncta* Etheridge; Roxo: 47.
. 1924 *Neritina etheridgei* Roxo: 47, nom. nov. pro *Neritina ziczac* Etheridge, 1879 non *Neritina zigzag* Lamarck, 1822: 185.
. 1924 *Neritina*, unnamed species; Roxo: figs B, B′.
. 1938 *Neritina (Vitta) ortoni* Conrad; de Greve: 61; pl. 5, figs 12–15.
v. 1938 *Neritina amazonensis* de Greve: 62; pl. 5, figs 4–6, 8.
v. 1938 *Neritina roxoi* de Greve: 64; pl. 5, figs 10, 11, 16.
. 1938 *Neritina (Vitta) etheridgei* Roxo; de Greve: 66; pl. 5, figs 1–3, 7, 9.
. 1938 *Neritina puncta* Etheridge; de Greve: 67 (discussed but not recorded as being present at Iquitos).
v? 1965 *Neritina* aff. *woodwardi* Guppy; Jung: 480; pl. 62, figs 12, 13.
. 1966 *Neritina amazonensis* de Greve; Willard: 66; pl. 62, fig. 3.



Figs 9–14 *Neritina ortoni* Conrad. Pebasian, Pichana, Peru; Hauxwell Colln. **9**, GG25473, shell figured by Woodward (1871: pl. 5, figs 2a, b), tilted front view × 2. **10**, GG25474, shell accompanying GG25473, top × 2. **11**, GG21783, side, showing sinuate outer lip, × 2.5. **12**a, b, GG21782, front, oblique view into aperture to show columella, × 2.5. **13**, GG21784, base × 2. **14**, GG21785, similar view to Fig. 11, but with outer lip broken away showing columella, × 2.5.

. 1966 *Neritina etheridgei* Roxo; Willard: 66, 67; pl. 62, figs 1, 2.
. 1966 *Neritina ortoni* Conrad; Willard: 66.
. 1966 *Neritina puncta* Etheridge; Willard: 66.

TYPE MATERIAL. Types of *N. ortoni* Conrad, 1871, Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell Collection) (NYSM, Clarke 1906). Not studied.

Lectotype of *N. puncta* Etheridge, 1879, selected herein. BMPD GG19992, Late Caenozoic, Pebasian, Canamá, Peru (Barrington Brown Collection); probably the specimen figured by Etheridge, pl. 7, fig. 9. Two accompanying, probably unfigured, shells, GG19993, GG21777, details as above, are paralectotypes.

Lectotype of *N. ziczac* Etheridge, 1879, selected herein. BMPD GG19994, Late Caenozoic, Pebasian, Canamá, Peru (Barrington Brown Collection); the original of his pl. 7, fig. 10 (front view). GG19995, details as above, figured by Etheridge, pl. 7, fig. 10a (rear view), is a paralectotype.

Holotype of *N. amazonensis* de Greve, 1938: pl. 5, figs 4, 5, 5, 8. PIMUZ 219, Late Caenozoic, Iquitos, Peru (Peyer Collection). ('Typus' of de Greve). PIMUZ 220, details as above, but not figured by de Greve, is a paratype.

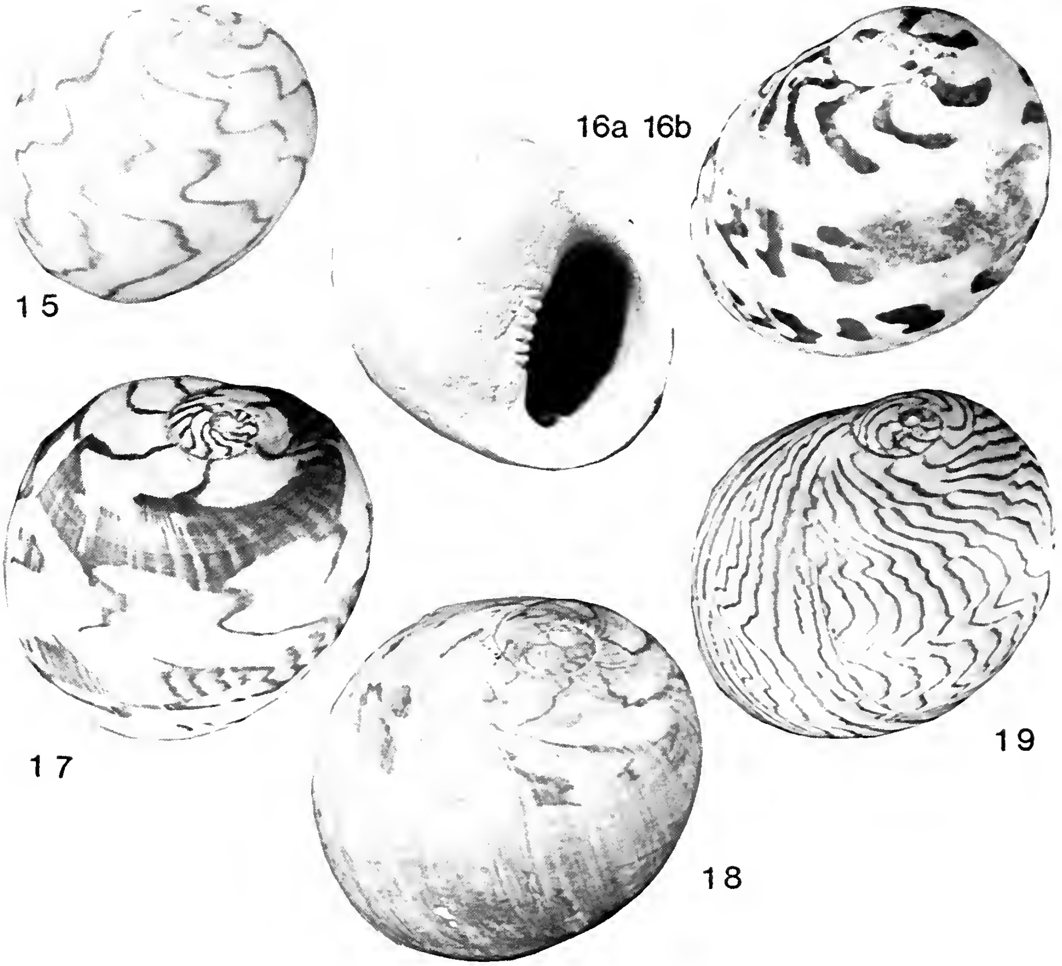
Holotype of *N. roxoi* de Greve, 1938: pl. 5, figs 11, 16. PIMUZ 216B, Iquitos, details as for *N. amazonensis*. Another shell figured by de Greve, pl. 5, fig. 10, is a paratype; these two are accompanied by a third unnumbered shell which was not mentioned by de Greve and is therefore not a paratype.

OTHER MATERIAL STUDIED. G25473, Late Caenozoic, Pebasian, Pichana, Peru (Hauxwell Colln), the shell figured by Woodward, 1871: pl. 5, figs 2a, b, and G25474, the accompanying shell. G24587/1–30, GG19997/1–20, GG21782–99, Pichana, same details. GG19996, a single operculum, extracted in 1982 from matrix of Hauxwell Colln from Pichana. GG12282/1–12, GG12283/1–25, GG21778–81, Late Cainozoic, Amazon Valley (Trechmann Colln). H 13639 (Basel NHM), Cantaure Formation, Late Burdigalian, Lower Miocene; Paraguana Peninsula, northern Venezuela (Jung 1965); see Fig. 25.

FURTHER OCCURRENCES. All late Caenozoic, Pebasian. Pebas (Gabb 1869, Boettger 1878, Willard 1966); Três Unidos, Peru (Roxo 1924); Iquitos (de Greve 1938, Willard 1966); Negro Urca and Rumi Tuni (Willard 1966). Late Caenozoic, Pebasian, upper Amazon Valley and ? Lower Miocene, northern Venezuela.

DIAGNOSIS. *Neritina* characterized by markedly angular, velatiform, junction between inner lip callus and basal ridge of shell; upper surface of shell varying between domed with sunken nuclear whorls to almost flat with exserted nuclear whorls; outer lip flared, with sinuous growth lines; inner lip denticulate except at upper and lower ends; colour patterning variable, commonly of zigzag lines but sometimes of variously shaped blotches and irregular reticulations; operculum lacking peg.

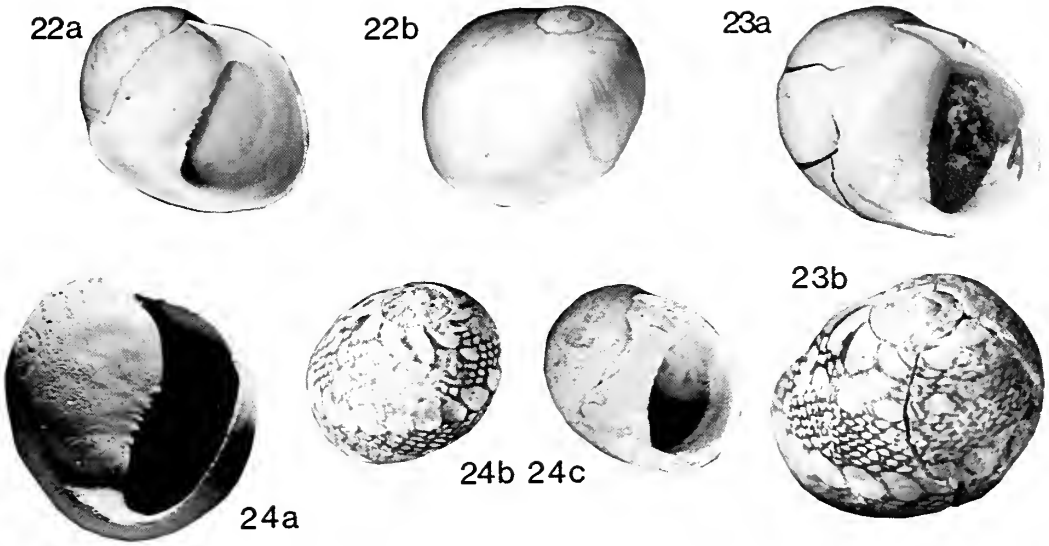
DESCRIPTION. The shell surface is smooth and porcellanous, but the growth lines are clearly visible. There are seldom more than four whorls. The spire varies: in most specimens it is almost flat except for the small, globular, first whorl which stands proud of the main shell surface. In these shells the suture describes a smooth spiral. In a relatively few other shells, the spire is domed, or papilliform, but the nuclear



Figs 15–19 *Neritina ortoni* Conrad. Pebasian, Pichana, Peru; Hauxwell Colln. **15**, GG21789, rear × 10. **16**a, b, GG21786, front and rear, × 6.7. **17**, GG21787, rear × 5. **18**, GG21790, rear × 3. **19**, GG21788, rear, showing most common form of colour patterning, × 5.

Figs 20–21 *Neritina ortoni* Conrad. Pebasian, Canamá, Peru. **20**a, b, two apertural views from different angles of GG19994, **lectotype** (selected herein) of *Neritina ziczac* Etheridge, figured by Etheridge (1879: pl. 7, fig. 10), × 2.5. **21**, rear view of GG19995, showing colour patterning, × 2.5.

whorl is sunken or almost so, and their suture describes a rather erratic spiral with angular changes of direction. In all shells the expansion rate is high, producing a flared outer lip, which, in side view, is markedly sinuous. Both the upper and lower junctions between the outer lip and the main body of the shell are reminiscent of *Velates*. As in *Velates*, an angular basal ridge starts at the left lower edge of the callus pad and runs parallel to the base of the shell along the lower margin of the inner lip. The outer lip is thickened at its upper junction with the inner lip. The inner lip appears straight when viewed from the front, but is curved to the right in side view. The number of denticles borne by the inner lip varies considerably, but only partly with shell size: between ten and sixteen denticles may be present on fully grown shells. The denticles



igs 22–24 *Neritina ortoni* Conrad. Pebasian, Iquitos, Peru; Peyer Colln (PIMUZ). **22a**, b, PIMUZ 219, holotype of *Neritina amazonensis* de reve, front and rear, × 2. **23a**, b, PIMUZ 216A, paratype of *Neritina roxoi* de Greve, front and rear, × 4. **24a–c**, PIMUZ 216D, holotype of *Neritina roxoi* de Greve, front and rear, × 4, oblique view into aperture, × 6.

re absent from both the top and bottom of the inner lip. The allus pad covers a large proportion of the apertural surface, pon which it has a slight flattening effect.

Colour patterning is visible on the majority of shells, but here is a strong tendency for the patterning to break down on he last whorl of the larger specimens. The most common attern is of zigzag lines. Patterns of both regular and rregular dark blotches are present in a minority of specimens. reversal of this also occurs: in some shells light blotches are eparated by a dark, rather irregular, net-like pattern.

A single damaged operculum was obtained from the matrix rom Pichana. It lacks the peg which branches off the pophysis in other species of *Neritina*.

IMENSIONS. In mm.	height	breadth
onrad 1871: pl. 10, fig. 5.	17	17
onrad 1871: pl. 10, fig. 11.	24	26
25473 (fig'd Woodward 1871: pl. 5, figs 2a, b)	22.3	24.0
25474 (found with G25473)	23.5	24.2
G19992, lectotype, *N. puncta* Etheridge, anamá	7.5	7.5
G19993, paralectotype, *N. puncta* Etheridge, anamá	6.4	6.4
G21777, as above.	8.4	–
G19994, lectotype, *N. ziczac* Etheridge, anamá.	16.5	16.5
IMUZ 219, holotype of *N. amazonensis* de reve, Iquitos.	14.2	16.0
IMUZ 216A, holotype of *N. roxoi* de Greve, quitos	8.4	8.4
I 13639 (Basel NHM), fig'd Jung, 1965 as *N.* ff. *woodwardi* Guppy; Cantaure Formation, enezuela.	13.5	15.0

EMARKS. Conrad (1871) remarked that Gabb (1869) had nly young shells, which were identified as *N. pupa* Linné, vailable for study. Conrad, who had fifteen shells of various ages, concluded that both his own and Gabb's material belonged to a single new species, *N. ortoni*. The living *N. pupa* was much smaller and its spire was not flattened.

The BMPD collections, including specimens newly extracted from matrix, contains about 100 shells from Pichana, far fewer than the over 250 quoted by Woodward (1871). Nevertheless, his conclusion that *N. ortoni* is the only *Neritina* occurring there is still supported. Spire shape appears to be a very variable feature, and Woodward's conclusion, based only on his Pichana sample, that only one species is present, is now expanded to cover all the references in the above synonymy. The sample from Pichana is predominantly of shells with zigzag colour patterning, though other patterns occur. The unlocalized samples (GG12282–3, Trechmann Colln) also have a preponderance of zigzag colour-patterned shells, but show marked variation in spire height, with about a third of the undamaged shells having the relatively high, domed, spire coupled with a sunken nucleus. In shape, these agree with the much smaller lectotype and two paralectotypes of *N. puncta* Etheridge, 1879, from Canamá. *N. ziczac* Etheridge, 1879, also from Canamá, and subsequently renamed as *N. etheridgei* by Roxo (1924), has the typical zigzag patterning of *N. ortoni*: there appear to be no differences between the two species, and it is difficult to understand why Etheridge described his material under a new name. De Greve (1938) used the name *N. etheridgei* Roxo for adults with zigzag markings and *N. ortoni* for juvenile shells up to 4.3 mm high with similar patterning. His *N. amazonensis* was based on large shells with little or no patterning, but such obsolescence is a regular feature of the larger shells at Pichana. *N. roxoi* de Greve was erected for shells from Iquitos resembling the unnamed specimen from Três Unidos figured by Roxo (1924: figs B, B′). These have domed spires and an irregular, diagonally reticulate pattern modified by larger clear oval patches arranged spirally. Somewhat similar patterning occurs rarely at Pichana (BMPD and Conrad, 1871*b*: pl. 10, fig. 5). This patterning appears to form a link between the zigzag lines of typical *N. ortoni* and the dark

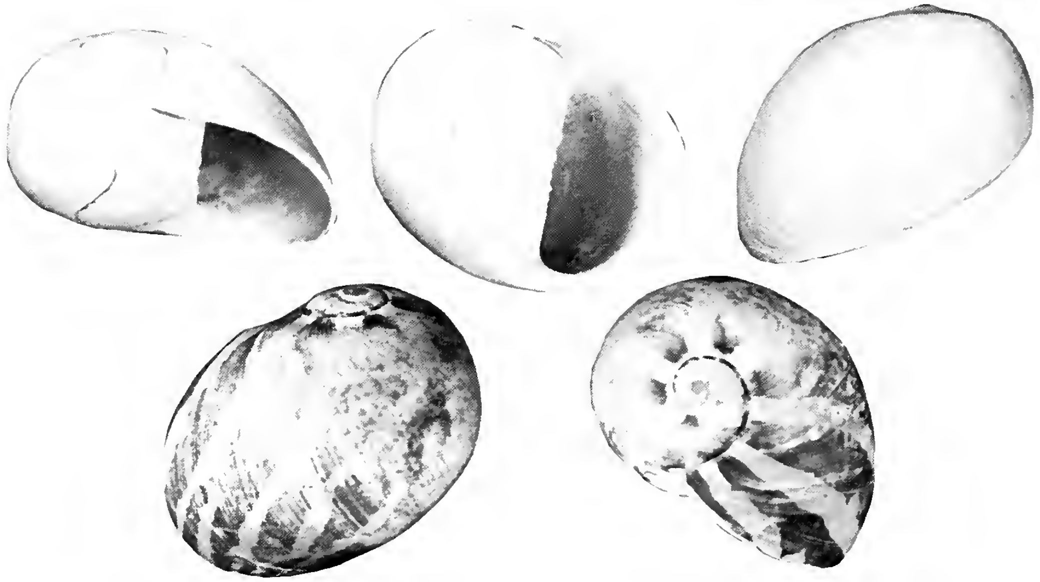
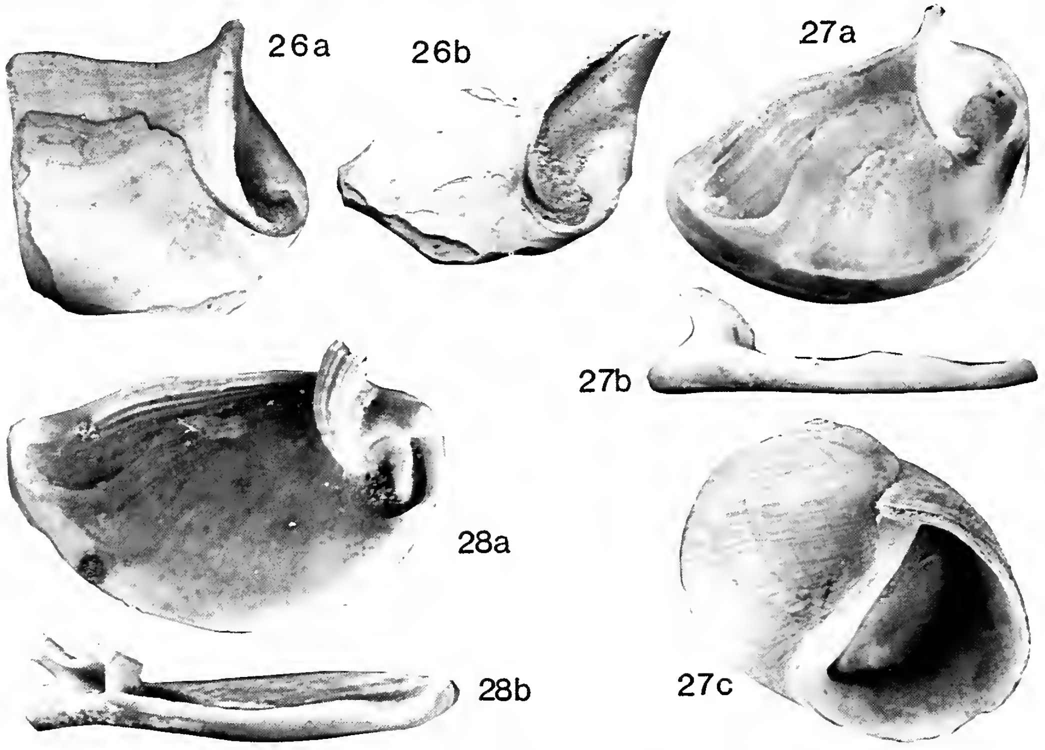


Fig. 25 *Neritina ?ortoni* Conrad. Lower Miocene, Late Burdigalian (planktonic foraminiferal zone N.8), Cantaure Formation, Paraguana Peninsula, northern Venezuela. Basel NHM, H 13639, figured Jung (1965: pl. 62, figs 12, 13) as *N.* aff. *woodwardi* Guppy, all × 2.5.



Figs 26–28 Operculae. **26**a, b, GG19996, broken operculum, presumed to be of *Neritina ortoni* Conrad, extracted from washings from Pebasian, Pichana, Peru, Hauxwell Colln. Plan and oblique views, × 10. **27**a–c, *Fluvinerita tenebricosa* C. B. Adams. ANSP 15359, paratype of *Nerita (Fluvinerita) alticolor* Pilsbry; Recent, Jamaica. **27**a, b, plan and side views of operculum × 8; **27**c, shell × 5. **28**a, b, *Neritina reclivita* Say. BMZD 1984223, Recent, Caribbean; plan and side views of operculum × 4.

spots which tend to coalesce into broad radiating spokes on the spire of *N. puncta*.

The most striking feature common to all the nominal species of Pebasian *Neritina* is the shallowness of the insertion of the inner lip within the aperture, particularly abapically where the basal ridge and the inner lip are almost flush with each other. These apertural features are reminiscent of those found in *Velates*, *Smaragdia*, and the shell identified as *N.* aff. *woodwardi* Guppy by Jung (1965), but are unknown in other Neritinae. However, the Eocene marine genus *Velates* may be distinguished by its characteristic patelliform aboral surface. *Smaragdia* differs in the way in which the central part of its inner lip is stepped to the left and by its small size. Its rather curved growth lines, however, resemble those of *N. ortoni*.

Examination of living species of *Neritina* from both the Pacific and Atlantic/Caribbean shores of South and Central America has revealed none particularly close to *N. ortoni*: in addition to lacking the velatiform aperture, they have operculae with pegs. *N. zebra* (Bruguière, 1792*a*) often has zigzag patterning, but the individual lines are more continuous, with fewer angulations, and generally broader. More important differences are its more evenly globose shape and its virtually straight outer lip. *N. zebra* appears to be confined to the Atlantic drainage system from Panama to north-western Brazil (von Martens 1879: 118, who added that, as far as is known, it lives in fresh running water). However, von Martens recorded it from the island of Curaçao, so it must clearly be able to tolerate some contact with salt water.

Nerita (Fluvinerita) alticolor Pilsbry (1932) [= *Neritina tenebricosa* C. B. Adams, 1852] lives in fresh-water streams of Jamaica and has an operculum which differs in detail from that of *N. ortoni* but does lack a peg. The shell, however, is relatively thick and also spirally striate. It is rather globose as well as lacking the apertural features of *N. ortoni*. It appears to have been correctly equated with *Nerita* rather than *Neritina* by Pilsbry, who had also studied its radula. Although *Fluvinerita* may be safely dismissed from further consideration as a possible relative of *N. ortoni*, it is of some interest as another example of a monospecific subgenus with no known close relatives.

Jung (1965: 480; pl. 62, figs 12, 13) identified a single specimen from the rich marine fauna of the Burdigalian (Zone N8) Cantaure Formation of the Paraguana Peninsula, northern Venezuela as *Neritina* aff. *woodwardi* Guppy (1866). This is now tentatively assigned to *N. ortoni*. Guppy's type specimen of *N. woodwardi*, from the Neogene of Jamaica, should be in BMPD (reg. no 64080) but appears to be lost. However, his illustrations (1866: 291; pl. 18, figs 4, 5) and those of Woodring (1928: 424; pl. 35, figs 7, 9) show a very different higher-spired shell, with a strongly curved columella on which the denticles are obscure. Jung's Venezuelan specimen has a low spire and flaring aperture. Above all, its comparatively velatiform apertural features resemble those of *N. ortoni*, though the angular junction between the callus pad and the base of the shell is not so sharp. A further difference is that the colour patterning is of a type not found in *N. ortoni*. Nevertheless, this Venezuelan specimen must be regarded as being very close to the Pebasian species, even if not conspecific.

Neritina is rare in the non-marine Neogene deposits of the Cuenca Basin, Ecuador (Bristow & Parodiz 1982: 34–37; BMPD collections), and, as Parodiz pointed out, none of the Cuenca species resemble the Pebasian fossils. Records of Neogene Neritidae from marine strata in South America and the Caribbean region are sparse (Canal Zone of Panama, Woodring 1957: 67; Dominican Republic, Maury 1917: 152; Venezuela, Weisbord 1962: 116). The subfamily is as yet unknown from the rich marine faunas of Peru and Ecuador described by Olsson in numerous papers, and in BMPD collections from Ecuador. A probable explanation for its rarity is that shells of sublittoral species have a greater chance of fossilization than those, such as *Neritina*, living either in the littoral zone or in fresh to brackish water.

Order **CAENOGASTROPODA** Cox, 1959

Superfamily **RISSOACEA** Gray, 1847

[Family Rissoina Gray, 1847: 150; Family Rissoidae, H. & A. Adams, 1854: 327; *nom. transl.* Thiele, 1929: 136]

Family **HYDROBIIDAE** Stimpson, 1865

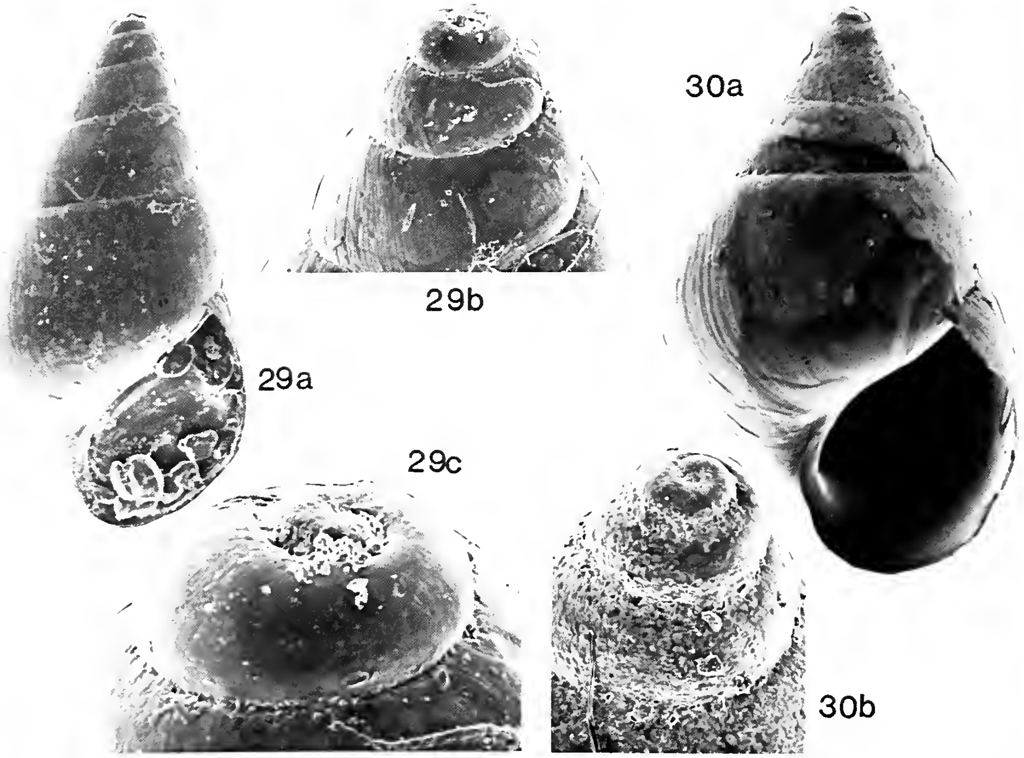
[Subfamily Hydrobiinae Stimpson, 1865*a*: 52, 1865*b*: 4, 39; *nom. transl.* Fischer, 1885: 725; = Paludestrinidae Newton, 1891: 226]

The assignment of fossil taxa to various subfamilies is perforce based entirely on shell characters. Several of these fossils do not fit comfortably into the taxonomic arrangements proposed in Taylor (1966), Davis & Pons da Silva (1984), Thompson (1984) and Hershler (1985).

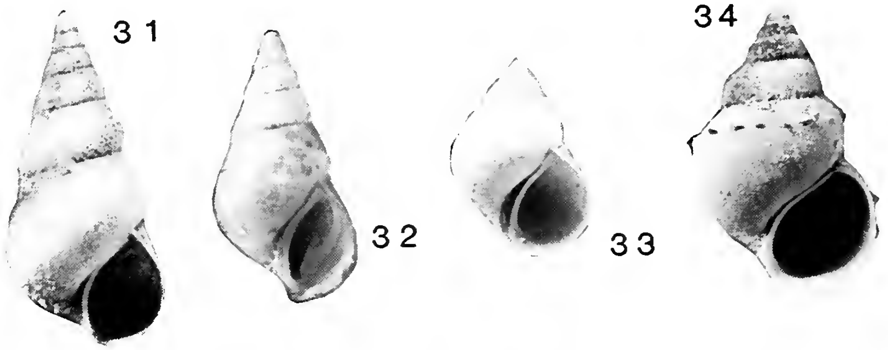
Subfamily **LITTORIDININAE** Thiele, 1928

[Tribus Littoridineae Thiele, 1928: 378; 1929: 141; *nom. transl.* Wenz, 1939: 571; = Subfamily Littoridininae 'nov.' Taylor, 1966: 182]

Taylor (1966), when proposing the Littoridininae as a new subfamily, was obviously unaware of its previous recognition (Wenz 1939, following Thiele, 1928). Paludestrinidae Newton (1891) was an unnecessary substitute name (see Cossmann, 1921: 95) for Hydrobiidae. Stimpson published Hydrobiinae twice in the same year: first, on 25 February, in the title only of his paper (1865*a*); in his second work (1865*b*), which appeared in August, full definitions were given. He did not mention *Littoridina* (type species by monotypy *L. gaudichaudi* Souleyet, 1852 (Fig. 39); Recent, Guayaquil, Ecuador), but in discussing *Paludestrina* d'Orbigny (1841: 8) proposed (1865*b*: 41) the name *Heleobia* for (Figs 31, 32) *Paludestrina culminea* d'Orbigny (1840: 36), almost certainly from Lake Titicaca, and its allies – species which subsequent authors have generally placed in *Littoridina. Heleobia* was treated as a synonym of *Littoridina* in Wenz (1939: 571), but has recently been resurrected by Davis *et al.* (1982: 168; Pons da Silva & Davis 1983: 131) for *Paludestrina australis* d'Orbigny and other species from Brazil, Uruguay and Argentina, on the grounds that their anatomy differs substantially enough from that described by Souleyet himself for *Littoridina gaudichaudi* to justify generic separation. No named specimens of *L. gaudichaudi* are available for comparison in BMZD. The type illustration of its shell, however, show it to be stouter and possibly with a heavier-lipped aperture than *Heleobia culminea* and the other South American species represented in BMZD. Thus, for the present, *Littoridina* is retained for its type species only, whilst all the smooth aciculate species which I have been able to examine and which are normally assigned to that genus – Taylor (1966: 182) estimated that there were about sixty living species – seem best accommodated in *Heleobia*. Haas (1955) erected several, mostly monotypic, new genera of Littoridininae from Lake Titicaca, apparently only on conchological grounds (collection, including types, in BMZD). The samples of all but *Brachypyrgulina* are very small. *Heleobia*, however, is abundant in the lake (BMZD colln). Both *Strombopoma* and *Rhamphopoma* (Fig. 32) Haas have shells typical of *Heleobia*, and *Heligmopoma* (Fig. 33) differs only in having a comparatively obtuse spire (spire angle 60°). *Brachypyrgulina* (Fig. 38) is characterized by its rectangular whorl profile, with a broad ramp and angular shoulder, whilst *Limnothauma* has a conical spire, a strong peripheral keel coinciding with the lower suture, and a broad, deep, umbilicus bordered by a basal keel. Hubendick, working on the anatomy of material from the same collection (1955: 322–326) reported that the verge, gill and radula of all of Haas's genera (with the exception of *Limnothauma*, which he did not examine and is known only by a single specimen)



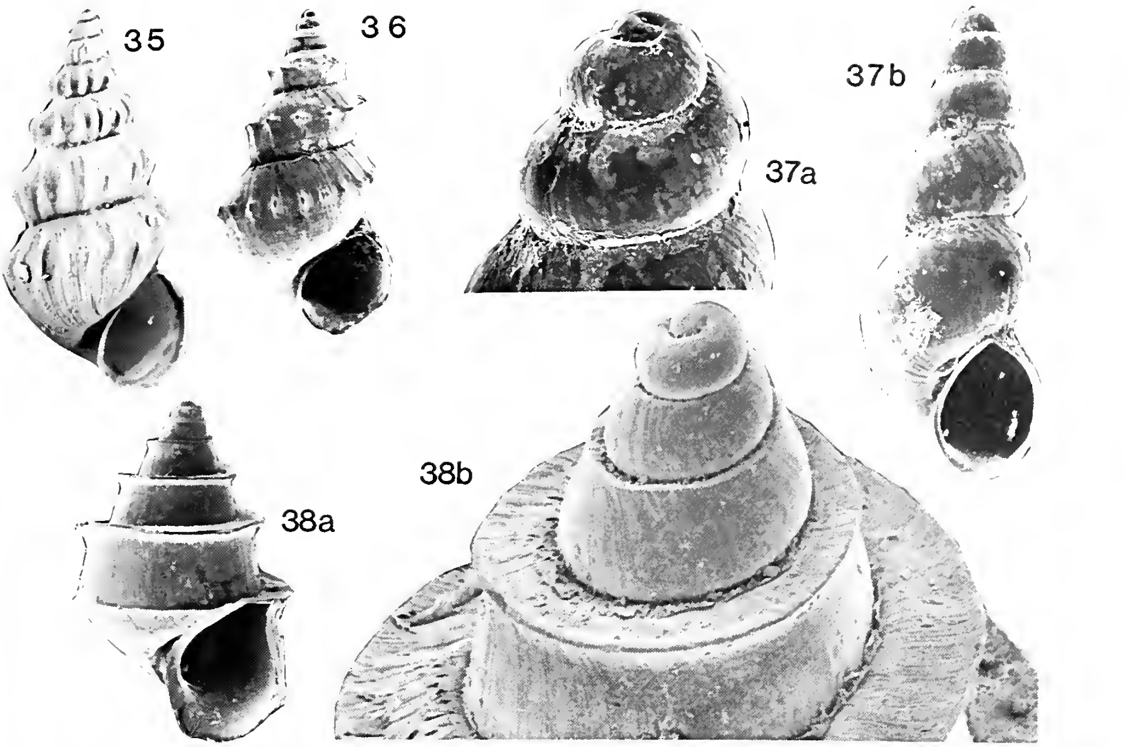
Figs 29–30 *Heleobia*. Recent, eastern Brazil. **29**a–c, *Heleobia australis* (d'Orbigny). BMZD 1958.4.10.7; front, × 20; early whorls, × 60; apex, × 200. Saco de Manguera, Rio Grande; E. C. Rios (Museo Oceanográfico de Rio Grande) Colln. **30**a, b, *Heleobia charruana* (d'Orbigny). BMZD 1984224; front, × 20; early whorls, × 60. Cananeir; given and determined by E. Marcus.



Figs 31–34 Recent Littoridininae. All in front view, × 8. **31**, *Heleobia culminea* (d'Orbigny). BMZD 1854.12.4.352, one of seven syntypes, labelled as holotype of *Paludestrina culminea* d'Orbigny. ? Lake Titicaca, Peru; d'Orbigny Colln, species no. 272. **32**, *Heleobia culminea* (d'Orbigny). BMZD 1956.xi.5.167, holotype of *Rhamphopoma magna* Haas; Chococoya, Lake Titicaca, depth 3.5 to 4.5 m. G. I. Crawfor Colln. **33**, *Heligmopoma umbilicata* Haas. BMZD 1956.xi.5.157, holotype; Siripata Bay, Lake Titicaca, depth 2.4 m. G. I. Crawford Colln **34**, *Potamopyrgus corolla* Gould. BMZD 1984225. Wanganui River, near Pipiriki, New Zealand.

had very uniform anatomy similar to that of *Littoridina* (i.e. *Heleobia*). He thought that though the operculae of *Strombopoma* and *Rhamphopoma* were of aberrant types, they might well have been derived from that of *Heleobia*. His conclusion (1955: 326) that these genera might have evolved in isolation in Lake Titicaca seems reasonable. This situation is probably analogous to the suspected adaptive radiation of the Thiaridae in Lake Tanganyika (see Wenz, 1939: 708–712).

Taylor (1966) placed some thirty high-spired species, including all the South American fossils originally described as *Dyris*, *Liris* and *Potamopyrgus*, into *Tryonia*, whose type species (Fig. 35) *T. clathrata* Stimpson (1865*b*), from th Pleistocene of Colorado, has rather sharp axial folds as wel as the carinate whorl profile. The whorls of *Liris* have mor evenly biconvex profiles, but the sculpture is similar to that o *Tryonia*. Taylor wrote that virtually all the species were known by their shells alone so that no 'trenchant characteris tics' of the genus were possible. Thus, evidence for supra specific classification is not available. There appear to be n sufficient reasons to accept that all these very differentl sculptured species are congeneric as Taylor suggested. Hi approach seems somewhat inconsistent, for at the same tim



igs 35–38 Recent Littoridininae. **35**, *Tryonia clathrata* Stimpson, type species of *Tryonia*. BMZD 1900.6.26.1643. ? Pleistocene; Colorado, U.S.A.; × 12. **36**, *?Tryonia coronata* (Pfeiffer), usually referred to either *Pyrgophorus* or *Lyrodes*. BMZD 1984226. Recent; Venezuela; × 10. **37**a, b, *Durangonella mariae* Morrison, 1945. BMZD 1951.11.1.222, paratype; front, × 20; oblique view of apex, × 60. ?Subfossil; Tlahuac, D.F., Mexico; pres'd Smithsonian Institution. **38**a, b, *Brachypyrgulina carinifera* Haas. BMZD 1956.xi.5.102; paratype; front, × 12.5; oblique view of spire, × 50. Sucuné, Lake Titicaca, Peru, depth 5 m.

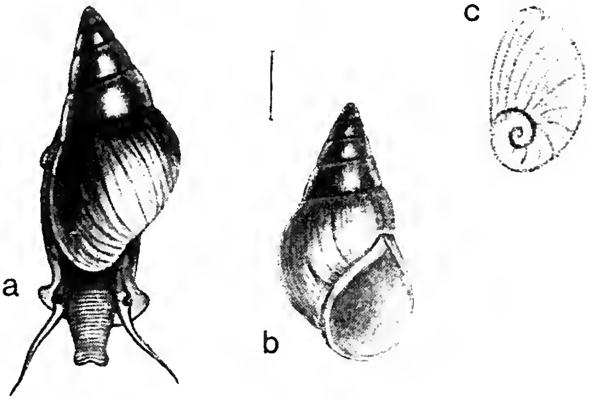


Fig. 39 *Littoridina gaudichaudi* (Souleyet). Recent; Guayaquil, Ecuador. Type illustrations copied at original size from Souleyet's (1852) figs 31–33; magnifications approximate. a, dorsal view of shell with live animal extended, × 3.75; b, ventral view of shell, × 3.75; c, operculum, × 6.

1966: 179, 182 *et seqq.*) he accepted all of Haas' Lake 'iticaca genera not only as distinct, but as belonging to two ubfamilies, the Cochliopinae and Littoridininae. Moreover, 'ryonia (*sensu* Taylor) would have a discontinuous geographical range (Taylor 1966: 183, text-fig. 14, map), and hough the pre-Pleistocene record is sparse, Taylor's list made without comment) implies that *Tryonia* was flourishing n both North and South America before the existence of the anamanian land bridge.

The apparent adaptive radiations in Lakes Titicaca and 'anganyika may be taken as examples of what might be xpected to occur in other groups, including fossils under onsideration. There is, however, justification for the provi- onal classification of fossils on a slightly different, pragmatic, asis. None of the fossil species under consideration, includ- ng *'Littoridina' crassa* (Etheridge), can be confidently assigned o living genera of Littoridininae as listed in Taylor (1966: 82–3). In the present paper *Dyris* is used for those species ith predominently spiral sculpture and *Liris* is retained for hose with predominently axial, as opposed to collabral, culpture. This generic arrangement is perhaps somewhat rbitrary and cannot claim to be more than a workable ompromise. This is partly dictated by lack of knowledge of he Recent fauna. Both the small size of the available ollections from such a vast region and the sparseness of the elevant literature suggest that small Mollusca of the Recent auna have been relatively neglected. In addition, two other pecies, in particular, suggest not only a common ancestry but lso a fairly close relationship between these two fossil genera. The type species of *Dyris* and *Liris* are very obviously distinct. The rare bicarinate and unicarinate shells in the Pichana sample here identified as belonging to *D. gracilis* Conrad – the type species of *Dyris* – do, however, approach the non-carinate *Liris* in shell morphology. The spirally ribbed *Dyris semituberculata* sp. nov. (p. 196) from La Tagua has weak and variable collabral folding, whilst *Dyris tuberculata* (de Greve 1938) from Iquitos has strong spiral and collabral sculpture. De Greve had assigned the latter species to *Liris* on the grounds that the peristome was detached from the body whorl as in the two other species occurring at Iquitos. This feature was also regarded as a generic distinction by Parodiz (1969: 119). However, this phenomenon is almost exclusively confined to Iquitos shells. It is linked with the spire angle reducing with growth, so that mature shells tend to be more acute, and is also often associated with the aperture being comparatively rounded as opposed to the normal tear-shape. *Liris* is thus a good example of how change in one character – in this case an increase in the whorl translation rate – may affect several others. The rather sporadic incidence of both detached peristomes and rounded apertures argues against either being a specific, let alone a generic, distinction.

To summarize, lack of comparative material makes it impracticable to postulate relationships between the various fossil and Recent genera. For example, it is accepted that the relationship between *Heleobia* and *Dyris* may be no more profound than that between *Heleobia* and *Brachypyrgulina*. In addition to *Heleobia*, favoured candidates as possible living relatives of the fossil genera include (Fig. 36) the Argentine *Lyrodes* (Doering 1884), the largely Central American *Pyrgophorus* (Ancey 1888) which is known from northernmost South America (Taylor, 1966: 194–196), and *Durangonella* (Morrison 1945) from Central Mexico (Fig. 37). *Lyrodes* is considered as distinct and characterized by fine spiral lirae: its type species, *L. guaranitica* Doering (subsequent designation by Pilsbry, 1911: 562) from Argentina, however, was placed in *Heleobia* (Pons da Silva & Davis 1983: 129).

Littoridininae range from fresh water through brackish (mangrove swamps and coastal lagoons) to marginal marine conditions, where they have been reported in association with genera such as *Brachydontes, Neritina, Nassarius* and *Thais* (Gaillard 1974*a*, *b*; Marcus & Marcus 1963*a*: 33, 1963*b*: 45–47).

Genus ***DYRIS*** Conrad, 1871

[= *Isaea* Conrad, 1871*b*, *non* Edwards, 1830; = *Conradia* Wenz, 1925, *non* A. Adams, 1860].

TYPE SPECIES. *Dyris gracilis* Conrad, 1871*b*; Late Caenozoic, Pebasian; Pichana, Peru. By monotypy.

DIAGNOSIS. Like *Heleobia*, but with predominantly spiral ribbing; peristome not detached.

OTHER SPECIES ASSIGNED. *Mesalia ortoni* Gabb, 1869, Pebas; *Isaea lintea* Conrad, 1871*b*, Pichana; *Hydrobia (Isaea) tricarinata* Boettger, 1878, Pebas; *Liris tuberculata* de Greve, 1938, Iquitos; *Dyris hauxwelli* sp. nov. (p. 192), Pichana. All Late Caenozoic, Pebasian, Upper Amazon Valley. *Potamopyrgus laciranus* Pilsbry & Olsson, 1935, Miocene, La Cira Formation, Upper Magdalena Valley, Colombia; *Dyris semituberculata* sp. nov. (p. 196), Late Caenozoic, La Tagua, Colombia.

GENERIC DISTRIBUTION. ? Neogene only, north-western South America. Unknown living.

REMARKS. The possible relationships between *Dyris* and living Littoridininae are discussed under the subfamily, above. Comparisons between *Dyris* and the living *Lyrodes* are discussed under *D. lacirana* (Pilsbry & Olsson), p. 195. Parodiz (1969) treated *D. gracilis*, *D. lintea* and *D. tricarinata* as conspecific, stating that he could observe clinal variation between the three in a sample from Três Unidos, and adding that the same variations could be observed in the numerous illustrations of Iquitos shells (de Greve 1938). It has now been possible to examine over 70 newly extracted shells from the sediment collected by Hauxwell from Pichana, as well as previously separated specimens in BMPD, which were presumably named by Woodward, and also the types of Conrad's two species, neither of which has been adequately illustrated before. This study suggests that, at Pichana, it is possible to recognize as distinct not only the three species named above, but also *D. hauxwelli* sp. nov. Further justification for separation is that the various species occur in different proportions – or in some cases, not at all – at different localities. The only quantitative guide to the relative rarity of these species at Pichana was afforded by the residue of matrix. When this was searched for the first time (additional specimens were obtained later in a subsequent search), the number of specimens obtained was as follows: *D. gracilis* (5), *D. lintea* (19), *D. tricarinata* (40), and *D. hauxwelli* (10). The original BMPD samples from Pichana (Woodward 1871: 102, 108, postscript) contain over fifty *D. tricarinata* and only seven fragments of *D. lintea*. Both *D. gracilis* and *D. hauxwelli* are absent: the former probably because of its rarity and the latter probably because of its small size. In contrast, at Iquitos, from the number of illustrations – de Greve gave no specimen counts in his text – it would appear that *D. lintea* and *D. tuberculata* are the two most common species. The other species appear to be rare at Iquitos, and the picture is further complicated by reidentifications herein. Thus *D. lintea* of de Greve (*pars*) = *D. gracilis*; *D. gracilis* of de Greve = *D. hauxwelli*. Although de Greve recorded *D. tricarinata* as occurring at Iquitos, it may be uncommon there, as his only illustrations of the species are of Boettger's types from Pebas.

Dyris gracilis Conrad, 1871 Figs 41–48, 454–455

*v 1871*b* *Dyris gracilis* Conrad: 195; pl. 10, fig. 8; pl. 11, fig. 7.
. 1878 *Hydrobia (Isaea) gracilis* (Conrad) Boettger: 493.
1879 *Dyris gracilis* Conrad; Etheridge: 86.
v. 1879 *Melania bicarinata* Etheridge: 88; pl. 7, fig. 7.
v. 1879 *Melania tricarinata* Etheridge: 87; pl. 7, fig. 6.
. 1926 *Hydrobia* (*Conradia*) *gracilis* (Conrad); Wenz: 1970.
? 1938 *Hydrobia (Conradia) lintea* (Conrad); de Greve: 83 (*pars*); pl. 1, figs 29, 30 (*non* figs 10, 28)
. 1966 *Tryonia bicarinata* (Etheridge) Taylor: 196.
. 1966 *Tryonia gracilis* (Conrad) Taylor: 197.
. 1969 *Dyris gracilis* Conrad; Parodiz: 118 (*pars*).

LECTOTYPE. Selected herein: NYSM 9192a, with height 5.9 mm. The accompanying NYSM 9192b, with height 4.9 mm, is a paralectotype. Both Late Caenozoic, Pebasian, Pichana (Hauxwell Colln). Holotype GG22421 (*ex* 97728) of *Melania tricarinata* Etheridge; Late Caenozoic, Canamá, Peru; Barrington Brown colln.

Lectotype (selected herein) GG22416 and two accompanying paralectotypes GG22417–8 (all *ex* 97724) of *Melania bicarinata* Etheridge; Late Caenozoic, Canamá, Peru; Barrington Brown Colln.

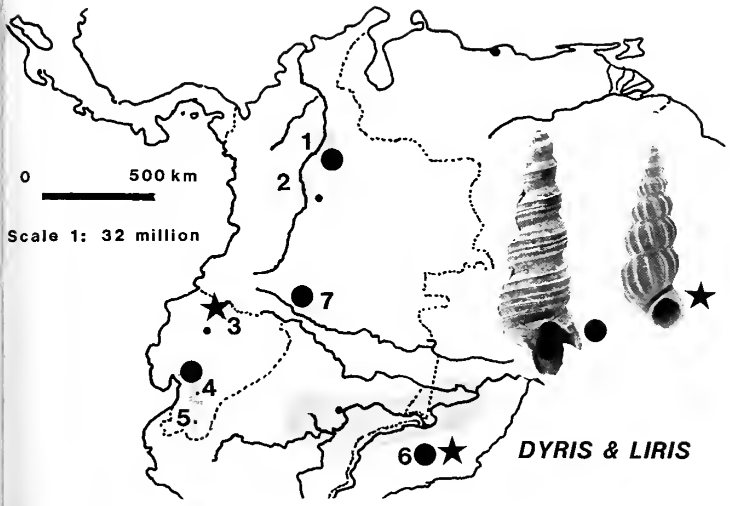
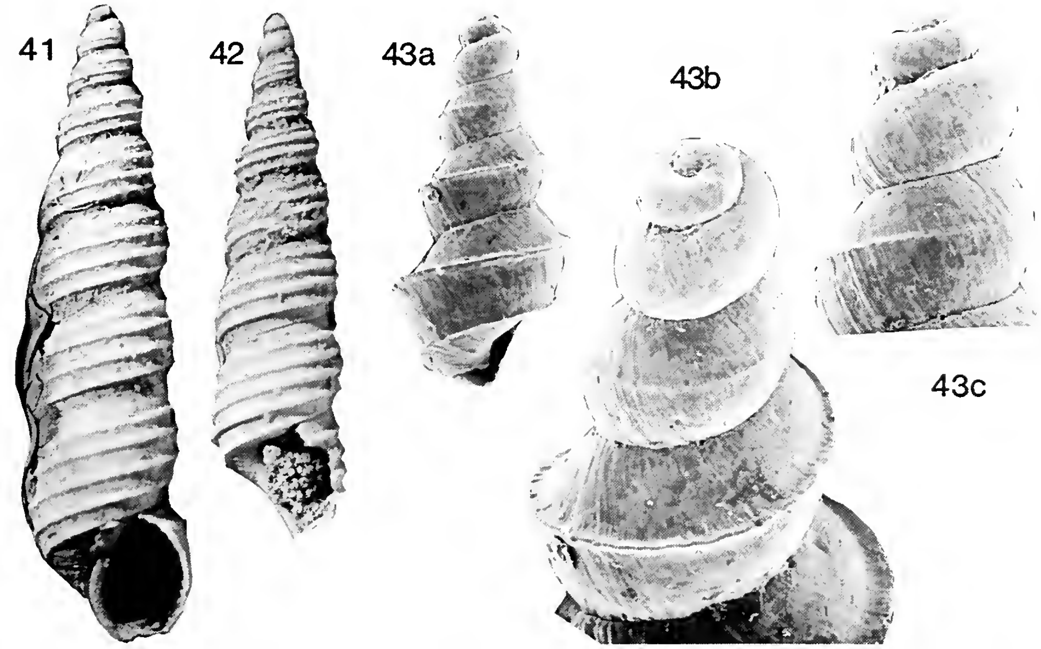


Fig. 40 Distribution of the extinct genera *Dyris* and *Liris*. Key as in Fig. 6, p. 177. ● = *Dyris*; ★ = *Liris*. Inset: left, *Dyris gracilis* Conrad, Pichana, Peru; right, *Liris scalarioides* (Etheridge); Puerto Nariño, Colombia.



Figs 41–43 *Dyris gracilis* Conrad. Pebasian; Pichana, Peru; Hauxwell Colln. **41**, NYSM 9192a, **lectotype** (herein selected), × 15. **42**, NYSM 9192b, paralectotype, × 15. **43**, GG19798: a, side view, × 40; b, oblique view of apex and spire whorls, × 100; c, side view of apex, × 100.

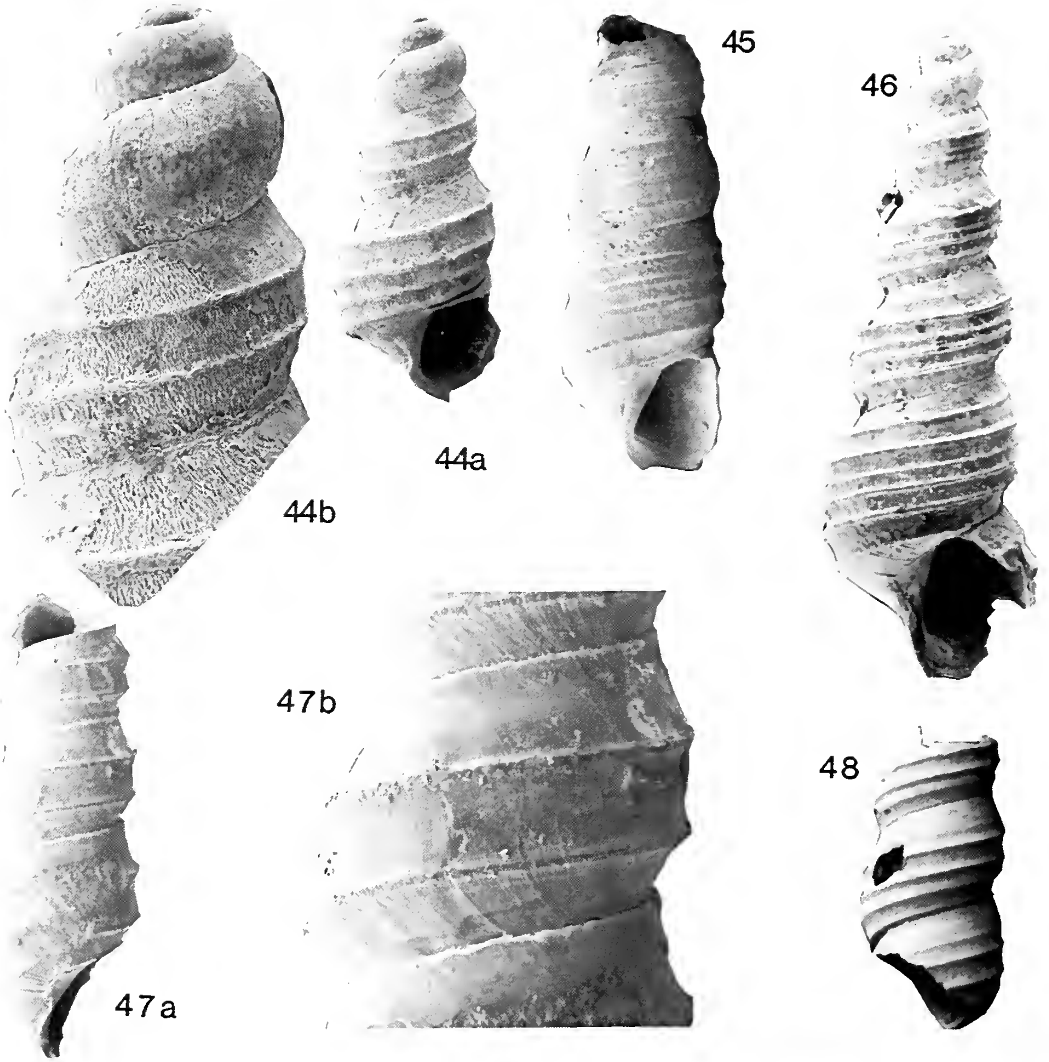
Other material studied. GG19796–8, GG21521–6, Late Caenozoic, Pebasian, Pichana (Hauxwell Colln, extracted 1982); GG21520, Puerto Nariño, Colombia (Weeda Colln).

Further occurrences. All Late Caenozoic, Pebasian. Pebas (Boettger 1878); Iquitos (de Greve 1938).

Diagnosis. Slender *Dyris* with a spire angle of between 13° and 17° bearing one to three fairly evenly spaced carinae, usually increasing to four or five on later whorls; aperture as little as a sixth of shell height.

Description. The tall apex is variable in height, comprising 2–2½ convex whorls which are smooth except for prosocyrt growth lines. A noticeable feature of the apex is the alteration of sutural slope in individual specimens. The last apical whorl is normally rather bulbous, and on it, one or more carinae develop at more or less the same time.

These are sometimes, but not always, joined fairly soon by up to three extra carinae. The carinae are sharp and separated by wide, concave, interspaces. Throughout growth a fairly distinct ramp and wide suprasutural groove persist, so that the whorl profile remains basically bicarinate. The growth lines change from prosocyrt on the apical whorls to reverse sigmoid on the later whorls and are more or less orthocline on the central portion of the whorl. In all shells, an additional carina marks the edge of the base of the whorl and is nearly or completely obscured by the following whorl, so that the sutural region is virtually smooth. The inner lip is just detached from the base, which is slightly concave and smooth except in one specimen, which bears a single weak spiral rib on its base.



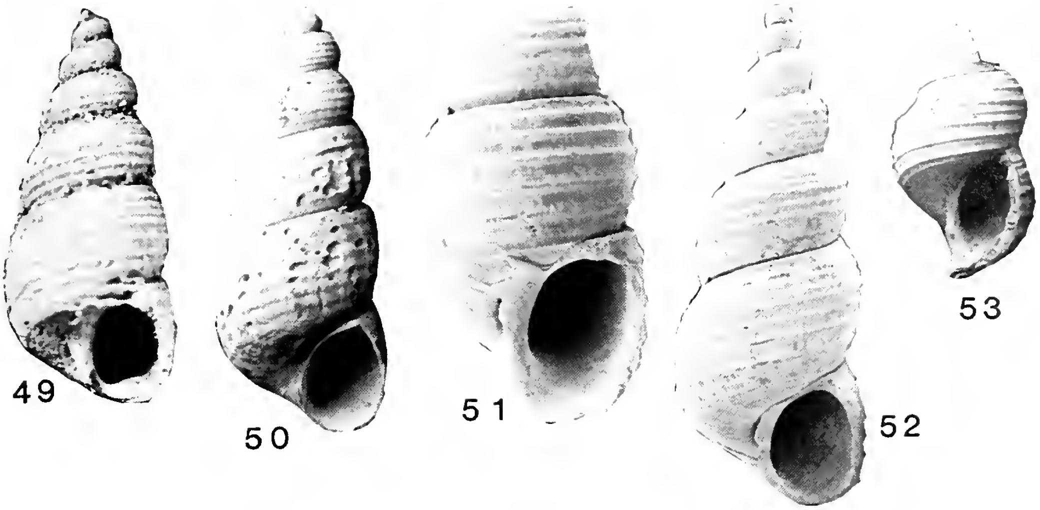
Figs 44–48 *Dyris gracilis* Conrad. Pebasian. **44–47**, Pichana, Peru; Hauxwell Colln. **44**, GG19797; a, front view, × 40; b, front view, early whorls only, × 100. **45**, GG21522; front view, × 15. **46**, GG19796; small specimen (h = 2.34 mm) resembling lectotype, × 40. **47**, GG21521; a, side view, × 15; b, penultimate whorl showing reverse sigmoid growth lines, × 50. **48**, GG21520; side view, × 15. Puerto Nariño, Colombia; Weeda Colln.

Dimensions. In mm.	h	br	hap	h/br	sa
Lectotype, NYSM 9192a, Pichana	5.9	1.5	1.2	3.9	15°
Paralectotype, NYSM 9192b, Pichana	4.9	1.4	–	3.5	15°
GG19796, Pichana	2.3	0.8	0.5	3.0	17°
PIMUZ 833, Iquitos (fig'd de Greve 1938: pl. 1, figs 29, 30, as *H. lintea*)	7.7	2.2	1.7	3.5	–
Lectotype, GG22416, of *Melania bicarinata* Etheridge, Canamá	4.8+	1.4	1.4	–	18°
Holotype, GG22421, of *Melania tricarinata* Etheridge, Canamá	5.2	1.5	–	3.5	18°

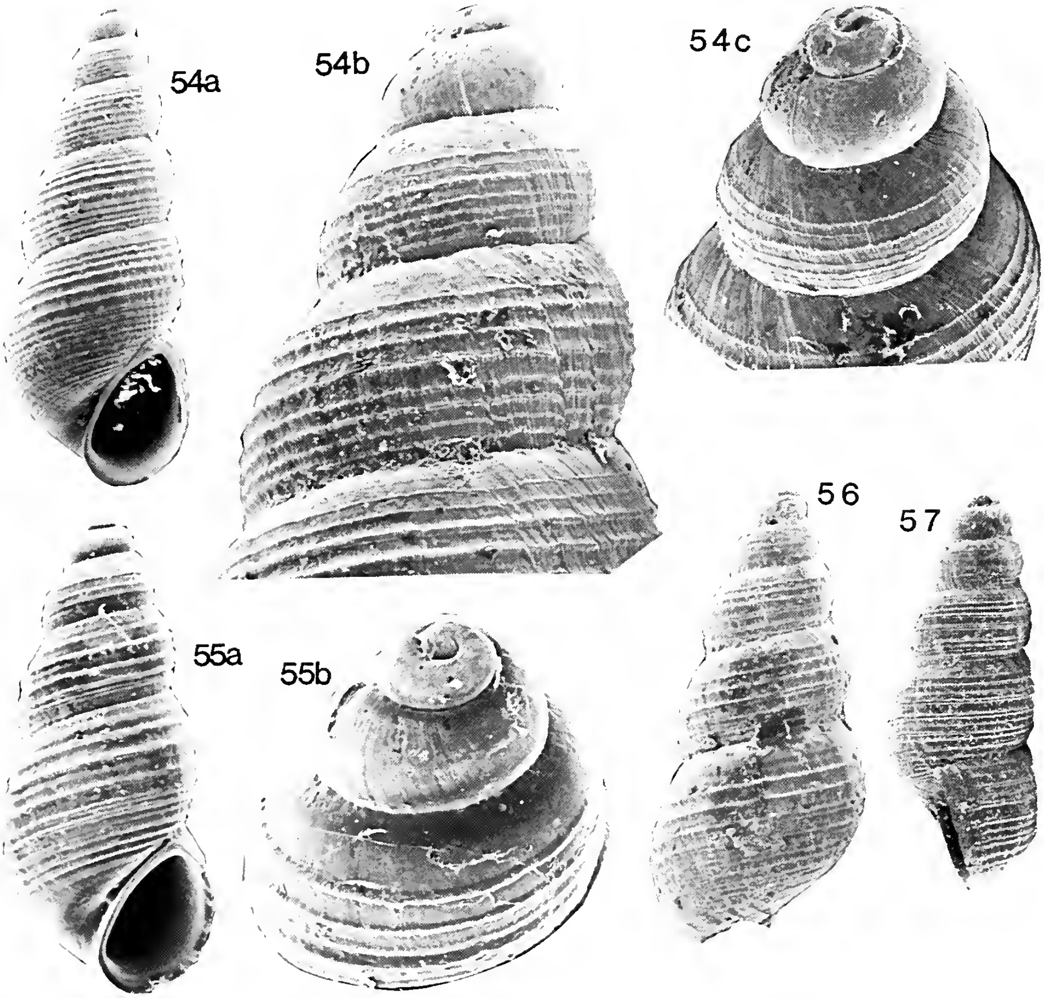
Note. Nearly all BMPD specimens are too fragmentary to measure.

Remarks. This is a very rare species represented at Pichana mainly by broken fragments. Parts of the synonymy must be treated with suspicion because Conrad's original illustrations are so small as to be useless by themselves. However, coupled with his description, which includes the statement that there are four carinae on the penultimate whorl and five (i.e. including the basal) on the last, it is reasonable to assume that NYSM 9192 is the type series. Boettger's (1878) reference seems convincing. Roxo (1924: 48), who was quoted in de Greve's (1938) synonymy, was, in fact, remarking that he had *not* found the species at Três Unidos.

All specimens in BMPD of *Dyris lintea* (Conrad) are spirally multistriate. De Greve, however (1938: pl. 1, figs 10–30), figured a series of shells exhibiting considerable variation in spiral sculpture as that species. PIMUZ 833 (1938: pl. 1, figs 29, 30) is here referred to *D. gracilis* because of its few spiral ribs, even though they are comparatively weak, and in spite of its basal disc being neither concave nor bordered by a spiral carina. De Greve (1938: pl. 3, figs 21–28) identified as *D. ? gracilis* shells here referred to *D. tricarinata* (Boettger),



igs 49–53 *Dyris lintea* (Conrad). Pebasian; Pichana, Peru; Hauxwell Colln. **49**, NYSM 9252, holotype; × 10. **50**, GG19794; × 10. **51**, G45294; × 15. **52**, G25293; × 15. **53**, GG19795; × 10.



igs 54–57 *Dyris lintea* (Conrad). Pebasian; Pichana, Peru; Hauxwell Colln. **54**, GG19790; a, front view, × 30; b, c, side and oblique views of arly whorls, × 100; note prominent growth line on second whorl, possibly marking position of aperture of larval shell. **55**, GG19791; a, front view, × 30; b, oblique view of apex, × 100. **56**, GG19792; rear view, × 30. **57**, GG19793; side view, × 30.

whilst his pl. 5, figs 30 and 37 are now assigned to *D. hauxwelli* sp. nov. (see p. 192). The distinctions between *D. gracilis* and *D. hauxwelli* are given under the latter. *D. tricarinata* (Boettger) may be easily separated from *D. gracilis* by its larger apical whorls, greater spire angle and different whorl profile.

Dyris lintea (Conrad, 1871) Figs 49–58

*v 1871 *Isaea lintea* Conrad: 193; pl. 10, fig. 6.
. 1878 *Hydrobia (Isaea) lintea* (Conrad) Boettger: 493.
. 1924 *Isaea lintea* Conrad; Roxo: 49.
. 1926 *Hydrobia (Conradia) lintea* (Conrad); Wenz: 1970.
. 1938 *Hydrobia (Conradia) lintea* (Conrad); de Greve: 83 (*pars*); pl. 1, figs 10–28 (*non* figs 29, 30).
. 1966 *Tryonia lintea* (Conrad) Taylor: 197.
. 1969 *Dyris gracilis* (Conrad); Parodiz: 118 (*pars*).
. 1980 *Hydrobia lintea* (Conrad); Costa: 879; pl. 1, figs 5, 6.
. 1981 *Hydrobia lintea* (Conrad); Costa: 639; pl. 1, figs 3, 4.

HOLOTYPE. NYSM 9252, Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell Colln).

OTHER MATERIAL STUDIED. All Late Caenozoic, Pebasian. G25293–7, Pichana, Peru (Hauxwell Colln); GG19790–5, GG21676–9, GG21680/1-5, Pichana, Peru (Hauxwell Colln, extracted 1982); GG19961, GG21519, GG21681–5, Puerto Nariño, Colombia (Weeda Colln).

FURTHER OCCURRENCES. All late Caenozoic, Pebasian. Pebas (Boettger 1878); Três Unidos (Roxo 1924, Costa 1981); Iquitos (de Greve 1938); CPCAN I, Tamanduá, CPCAN II, Poreré, CPCAN III, São Paulo de Olivença, Afloramento em Italaia do Norte (Costa 1980). Upper Amazon Basin only.

DIAGNOSIS. *Dyris* up to 16 mm high with evenly convex whorls; sculptured with between six and ten spiral ribs per whorl on early whorls; later whorls with spiral grooves.

DESCRIPTION. The description of the early whorls is based on the newly extracted juveniles from Pichana, as all the adults are damaged. The apex of 2–2¼ whorls is naticiform and has a height and breadth of about 0.3 mm. Spiral ribbing develops rapidly on the next whorl and the full number of ribs is developed by the sixth whorl. There are 9–10 whorls in all. The spiral ribs are narrow and separated by convex interspaces. The arrangement of the ribbing is normally fairly regular and of even strength, but more variation is shown in de Greve's illustrations (1938) of Iquitos shells and also in the specimens from Puerto Nariño.

DIMENSIONS. In mm.	h		br	hap	h/br	sa
Holotype NYSM 9252	5.5		2.4	*c.* 1.3	2.25	30°
G25293	5.1		2.1	1.4	2.43	30°–38°
G25294	3.8		1.6	–	–	–
G25295	2.7		–	–	–	38°
(penultimate whorl)			(1.1)			
GG19790	2.40		0.95	0.76	2.53	25°
GG19791	2.25		1.00	0.67	2.25	–
GG19792	2.15		1.00	–	2.15	28°
GG19793	1.87		0.71	–	2.63	–
GG19961	10.5	(e 15+)				18°
GG21519	6.4	(e 12+)	3.2	–	–	–

All Pichana, except GG19961, GG21519 (Puerto Nariño).

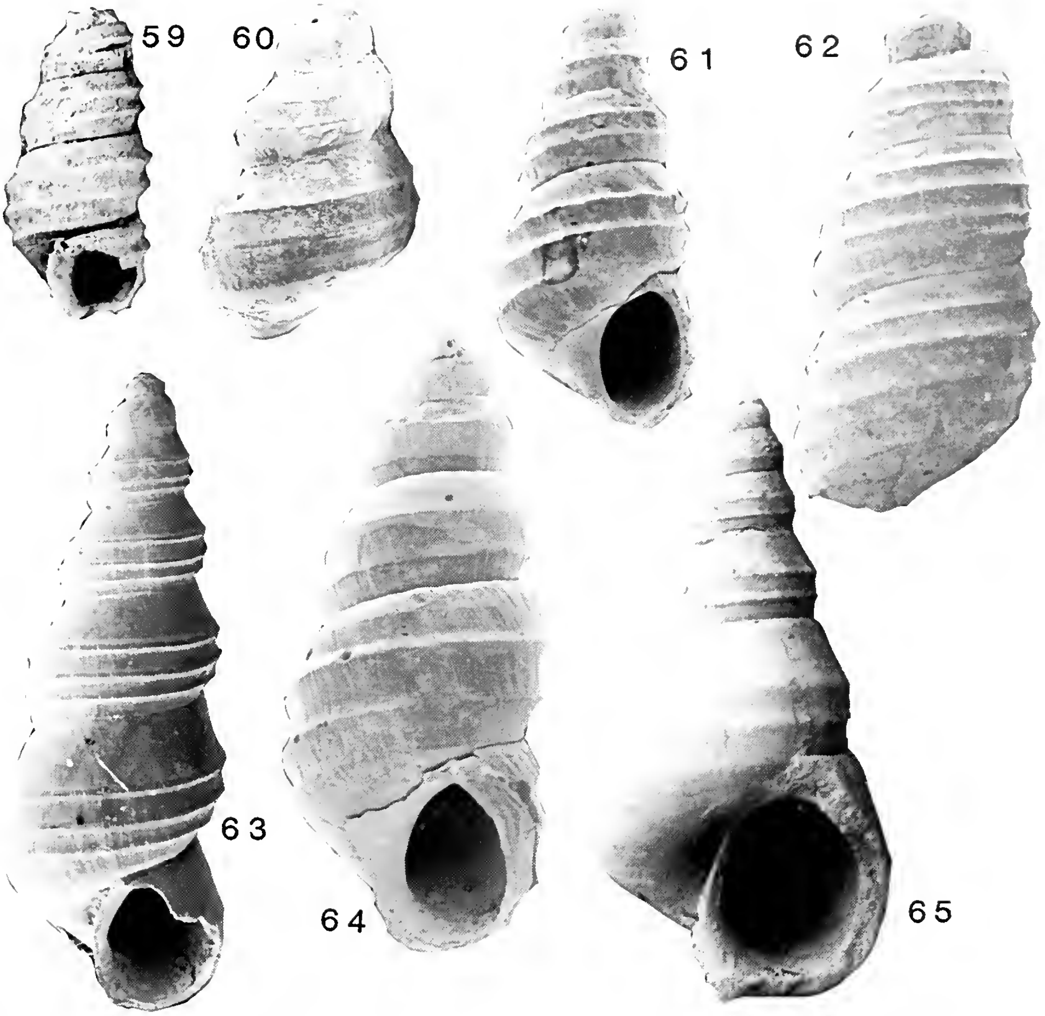
Fig. 58 *Dyris lintea* (Conrad). Pebasian; Puerto Nariño, Colombia; Weeda Colln. GG19961; front view, × 6.

REMARKS. Careful examination suggested that the newly extracted, and often almost perfectly preserved, small shells from Pichana belonged to this species, otherwise known only from rather incomplete adults, all of which, including the worn holotype, lack the early whorls. The penultimate whorl of GG25295 has a breadth of 1.1 mm and both its profile and sculpture appear very similar to those of the specimens here considered to be only partly grown. The large shells from Puerto Nariño are also referred to this species: the typical spiral ribbing is exhibited on the early whorls of GG19961 (Fig. 58), though this is replaced by spiral grooving on later whorls of both this specimen and GG21519. But these determinations, both of the small Pichana shells and the large Puerto Nariño specimens, cannot be regarded as definite because of the lack of well preserved specimens providing a continuous view of how the sculpture develops. Elsewhere, *D. hauxwelli* sp. nov. is separated from the co-occuring *D. tricarinata* (Boettger). The apical whorls of both are preserved and it is clear that the former is a much smaller species. It is felt that the specimens available provide no similar grounds to justify splitting into two species the large and small individuals here all assigned to *D. lintea*.

D. lintea is easily distinguished from other known species of *Dyris* by its more numerous spiral ribs and the fact that they are fairly evenly dispersed over the whorl surface of the spire whorls, which are evenly biconvex. Aciculate specimens of this species most closely resemble *D. gracilis* Conrad, but in the latter the spiral sculpture may be described as consisting of sharply crested carinae, which are less numerous than the ribs of *D. lintea*.

Dyris tricarinata (Boettger, 1878) Figs 59–78

v. 1871*b* *Isaea ortoni* (Gabb) Conrad: 193 (*pars*); pl. 10, fig. 10 (*non* pl. 10, fig. 13)
v. 1871 *Isaea tricarinata* Conrad; Woodward: 108 (*nom. nud*).
*. 1878 *Hydrobia (Isaea) tricarinata* Boettger: 492; pl. 13, figs 10a, b, 11a–c.
. 1926 *Hydrobia (Conradia) tricarinata* Boettger; Wenz: 1971.
. 1938 *Hydrobia (Conradia) tricarinata* Boettger; de Greve: 81; pl. 1, figs 7–9.



igs 59–65 *Dyris tricarinata* (Boettger). Pebasian; Pichana, Peru; Hauxwell Colln. **59**, shell figured by Conrad (1871*b*: pl. 10, fig. 10) as *Isaea rtoni* (Gabb), NYSM 9253; front view, × 10. **60**, GG21692; rear, × 25. **61**, GG21693; front, × 20. **62**, GG21690; rear, × 20. **63**, G25289; front, × 15; see also Fig. 66. **64**, GG21691; front, × 20. **65**, G25290; front, × 15.

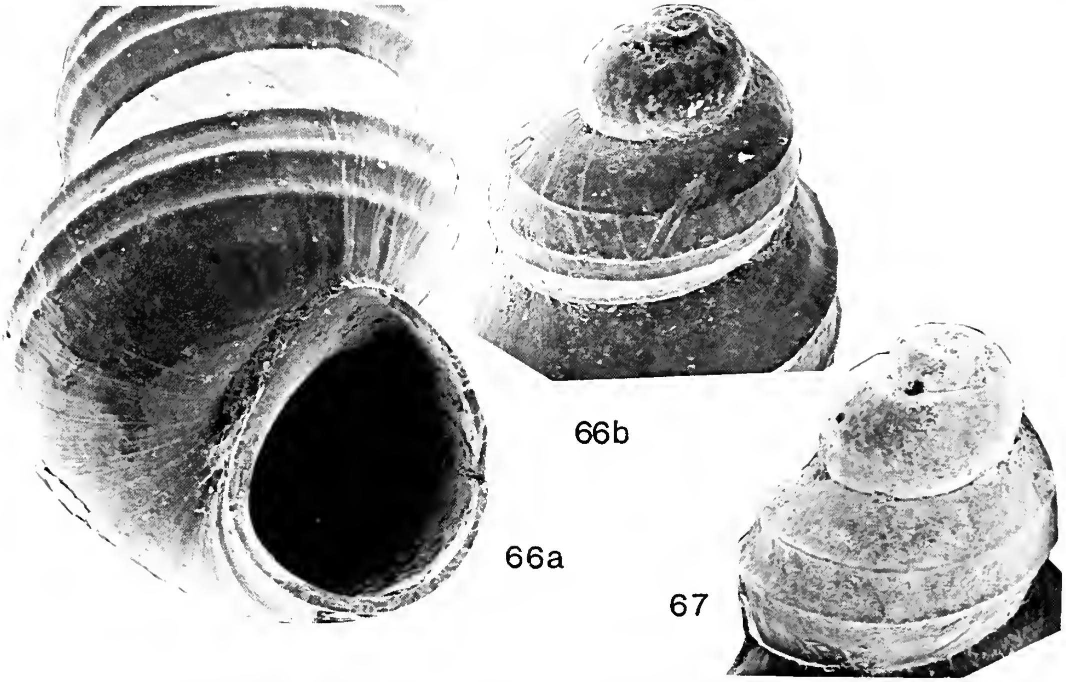
. 1966 *Hydrobia tricarinata* Boettger; Willard: 65; pl. 62, figs 4–6.
. 1966 *Tryonia tricarinata* (Boettger) Taylor: 197.
. 1969 *Dyris gracilis* Conrad; Parodiz: 118 (*pars*).
. 1980 *Hydrobia tricarinata* Boettger; Costa: 878; pl. 1, figs 5, 6.
. 1982 *Dyris* cf. *gracilis* 'form' *carinata* (Boettger); Bristow & Parodiz: 16, 41.

'YPE MATERIAL. Types of *Hydrobia tricarinata* Boettger not tudied. Senckenburg Museum, Frankfurt. One of Boettger's pecimens (1878: pl. 13, fig. 11), was designated by de Greve 1938) as 'Typus' (= Lectotype) and another (1878: pl. 10, g. 10) as Paratype. Both Late Caenozoic, Pebasian; Pebas, 'eru.

IATERIAL STUDIED. Late Caenozoic, Pebasian: G25289–90, ;G21686–8, GG21689/1–30, Pichana, Peru (Hauxwell Colln); ;G21690–4, GG21695/1–20, Pichana, Peru (Hauxwell Colln, xtracted 1982); NYSM 9253, six shells, including the shell gured by Conrad (1871: pl. 10, fig. 10), Pichana, Peru Hauxwell Colln); GG21527–9, Puerto Nariño, Colombia (Weeda Colln). Late Caenozoic: GG19840–9, GG19958, 1.5 km upstream from La Tagua, Colombia (Weeda Colln); GG19936, Loc. 33, 480–560 cm, La Tagua (Eden Colln); GG19929–32, Loc. 54, La Tagua (Eden Colln). ? Upper Miocene (Bristow & Parodiz, 1982: 17), San Cayetano Formation, Loja Basin, Ecuador: GG19809, GG21706–15, Loc. JW 424, Grid ref. 008 582 (Bristow & Parodiz, 1982: 16, 41). G43325–6, Loja (Prof C. Carrion Colln, 1926) are in similar matrix and are probably from the same horizon.

FURTHER OCCURRENCES. Late Caenozoic, Pebasian: Pebas (Boettger 1878, de Greve 1938); CPCAN III, São Paulo de Olivença (Costa 1980); Iquitos (de Greve 1938, Willard 1966). Três Unidos (Roxo 1924) is doubtful. Late Caenozoic, Pebasian, Upper Amazon Basin; Late Caenozoic, La Tagua, Colombia; Loja Basin, Ecuador.

DIAGNOSIS. *Dyris* with large blunt apex; lower half of subsequent whorls sculptured with two or three, or rarely more, prominent spiral carinae; upper half of whorl forming broad, smooth, steeply sloping ramp.



Figs 66–67 *Dyris tricarinata* (Boettger). Pebasian; Pichana, Peru; Hauxwell Colln. **66**, G25289; a, oblique view of apertural region, × 30; b, oblique view of apex, × 66; see also Fig. 63. **67**, GG21692; oblique view of apex, × 50.

DESCRIPTION. The apex consists of 2–2½ biconvex whorls which rapidly increase in size, and are smooth except for opisthocyrt growth lines. Spiral sculpture of sharp, coarse ridges or carinae quickly develops and, in the next whorl or so, these strengthen to superimpose the very variable but basically bicarinate adult whorl profile upon the biconvex smooth profile of earlier whorls. Perhaps the most constant feature is the ramp which occupies virtually all the adapical half of the whorl and slopes steeply at 60°–70°. In some specimens from La Tagua the spiral ribs are more numerous but weaker, so that the profile reverts to biconvex for the last whorl or so. In a small proportion of shells from Pichana the spiral carinae are of irregular strength, giving a slightly frilly appearance. The peristome is rimmed and sometimes slightly detached.

DIMENSIONS. In mm.	h	br	hap	h/br	sa
Lectotype, Pebas (from de Greve, 1938)	5.3	2.25	1.5	2.36	21°
G25289, Pichana	5.8	2.2	1.5	2.32	22°
G25290, Pichana	6.2	3.1	2.0	2.0	45°
GG19936, La Tagua, 33/480–560 cm	5.5	2.2	1.4	2.1	25°
GG19840, 1.5 km upstream from La Tagua	4.9	2.2	1.4	2.23	28°
GG19841, as above.	5.3	2.2	1.5	2.4	28°
GG19842, as above.	4.4	1.2	–	3.67	25°
GG21528, Puerto Nariño.	3.2	1.6	–	2.0	26°
GG21527, Puerto Nariño.	2.8	1.4	–	2.0	26°

REMARKS. De Greve (1938), when designating types, refigured Boettger's (1878) type material from Pebas, but none of his own from Iquitos. De Greve's measurements are highly suspect: he gave two views of the lectotype at different magnifications, but neither agrees with the dimensions that he gave (1938: 83) in his text and which are quoted here. Conrad thought that this species was the young of *Mesalia ortoni* Gabb (see Fig. 59) and, in response to this, the five shells originally registered as G25290 were originally labelled '*Isaea tricarinata* Conrad, possibly the young of *I. ortoni*': this is the sample discussed by Woodward (1871: 108, PS). Boettger, who was aware of the views of Conrad and Woodward, validated the name.

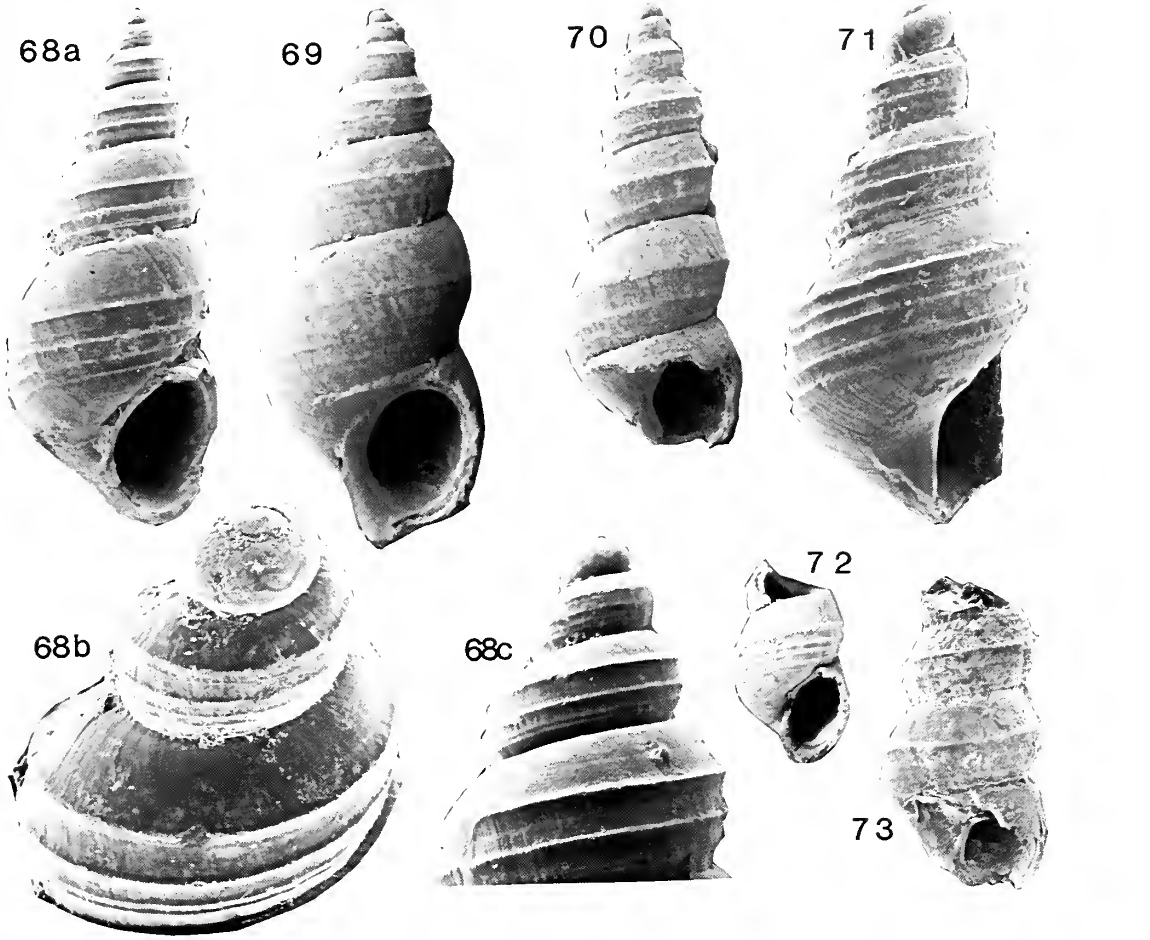
Three other species, *D. lacirana* (Pilsbry & Olsson), *D. semituberculata* sp. nov. (p. 196), and *D. hauxwelli* sp. nov. (below), are similar to *D. tricarinata* in that their spiral ribbing is confined to the lower part of the whorl. *D. lacirana* is known only from poorly preserved material but apparently has a more rounded whorl profile with the ramp less well differentiated, partly because of its weaker ribbing and partly because the ramp itself is slightly convex rather than concave. *D. semituberculata* from La Tagua is distinguished by its collabral folds which produce a much more frilly effect than seen in a small proportion of specimens from Pichana. *D. hauxwelli* is much smaller, with smaller apical whorls and a distinctly biconic whorl profile.

The material (GG18909, GG21706–15, GG43325–6) from the San Cayetano Formation, Ecuador, consists of numerous external moulds on bedding planes in a fine marl. No other species are known to occur in these samples. These specimens are referred to *D. tricarinata* on their size (up to 5 mm in height) and on the character of their ribbing, though their whorl profiles appear to be more pagodiform or biconic than that of the typical Pebasian material. This may, however, be the result of distortion and the fact that sections on bedding planes are seldom sagittal.

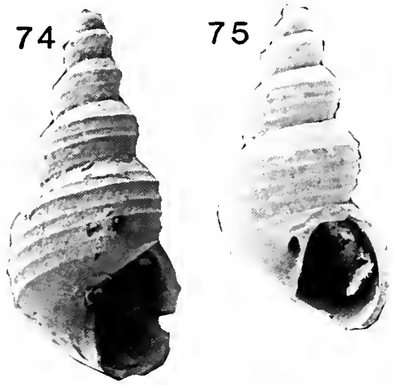
Roxo's record (1924) of the species from Três Unidos is treated as doubtful because it was not confirmed in either of Costa's two recent papers (1980, 1981).

Dyris hauxwelli sp. nov. Figs 79–85

v. 1871*b* *Isaea ortoni* (Gabb); Conrad: 193 (*pars*).
v. 1938 *Dyris (?) gracilis* Conrad; de Greve: 86; pl. 3, figs 21–28; pl. 5, figs 30, 37.
v. 1939 *Dyris gracilis* Conrad; Wenz: 572, fig. 1548.



Figs 68–73 *Dyris tricarinata* (Boettger). Late Caenozoic; La Tagua, Colombia. **68–70**, 1.5 km upstream from La Tagua; Weeda Colln. **68**, GG19840; a, front, × 15; b, oblique view of apex, × 75; c, side view of early whorls, × 40. **69**, GG19841; front, × 15. **70**, GG19842; × 15. **71–72**, Loc. 54; Eden Colln. **71**, GG19930; × 40. **72**, GG19929; × 12. **73**, GG19936; × 15; Loc. 33/480–560; Eden Colln.



Figs 74–75 *Dyris tricarinata* (Boettger). Pebasian; Puerto Nariño, Colombia; Weeda Colln. **74**, GG21527; front, × 20. **75**, GG21528; front, × 15.

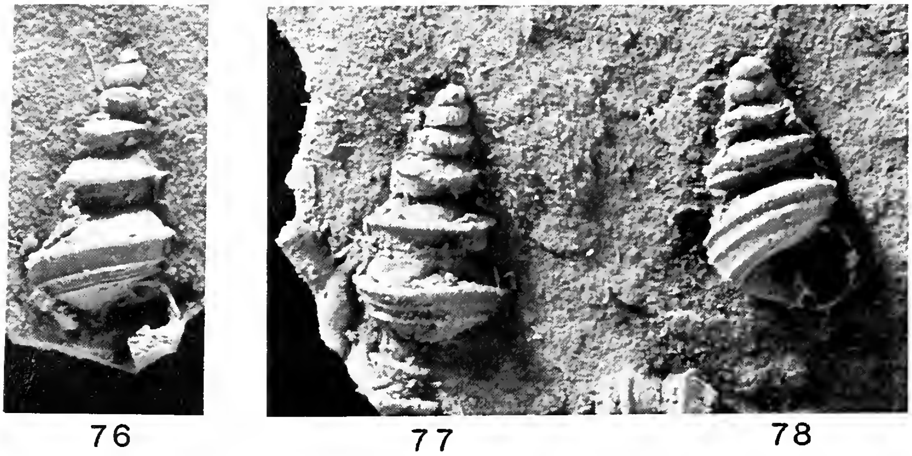
HOLOTYPE. GG19792, Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell Colln, extracted 1982). The following are paratypes; all Late Caenozoic, Pebasian. GG19793, GG21627–9, GG21696–705, Pichana, as above; NYSM 9253, one of seven hells misidentified by Conrad as *Isaea ortoni* (Gabb) – the emaining six are now reidentified as *D. tricarinata* (Boettger). GG19799, GG19960, Canamá (C. Barrington Brown Colln, extracted 1982); PIMUZ 491A, unfigured by de Greve (1938); PIMUZ 497C, de Greve, pl. 5, fig. 30 which was copied by Wenz (1939: fig. 1548); PIMUZ 491B, de Greve, pl. 5, fig. 37, all Iquitos. No other records.

NAME. From Juan Hauxwell's Collection, purchased by the BM in 1870.

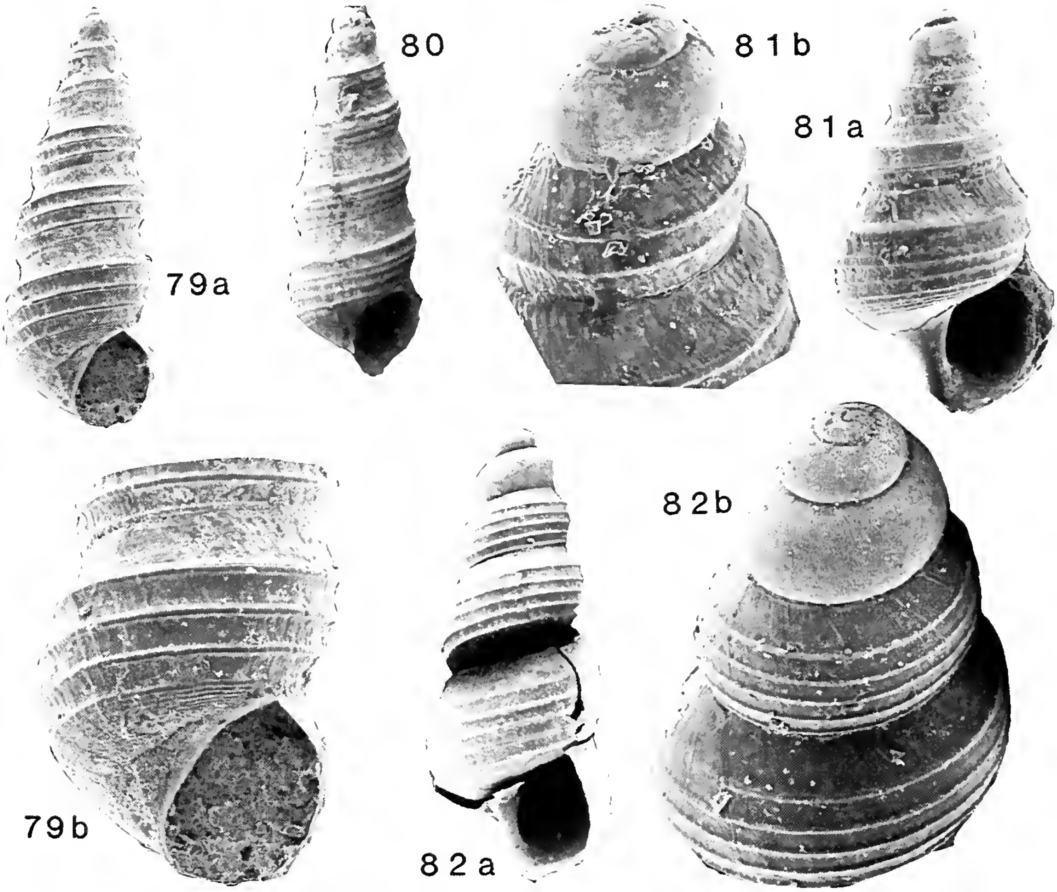
DISTRIBUTION. Late Caenozoic, Pebasian only. Upper Amazon basin only.

DIAGNOSIS. Like *Dyris tricarinata*, but much smaller, attaining the same number of whorls in half the height and with a markedly pagodiform whorl profile.

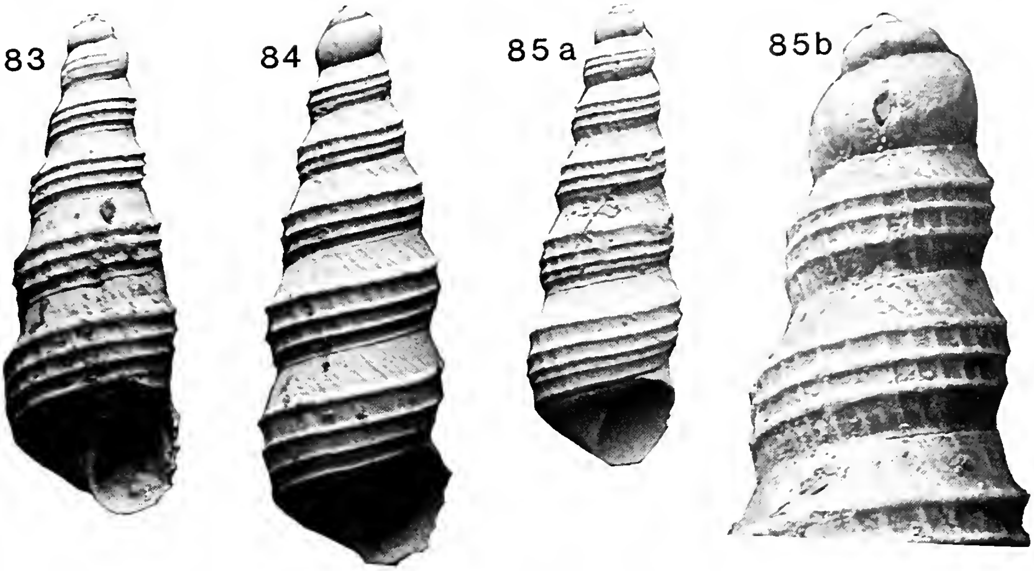
DESCRIPTION. This species has a height of under 3 mm and has about eight whorls. The spiral ribs, which are first seen on the third whorl, are relatively prominent for its size; that at the periphery is normally the strongest and those below it are progressively weaker towards the abapical suture. There are normally three or four ribs on each whorl but a small proportion of Pichana shells and the two from Canamá have five or six. Very weak threads can be seen on the base of the body whorl of the Iquitos shells and on some of those from Pichana. On the Iquitos shells, some of the growth lines are sufficiently strong to produce the appearance of collabral ribbing.



Figs 76–78 *Dyris tricarinata* (Boettger). San Cayetano Formation, presumed Miocene; Loc. JW 424, Loja Basin, Ecuador; all × 10. **76**, GG21706. **77**, GG21707. **78**, GG21708.



Figs 79–82 *Dyris hauxwelli* sp. nov. Pebasian. **79–81**, Pichana, Peru; Hauxwell Colln. **79**, **holotype**, GG19792; a, front, × 25; b, apertural region, × 50. **80**, paratype, GG21627; front, × 25. **81**, GG21628; a, front, × 40; b, oblique view of apex, × 100. **82**, GG19799; Canamá, Peru; Barrington Brown Colln. a, front, × 40; b, oblique view of apex, × 75.



Figs 83–85 *Dyris hauxwelli* sp. nov. Pebasian; Iquitos, Peru; originally identified by de Greve (1938) as *Dyris gracilis* Conrad. **83**, PIMUZ 491a; front, × 30. **84**, PIMUZ 491b, figured by de Greve (1938: pl. 5, fig. 37); front, × 30. **85**, PIMUZ 497c; a, front, × 30; b, apical whorls, × 75, figured by de Greve (1938: pl. 5, fig. 30).

IMENSIONS. In mm.	h	br	hap	h/br	sa
olotype, GG19792, Pichana.	2.32	0.90	0.53	2.58	21°
G21627, Pichana.	2.60	0.95	0.70	2.74	22°
G21628, Pichana.	1.38	0.75	–	1.84	32°
G21629, Pichana.	1.3	0.7	–	1.85	32°
G19799, Canamá.	2.1	0.83	0.5	2.53	24°
IMUZ 497C, Iquitos.	2.1	0.7	0.4	3.0	18°
IMUZ 491B, Iquitos.	2.5	0.8	0.4	3.1	20°
IMUZ 491A, Iquitos.	2.3	0.8	0.5	2.9	18°

EMARKS. The differences between similar species of *Dyris* vith smooth ramps are discussed under *D. tricarinata* Boettger), p. 192. No difficulty was encountered in separating *). hauxwelli* from *D. tricarinata* in the newly extracted 3MPD material from Pichana. It is probable that this small pecies has been overlooked by earlier workers and that it is nore widespread than indicated here. For example, de Greve 1938) had separated his specimens from *D. tricarinata* but ad identified them as *D.* (?) *gracilis*. Had he been able to xamine the types of that very different species, he would robably have concluded that his material belonged to an ndescribed species.

)yris lacirana (Pilsbry & Olsson, 1935) Fig. 86

v 1935 *Potamopyrgus laciranus* Pilsbry & Olsson: 9; pl. 5, fig. 6.
. 1966 *Tryonia lacirana* (Pilsbry & Olsson) Taylor: 197.
. 1969 *Lyrodes laciranus* (Pilsbry & Olsson) Parodiz: 117; pl. 16, fig. 4 (a copy of the type illustration).

IOLOTYPE. ANSP 13074, Miocene, La Cira Formation; near opffs, La Cira district, Colombia (W. W. Waring Colln). he numerous accompanying specimens, all on blocks of ndurated haematitic sandstone (co-occurring with paralectoypes of *Pachydon abundans* (Pilsbry & Olsson), herein placed in the synonymy of *P. cebada* (Anderson, 1928): see p. 311) are paratypes.

OTHER RECORDS. ‘Also at many localities near La Cira’ (Pilsbry & Olsson 1935: 9).

DISTRIBUTION. Only known from the La Cira Formation, as above. This formation was dated as either late Oligocene or early Miocene by Pilsbry & Olsson (1935), but is here regarded as Miocene.

DIAGNOSIS. *Dyris* with spiral ribs increasing from two to five with growth and confined to the lower half of whorl; whorl profile biconvex to weakly carinate at mid whorl-height.

DESCRIPTION. All the specimens are damaged: neither the apical whorls nor the aperture are properly known and the ribbing can only be examined on small, isolated, areas of shell surface. The spiral ribs, which are absent from the upper part of the whorl, are weak and increase in number from two or three on early whorls to five on the last whorl. On early whorls, the uppermost rib is just above the periphery but on later whorls it descends as low as the periphery. The whorl profile is usually evenly biconvex, though exceptionally the topmost rib forms a weak carina.

DIMENSIONS. In mm.	h	br	hap	sa
Holotype, ANSP 13074	3.9	1.8	–	30°

REMARKS. Comparisons with similar species are given under *D. tricarinata*, p. 192. The similarities are sufficient to suggest that this species should be assigned to *Dyris* as opposed to any of the genera used by previous authors. *Potamopyrgus* is based on a living New Zealand species, *Melania corolla* Gould, 1847. Its whorls are coronated with spines, and it seems unlikely that the genus occurs in South America. *Lyrodes* is widespread in South America at the present day

Fig. 86 *Dyris lacirana* (Pilsbry & Olsson). La Cira Formation, dated herein as Miocene; near Zopffs, Middle Magdalena Valley, Colombia; W. W. Waring Colln. Holotype, ANSP 13074; × 15. Note that the type illustration of Pilsbry & Olsson (1935: pl. 5, fig. 6) appears to be a reconstruction, and is probably based partly on this specimen.

(Parodiz 1969: 117). It differs from *Dyris* in being thinner-shelled, translucent and very finely spirally striate.

Pilsbry & Olsson's original figure was copied by Parodiz (1969). It is a reconstruction which cannot be matched with any of the ANSP specimens seen. It bears some resemblance to the specimen which has been isolated as holotype (ANSP 13074; Fig. 86) but this has one less whorl than the illustration. However, both the character of the ribbing and the whorl profile are accurately represented.

Dyris semituberculata sp. nov. Figs 87–102

HOLOTYPE. GG19853, Late Caenozoic; 1.5 km upstream from La Tagua, Colombia (Weeda Colln). The following are paratypes: GG19850/1–3 (juveniles), GG19854–5, GG21620–5, GG21626/1–10 (all as above); GG19937–9, GG19940/1–5, Loc. 54, La Tagua (Eden Colln); GG21716, GG21226–9, Loc. 33/480–560 cm, La Tagua (Eden Colln).

NAME. Distinct from *tuberculata*, with less marked sculpture.

DIAGNOSIS. *Dyris* with collabral sculpture on later whorls, consisting of about twenty folds or wrinkles per whorl; ramp smooth, with carinate shoulder below, both sometimes lost on later whorls as they become biconvex; spiral sculpture variable, up to about nine ribs per whorl.

DESCRIPTION. The sculpture is very variable and has a strong influence on the equally inconstant whorl profile. The first whorl is very small in comparison with the second which is bulbous, strongly biconvex, and twice as broad as high. The spiral sculpture first develops on the next whorl, as a carina with a broad ramp above. A second carina soon forms, thus making the whorl profile convexly bicarinate. Up to nine spiral ribs of varying strength may form on the spire whorls. As their number increases they tend to weaken and the whorl profile becomes biconvex with the periphery lying at mid whorl-height in most specimens. In some, however, a carinate shoulder with a comparatively smooth ramp above persists. About five more spiral ribs are present on the upper part of the base of the body whorl. Collabral sculpture does not appear until the fifth whorl and consists of low amplitude folds, often rather pinched at both sutures. The peristome is only lightly pressed against the body whorl, but is not detached. The base is usually almost umbilicate.

DIMENSIONS. In mm.	h	br	hap	h/br	sa
Holotype, GG19853, 1.5 km upstream of La Tagua.	5.8	2.2	1.5	2.45	30°
Paratype, GG21716, Loc. 33/480–560, La Tagua.	5.5	2.5	1.4	2.2	–

Note. The majority of specimens are too incomplete to provide meaningful measurements.

REMARKS. In *D. tuberculata* (de Greve), the collabral sculpture consists of much stronger but less numerous folds and its peristome is often detached. Juveniles of *D. semituberculata* and *D. tricarinata* (Boettger) are similar, but the early whorls of the new species are smaller and have a much more angular profile. A biconvex profile of later whorls is a common feature of *D. semituberculata* but rare in *D. tricarinata*. In the latter, the sculpture never develops such a strongly frilly appearance.

Dyris tuberculata (de Greve, 1938) Fig. 103

* 1938 *Liris tuberculata* de Greve: 96; pl. 2, figs 32–35; pl. 3, figs 1–20; text-figs 19–22.
. 1939 *Liris tuberculata* de Greve; Wenz: 572, fig. 1549 (copy of de Greve, pl. 3, fig. 10?).
1966 *Liris tuberculata* de Greve; Willard: 69, 93.
. 1966 *Tryonia tuberculata* (de Greve) Taylor: 197.
. 1969 *Liris tuberculata* de Greve; Parodiz: 120.

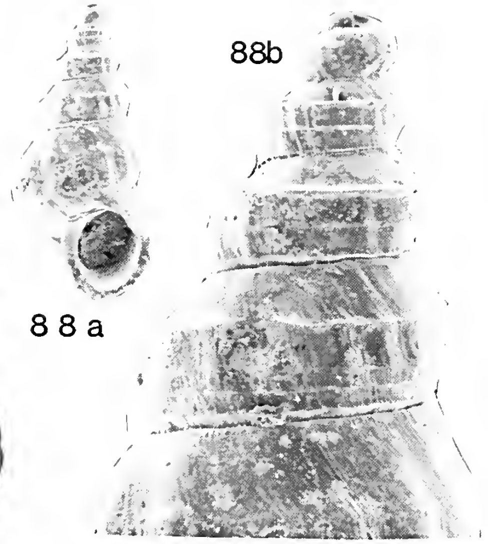
HOLOTYPE. PIMUZ 423, Late Caenozoic, Pebasian; Iquitos, Peru (de Greve 1938: pl. 2, figs 32–34) (Peyer Colln). About a dozen specimens (de Greve 1938), same details as holotype, are paratypes.

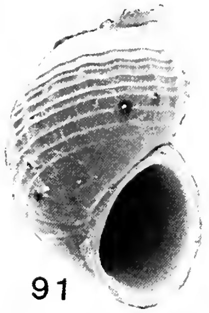
OTHER MATERIAL. A specimen (Fig. 103) was found loose with PIMUZ 317, *Hemisinus kochi* (Bernardi) (p. 241), from Iquitos; same details as above.

DISTRIBUTION. Late Caenozoic, possibly confined to Pebasian of Iquitos, Peru. A doubtful record is from the late Caenozoic, Rio Aguaytia, about 25 km from confluence with Rio Ucayali, *c.* 100 km south of Contamana (Willard 1966).

DIAGNOSIS. *Dyris* with bicarinate whorls and 14–20 strong collabral ribs; peristome frequently detached.

DESCRIPTION. The spire angle decreases markedly with growth in individual shells and also varies between 14° and 34° within the species. The first two whorls are smooth, strongly biconvex, and tilted about 45° to the shell axis. Two weak spiral ribs are developed on the next whorl. The first traces of collabral sculpture consist of up to twenty nodes per whorl, set at regular intervals. By the fourth whorl these nodes develop into short collabral ribs in the peripheral region bounded by the two spiral carinae. On the fifth and sixth whorls, the collabral ribs gradually spread onto both the ramp and the lower part of the whorl. By the seventh whorl both the sculpture and the bicarinate whorl profile have assumed their adult form. Secondary spiral ribs are present. One occurs near the periphery, between the two spiral carinae:



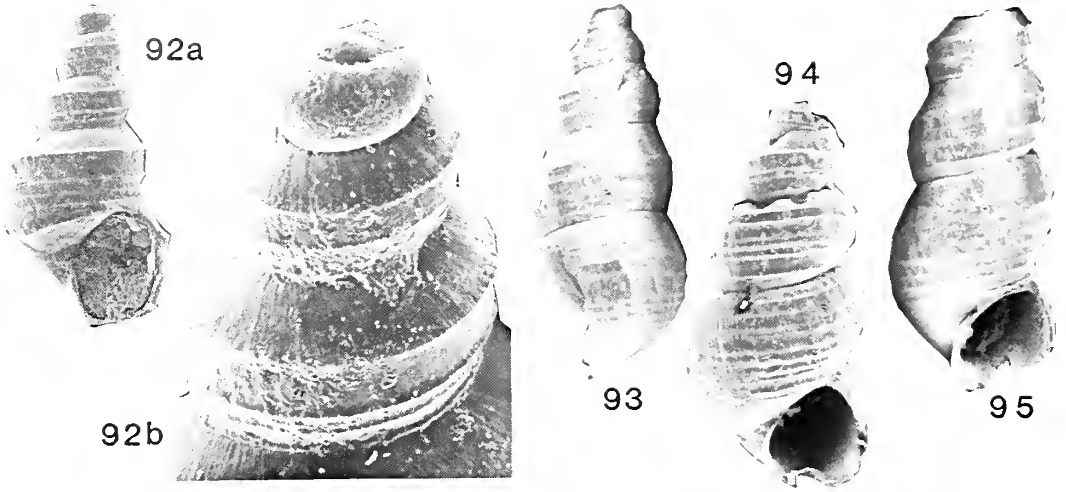


Figs 87–91 *Dyris semituberculata* sp. nov. Late Caenozoic; 1.5 km upstream from La Tagua, Colombia; Weeda Colln. **87**, **holotype**, GG19853; front, × 15. **88–91**, paratypes. **88**, GG21623; a, front, × 12.5; b, early spire whorls, × 50. **89**, GG21621; front, × 20. **90**, GG 19854; a, front, × 20; b, penultimate whorl, × 40. **91**, GG21625; front, showing undamaged aperture, × 10.

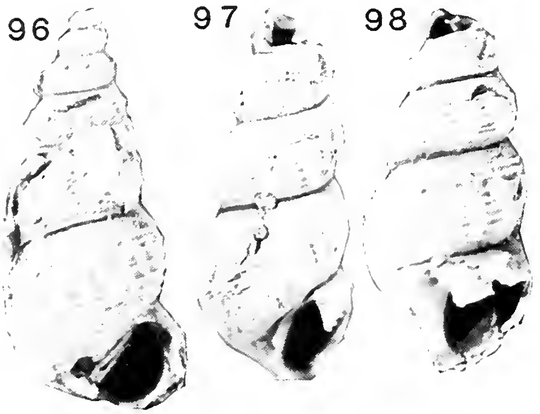
another quite strong rib lies between the lower carina and the lower suture. A further carina lies at the lower suture; it is only partly exposed, except on the body whorl of specimens with detached peristomes, when it is revealed to be extremely strong, forming a flange which separates the side from the base of the whorl. The *c*. 20 collabral nodes on the early whorls reduce to 14–16 collabral ribs on the later whorls. In section, these ribs are of an angular, zigzag pattern, except near both sutures where they broaden into low semiangular folds. As far as can be seen, the ribbing runs parallel to the growth lines, and is therefore collabral. The growth lines are weak, except on the base. In the single studied specimen, the sculpture is reduced in strength on the last whorl as it approaches the aperture. The base of the whorl is convex and lacks ribbing. The peristome is detached in some, but not all,

DIMENSIONS. In mm.	h	br	h/br	sa
PIMUZ 423, holotype (de Greve 1938: pl. 2, figs 32–34).	5.4 (4.6)	2.3	2.35	(30°–22°)
PIMUZ 418D (pl. 3, fig. 5).	5.5	1.9	2.89	(18°)
PIMUZ 430 (pl. 3, fig. 7).	5.5	2.3	2.39	(34°)
PIMUZ (studied herein).	4.6	1.65	2.79	22°

Note. Except for the un-numbered specimen studied herein, the figures are taken either from de Greve's (1938) text or from his plates; the latter are given in brackets. The discrepancies are particularly great in the case of the holotype.



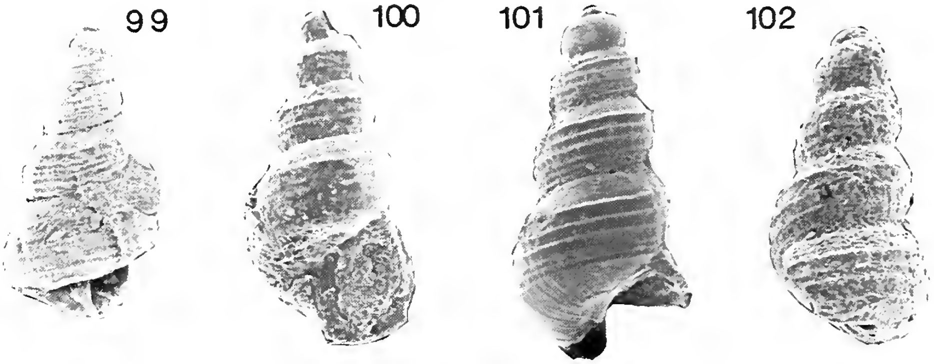
Figs 92–95 *Dyris semituberculata* sp. nov. Late Caenozoic; 1.5 km upstream from La Tagua, Colombia; Weeda Colln. Paratypes. **92**, GG21624; a, front, × 25; b, oblique view of early spire whorls, × 100. **93**, GG21622; side, × 15. **94**, GG19855; front, × 15. **95**, GG21620; front, × 15.



Figs 96–98 *Dyris semituberculata* sp. nov. Late Caenozoic; Loc. 54, La Tagua, Colombia; Eden Colln. Paratypes, all × 12.5. **96**, GG19937. **97**, GG19938. **98**, GG19939.

of the specimens figured by de Greve (1938). The rounded outer lip and semi-straight inner lip are joined below in an even curve and above at an angulation. The aperture tends to be more rounded in specimens with detached peristomes.

REMARKS. This species differs from *D. semituberculata* sp. nov. (p. 196) in having much stronger and more regular sculpture and fewer collabral ribs. *Liris tuberculata* de Greve is here transferred to *Dyris*, because of its apparent affinity with *D. semituberculata* and the close resemblance of its early whorls to those of specimens PIMUZ 491B and 497C from Iquitos. These were figured by de Greve (1938: pl. 5, fig. 37 and pl. 5, fig. 30, respectively) as *Dyris gracilis* Conrad, but are here reidentified as *D. hauxwelli* sp. nov. (p. 192). Although these specimens differ from ones from Pichana, the type locality of *hauxwelli*, in having prominent collabral striae they are unmistakably *Dyris* rather than *Liris*.



Figs 99–102 *Dyris semituberculata* sp. nov. Late Caenozoic; Loc. 33/480–560, La Tagua, Colombia. Paratypes. **99**, GG21226; × 20. **100**, GG21227; × 30. **101**, GG21228; × 40. **102**, GG21229; × 50.

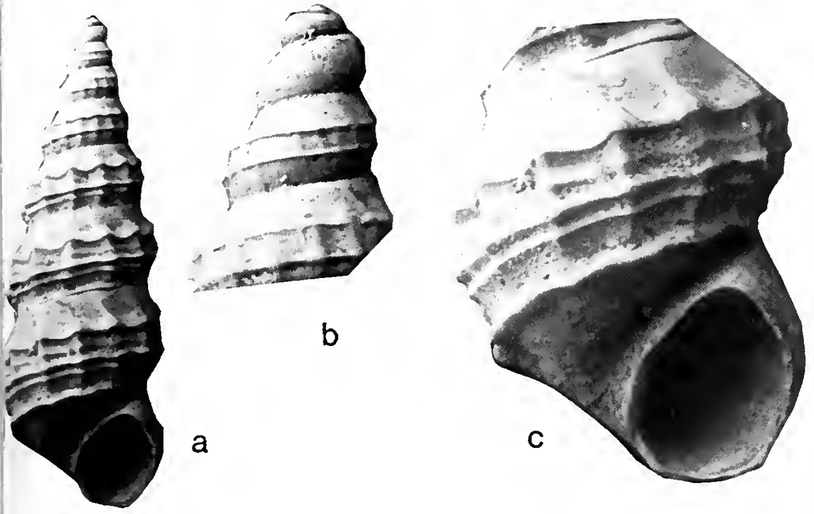
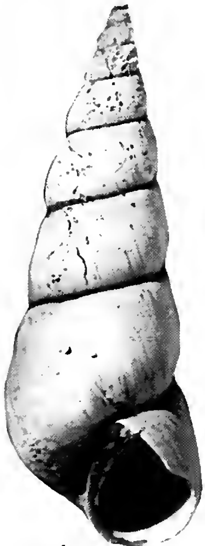
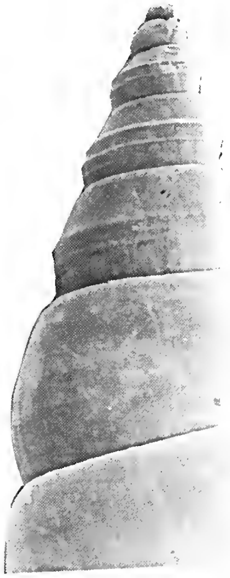


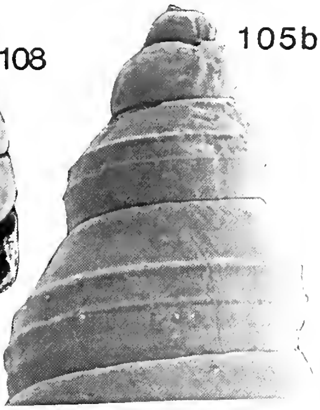
Fig. 103 *Dyris tuberculata* (de Greve). Pebasian; Iquitos, Peru. PIMUZ, unregistered. a, front, × 15; b, early spire whorls, × 50; c, body whorl and aperture, × 30.

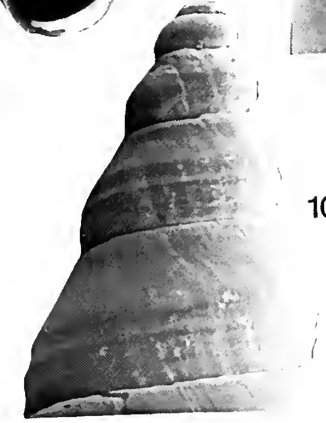

104

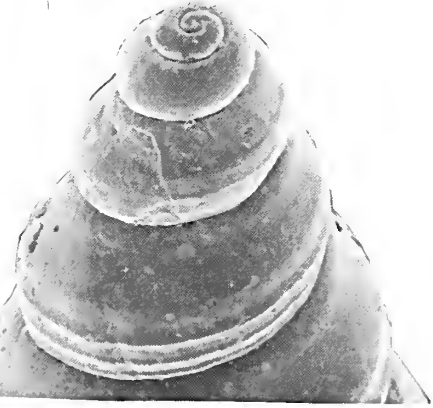

107


105a

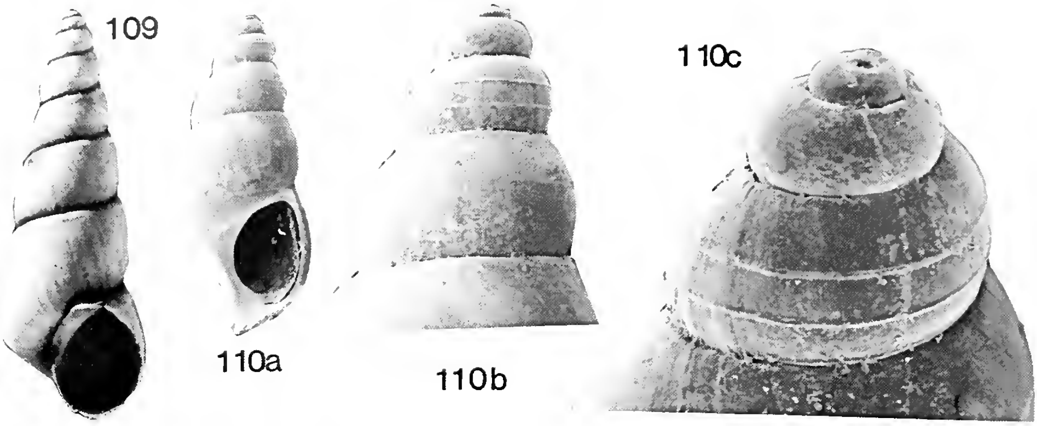

108


105b


106a


106b

Figs 104–108 *Dyris ortoni* (Conrad). Pebasian; Pichana, Peru; Hauxwell Colln. **104**, G25291; front, × 6. **105**, GG21632; a, × 15; b, × 30. **06**, GG21631; a, × 30; b, × 50. **107**, G25472, specimen figured by Woodward (1871: pl. 5, fig. 4) as *Odostomia* sp.; front, × 6. **108**, G25292; front, × 5.



Figs 109–110 *Dyris ortoni* (Conrad). Pebasian; Puerto Nariño, Colombia; Weeda Colln. **109**, GG19911; front, × 6. **110**, GG19912; a, front, × 10; b, early whorls, × 25; c, oblique view of apex, × 50.

Dyris ortoni (Gabb, 1869) Figs 104–112

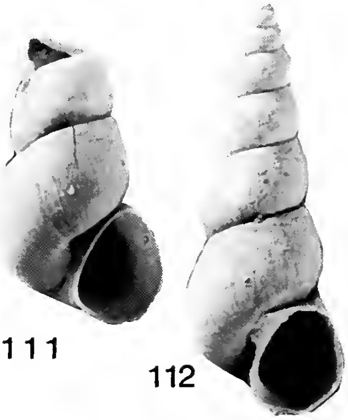
*. 1869 *Mesalia ortoni* Gabb: 198; pl. 16, fig. 3.
. 1871*b* *Isaea ortoni* (Gabb) Conrad: 193 (*pars*); pl. 10, fig. 13 (*non* pl. 10, fig. 10).
v. 1871 *Odostomia* ? Woodward: 103; pl. 5, figs 4a, b.
v. 1871 *Isaea (Mesalia) ortoni* (Gabb); Woodward: 108.
. 1878 *Hydrobia (Isaea) ortoni* (Gabb) Boettger: 490; pl. 13, figs 8a, b, 9a, b.
. 1878 *Hydrobia (Isaea) confusa* Boettger: 491; pl. 13, figs 4–7.
. 1924 *Isaea (Mesalia) ortoni* Gabb; Roxo: 49.
. 1926 *Hydrobia (Conradia) confusa* Boettger; Wenz: 1970.
. 1926 *Hydrobia (Conradia) ortoni* (Gabb); Wenz: 1971.
. 1938 *Hydrobia (Conradia) ortoni* (Gabb); de Greve: 79; pl. 1, figs 5, 6.
. 1938 *Hydrobia (Conradia) confusa* Boettger; de Greve: 80; pl. 1, figs 1–4.
. 1966 *Hydrobia confusa* Boettger; Willard: 65–68; pl. 63, figs 3, 4.
. 1966 *Isaea ortoni* (Gabb); Willard: 66–68, pl. 63, figs 1, 2.
. 1966 *Tryonia confusa* (Boettger) Taylor: 197.
. 1966 *Tryonia ortoni* (Gabb) Taylor: 197.
. 1969 *Dyris ortoni* (Gabb) Parodiz: 118.

Type material. *Mesalia ortoni* Gabb (1869), described from Pebas, Peru. Presumed lost, as it is not listed as present in ANSP by Richards (1968).

Types of *Hydrobia confusa* Boettger (1878) not studied. Senckenburg Museum, Frankfurt (refigured by de Greve, 1938).

Material studied. All Late Caenozoic. G25291–2, GG21631–4, GG21717–25, about 20 specimens, Pichana, Peru, Hauxwell Colln; GG19910–5, GG21726–35, about 60 specimens, Puerto Nariño, Colombia, Weeda Colln. G25472, Pichana, figured as *Odostomia*? by Woodward (1871), Hauxwell Colln.

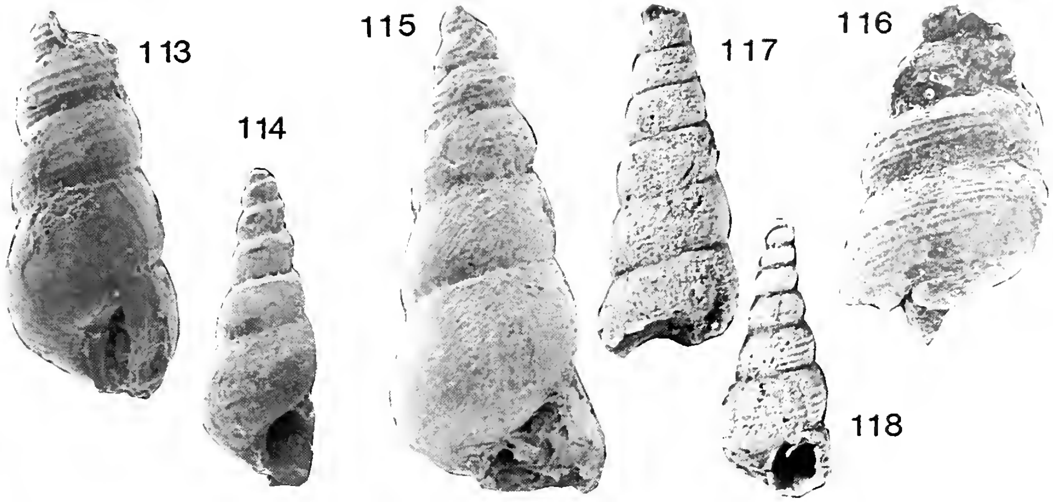
Further occurrences. Late Caenozoic, Pebasian; Amazon Basin. Pebas (Gabb 1869, Boettger 1878); Três Unidos (Roxo 1924); Iquitos (de Greve 1938). Iquitos (Willard 1966: 65); Rio Marañon, 10 km above Iquitos (1966: 66); Rumi Tuni, 225 km north of Iquitos (1966: 67); 30 km north o Iquitos (1966: 68). No other records.



Figs 111–112 *Dyris ortoni* (Conrad). Pebasian; Puerto Nariño, Colombia; Weeda Colln. Both × 6. **111**, GG19913. **112**, GG19910.

Diagnosis. Large, mainly smooth, high-spired *Dyris*, with spire angle between 15° and 33°, normally decreasing with growth; weak spiral sculpture usually confined to early whorls.

Description. The first two whorls are smooth, naticoid, an form a comparatively obtuse apex. The succeeding two o three whorls are also normally slightly less acute than the rest of the spire. Spiral sculpture is usually present and seldom consists of more than three randomly placed ribs which are normally confined to the third to fifth whorls. The uppermost rib forms an angulated shoulder, above which there is broad, fairly steep, ramp. In most specimens, the rest of the shell is smooth except for clearly visible but weak growth lines. In a very small proportion of the shells from Puerto Nariño, up to about ten spiral ribs are present on all but a few of the earliest whorls. The whorl profile is broadly biconve with the periphery well below half whorl height. The profile is often slightly flattened above the periphery and the maximum convexity occurs near the incised sutures. The aperture is fairly small, a third of shell height or less, tear-shaped pointed above and rounded below. The inner lip is flared an



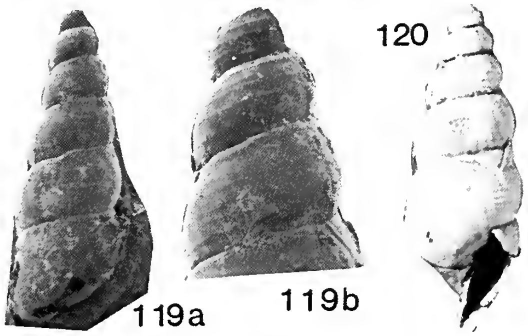
Figs 113–118 *Dyris* sp. Late Caenozoic; Loc. 33/480–560, La Tagua, Colombia; Eden Colln. **113**, GG19933/1; × 20. **114**, GG19933/2; × 20. **115**, GG19933/3; × 25. **116**, GG19933/4; × 15. **117**, GG19948/1; × 12. **118**, GG19948/2; × 12.

lightly detached from the base of the body whorl, exposing a mall umbilicus.

IMENSIONS. In mm.	h	br	hap	h/br	sa
ype of *Mesalia ortoni* Gabb; ebas (from Gabb, 1869, = 0.35").	8.9	–	–	–	24°
ectotype of *Hydrobia confusa* oettger; Pebas (from de Greve, 938: pl. 1, fig. 1).	11.0	4.1	3.2	2.7	26°
pecimen figured by Boettger 1878) as *H. ortoni* (from de reve, 1938: pl. 1, fig. 5).	9.8	3.3	2.2	4.5	20°
25291, Pichana.	13.4	4.5	3.3	3.0	22°
25292, Pichana.	6.7	2.9	2.2	2.3	32°
G21631, Pichana.	9.5	3.6	–	–	–
25472, *Odostomia*? of Voodward (1871)	5.7+	2.7	2.0	–	–
G19910, Puerto Nariño.	9.5	3.4	2.6	2.8	22°
G19911, Puerto Nariño.	7.6	2.8	2.4	2.7	22°
G19912, Puerto Nariño.	4.7	2.2	–	–	32°

EMARKS. One of the specimens figured by Conrad (1871: l. 10, fig. 13) is of this species but has not been seen and may e lost. The other (NYSM 9253) is of *Dyris tricarinata* Boettger). The rich samples from both Pichana and Puerto ariño suggest that *Hydrobia confusa* Boettger is merely a ss aciculate form of *ortoni*, and, following Parodiz (1969), is laced in synonymy. The two forms nearly always occur ogether. De Greve (1938) records both *Hydrobia ortoni* and *. confusa* from Iquitos and refigured Boettger's (1878) aterial from Pebas. The spire angles measured from de reve's pl. 1 range from 15° to 19° for *H. ortoni* and between 8° and 33° for *H. confusa*: not between 30° 30′ and 39° 30′ as iven in his text. The most acutely spired example of *. ortoni* that de Greve figured (1938: pl. 1, fig. 6) has a arkedly obtuse apex.

D. ortonii may be recognized by its large size and compara- ve smoothness. The spirally sculptured early whorls distin- uish it from the smooth-shelled living *Heleobia* and *Littoridina*, whilst living *Lyrodes* has weaker but more persistent spiral sculpture covering a much greater proportion of the shell surface.



Figs 119–120 *Dyris* sp. Late Caenozoic; La Tagua, Colombia; Eden Colln. **119**, Loc. 33/560, GG 19932/1; a, × 10; b, early whorls to show spiral ribbing, × 25. **120**, Loc. 54, GG19949; × 15.

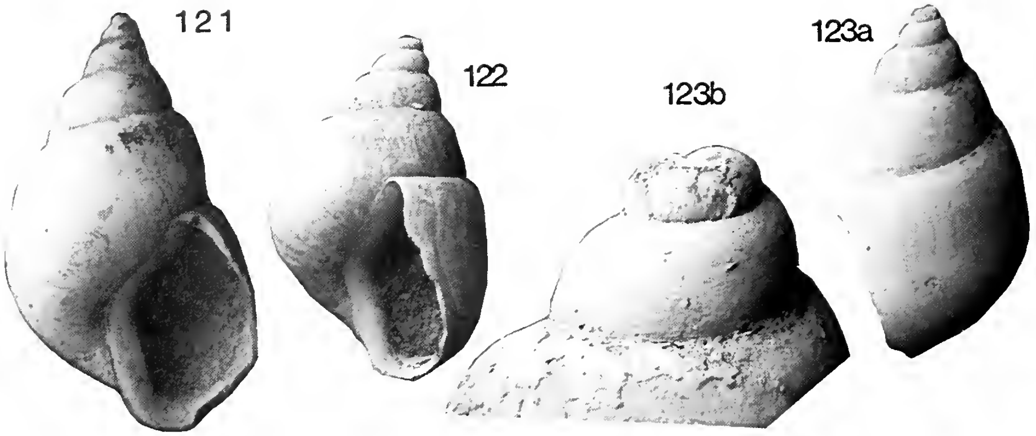
***Dyris* sp.** Figs 113–120

v. 1982 *Dyris gracilis* Conrad; Nuttall *in* Bristow & Parodiz: 20.

v. 1982 *Hydrobia* cf. *ortoni* (Gabb); Nuttall *in* Bristow & Parodiz: 20.

MATERIAL STUDIED. All Late Caenozoic, La Tagua (Eden Colln). GG19932/1–2, Loc. 33, 560 cm; GG19933–4, GG19935/1–6, GG19948/1–5, Loc. 33, 480–560 cm; GG19949/1–3, Loc. 54.

REMARKS. The material is too poorly preserved and fragmentary to justify formal description. The above samples consist of small aciculate gastropods, with fine spiral sculpture: some specimens are virtually smooth, but this is probably the result of wear. It is not entirely certain that only one species is present (see above synonymy). Nuttall *in* Bristow & Parodiz (1982) referred the spirally-ribbed specimens to *D. gracilis* and the smooth shells to *Hydrobia* cf. *ortoni*. These determinations were made before type and other well documented



Figs 121–123 *Littoridina crassa* (Etheridge). Pebasian; Canamá, Peru; Barrington Brown Colln. **121**, GG19993/1, lectotype, figured by Etheridge (1879: pl. 7, fig. 11) as *Hydrobia dubia* Etheridge, and by Kadolsky (1980: figs 13, 14) as *Littoridina crassa*; front, × 10. **122**, paralectotype, GG19993/2; between front and side view, × 10, to show columella and outer lip. **123**, paralectotype, GG19993/3; a, side, × 10; b, apical whorls from side, × 30.

material could be examined. By extrapolation from broken fragments, the height would appear to be about 5 mm and the breadth 1.6 mm. The apex is blunt, but the spire angle averages only about 20°. About six spiral threads may be counted with difficulty, and their spacing is variable. In some specimens they occur over the whole surface of each whorl, but in others they are closely spaced and confined to below the periphery.

These specimens cannot be matched with any described species, though they have some resemblance to juvenile shells of *D. lintea*, which, however, are considerably less aciculate.

Genus *LITTORIDINA* Souleyet, 1852

?Littoridina crassa (Etheridge, 1879) Figs 121–123

*v 1879 *Assiminea crassa* Etheridge: 86.
* 1879 *Hydrobia dubia* Etheridge: 86; pl. 7, fig. 11.
v. 1980 *Littoridina crassa* (Etheridge) Kadolsky: 371, figs 13, 14.
v. 1982 *Toxosoma eboreum* Conrad; Parodiz *in* Bristow & Parodiz: 41 (*pars*, *non* fig. 16).

LECTOTYPE of *Assiminea crassa* Etheridge, GG19833/1 (*ex* BMPD 97225), Late Caenozoic, Pebasian; Canamá (C. Barrington Brown Colln), selected by Kadolsky, 1980: 371, fig. 13. GG19833/2, 3, information as above, are paralectotypes. The type specimens of *Hydrobia dubia* Etheridge, 1879, are presumed either lost or mixed by mistake with the type specimens of *A. crassa* from the same locality, horizon and collection. One was figured by Etheridge (1879: pl. 7, fig. 11) and copied by Kadolsky (1980: fig. 14). No further occurrences known.

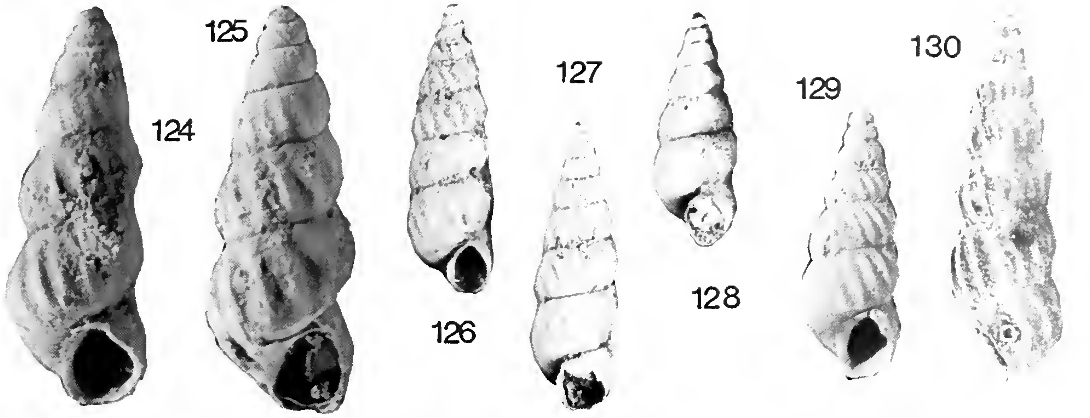
DIMENSIONS. In mm.	h	br	hap	h/br	sa
GG19833/1, Canamá.	5.9	3.7	2.5	1.59	55°
GG19833/2, Canamá.	4.9	3.1	2.3	1.56	–
GG19833/3, Canamá.	4.6	3.0	2.2	1.53	–

REMARKS. The three specimens BMPD 97225 were labelled as '*Assiminea crassa* Etheridge' by L. R. Cox, but in common with the other surviving specimens in Barrington Brown's collection from Canamá, there is no earlier label. In view of the obvious similarity between the specimens labelled *A. crassa* and Etheridge's type illustration of *H. dubia*, I concur with Kadolsky's decision to synonymize the two. Parodiz *in* Bristow & Parodiz (1982) placed *Hydrobia (Paludestrina) dubia* Etheridge in the synonymy of *Toxosoma eborea* Conrad, and thought that Etheridge's species resembled in particular specimens from Iquitos, figured by de Greve (1938: pl. 5, figs 24, 29, 33, 34) as *Pseudolacuna macroptera* Boettger. *Toxosoma eborea* has a columellar fold, whereas the present species does not. There is no basis for the synonymy suggested by Parodiz and there is no doubt that de Greve's specimens all belong to *T. eborea*.

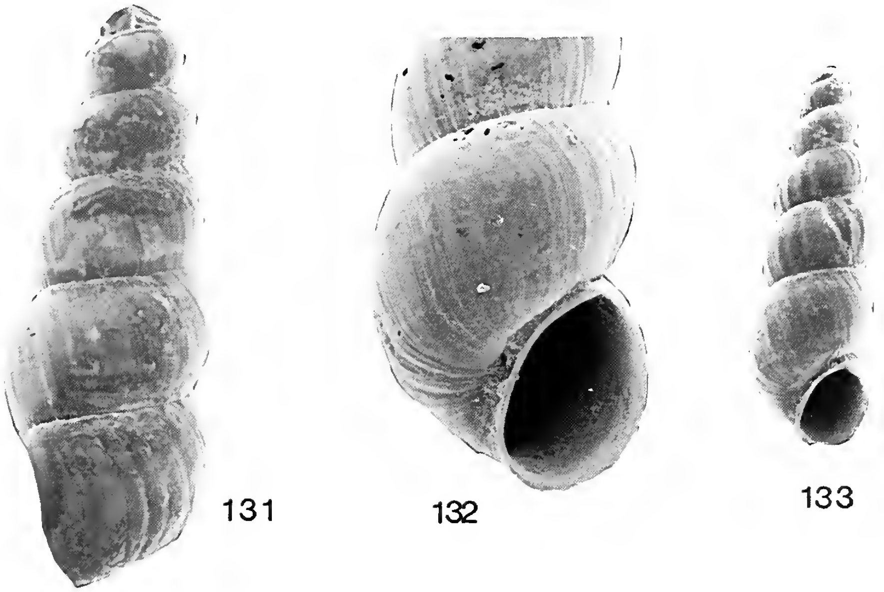
This species cannot be placed in any described genus with complete confidence. Following Kadolsky, who also expressed reservations on this point, it is very tentatively assigned to *Littoridina*. It may be distinguished from comparatively smooth species of *Dyris* such as *D. ortoni* Conrad by its complete lack of sculpture, apart from slightly sinuous but basically orthocline growth lines. In addition, its inner lip is not rimmed: it is more strongly calloused than that of *Dyris*, *Liris* and *Heleobia* but not as strongly as in either *Eubora* or *Potamolithus*. An important feature is the shape of this lip. In all the above-mentioned genera, the inner lip forms a fairly uniform curve whose centre lies well to the right of the columella. In '*L.*' *crassa*, on the other hand, the lower part of this lip, formed by the columella, is straight and leans slightly to the right, whilst the upper, parietal region, bulges strongly to the right. The outer lip is damaged in all three specimens: growth lines suggest, however, that no more than an extremely weak broad sinus is situated just to the right of the base of the columella. A posterior notch is present.

Genus *LIRIS* Conrad, 1871

TYPE SPECIES. *Liris laqueata* Conrad, 1871*b*, Late Caenozoic, Pebasian; Pichana, Peru (= *Turbonilla minuscula* Gabb, 1869, Pebas). By monotypy.



Figs 124–130 *Liris minuscula* (Gabb). Pebasian. **124–125**, Pebas, Peru; Orton Colln. **124**, ANSP 31397a, **lectotype** (of *Turbonilla minuscula* Gabb), here selected; front, × 15. **125**, ANSP 31397b, accompanying paralectotype; front, × 15. **126–130**, Pichana, Peru; Hauxwell Colln. **126**, NYSM 9259a, **lectotype** of *Liris laqueata* Conrad, here selected; front, × 10. **127**, NYSM 9259b, accompanying paralectotype; front, × 10. **128**, NYSM 9259c, accompanying paralectotype; front, × 10. **129**, GG21641; front, × 15. **130**, GG19969; side, × 25.



Figs 131–133 *Liris minuscula* (Gabb). Pebasian; Pichana, Peru; Hauxwell Colln. **131**, GG21640; side, × 40. **132**, GG21642; body whorl and aperture, × 50. **133**, GG19965; front, × 25.

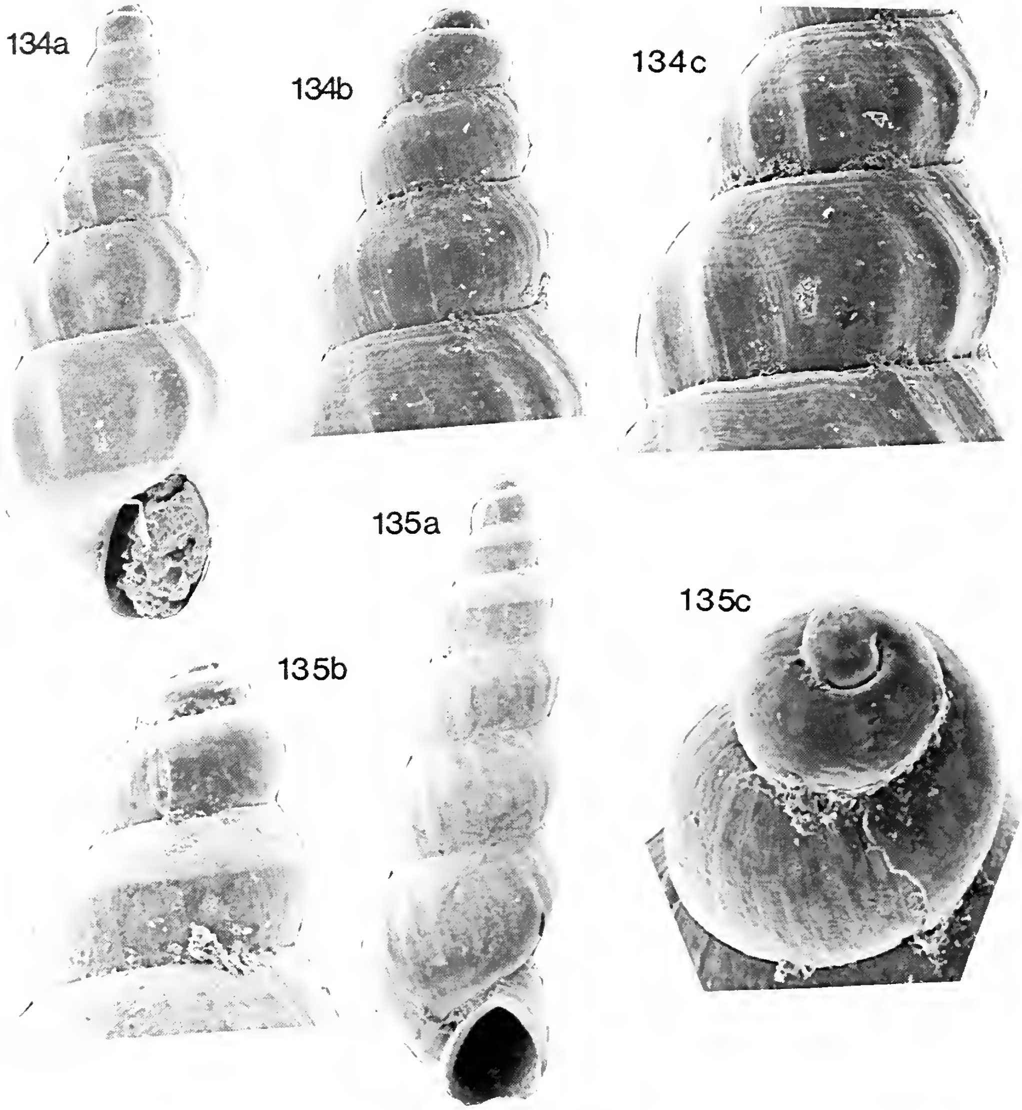
Diagnosis. Littoridinid with *c.* 12–18 axial, apparently not quite collabral, folds per whorl; growth lines prosocline; spiral sculpture absent or weak, often confined to early whorls.

Other species assigned. Late Caenozoic, Pebasian: *Liris acicularis* sp. nov., Pichana, Peru; *Melania scalarioides* Etheridge, 1879, Canamá; ?Miocene, Tumbatú Formation, Chota Basin, Ecuador; *Liris* sp. (p. 208)

Generic distribution. Late Caenozoic, Pebasian; Upper Amazon Basin. Pebas (Gabb 1869, Boettger 1878, Willard 1966); Pichana (Conrad 1871*b*); Iquitos (de Greve 1938, Willard 1966); ?Cachoera das Tracoas, Brazil (Roxo 1924); Três Unidos, Peru (Roxo 1924, Costa 1980); Puerto Nariño, Colombia. ? Miocene, Chota Basin, Ecuador. Unknown living.

Remarks. *Liris* resembles the living North American genus *Tryonia* (type species, *T. clathrata* Stimpson, 1865*b*). However, the latter has a more obtuse spire, and its folds are noticeably noded at the periphery and are truly collabral. Furthermore, its outer lip is bent forward adapically, whilst in *Liris* the reverse is true, with the growth lines disposed at a greater angle from the vertical than the folds. The aperture of *Tryonia* is relatively larger than that of *Liris*.

Comparison of the originally poorly illustrated type specimens of *Turbonilla minuscula* Gabb and of *Liris laqueata* Conrad with BMPD material from Pichana show that the two are synonymous, as was first suspected by Boettger (1878). On the other hand, de Greve (1938) was correct in recognizing that two quite similar species occurred together at Iquitos. All those that he figured as *L. minuscula* are now however referred to *L. scalarioides* (Etheridge) and those that he



Figs 134–135 *Liris minuscula* (Gabb). Pebasian; Pichana, Peru; Hauxwell Colln. **134**, GG19964; a, front, × 40; b, early whorls, × 90; c, middle whorls, × 75. **135**, GG19967; a, front, × 40; b, early whorls, × 115; c, oblique view of apex, × 190.

figured as *L. laqueata* are here placed in *L. minuscula*. Similarly, the distinctions given by Parodiz (1969: 119, 120) between *L. minuscula* and *L. laqueata* apply respectively to *L. scalarioides* and *L. minuscula* instead. These reidentifications also result in the locality data for the various species given by Taylor (1966: 197) being sometimes incorrect.

The unfigured references of Willard (1966) can, in view of the confusion over specific determinations, be treated only as evidence for the presence of the genus at his localities. Thus, the authenticated distribution of this genus is very restricted. It appears, unlike *Dyris*, to be almost entirely confined to the 'classic' Pebasian localities of the Upper Amazon Basin. The one exception so far known is the record from the Tumbatú Formation of Ecuador.

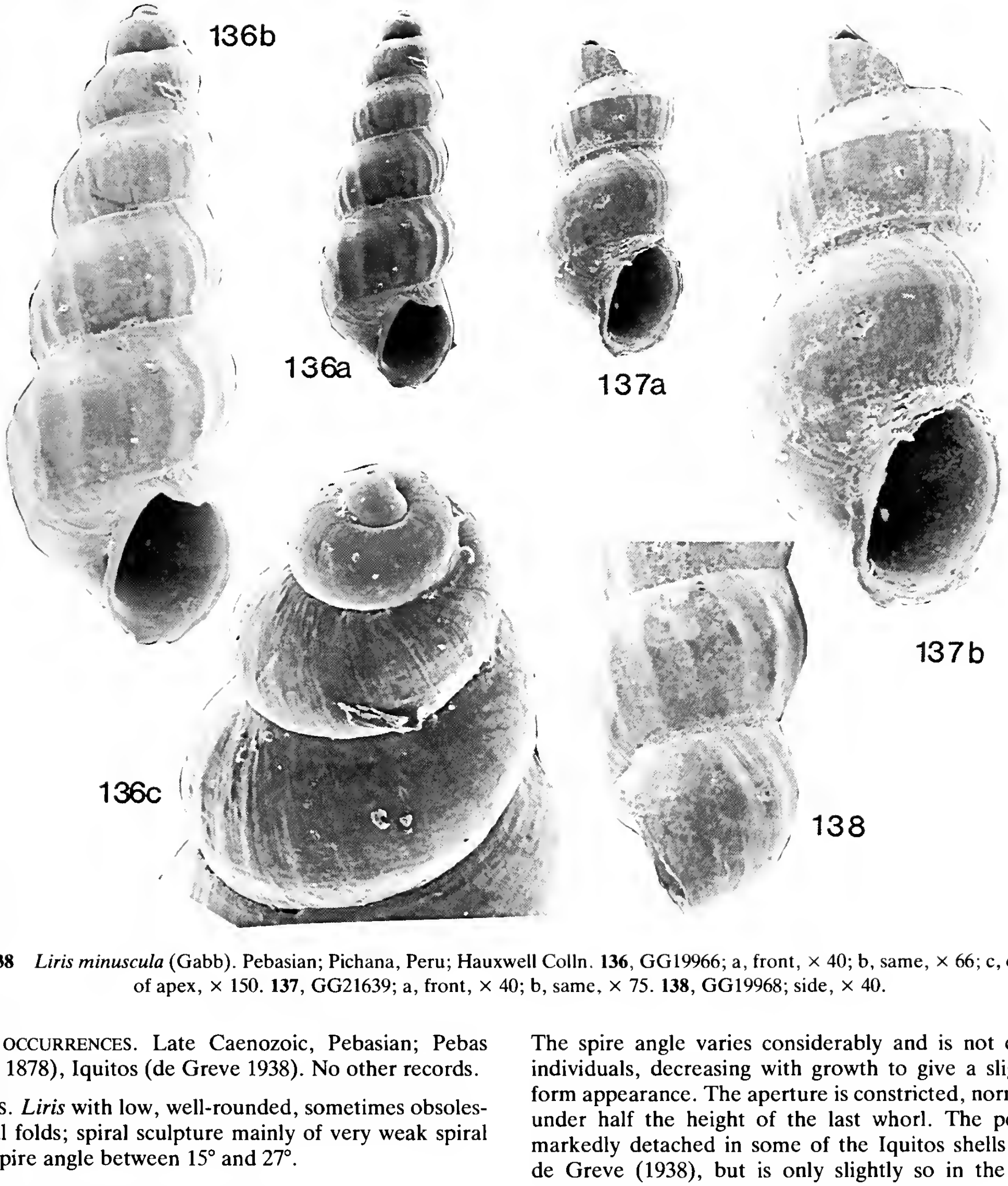
Liris minuscula (Gabb, 1869) Figs 124–138

*v 1869 *Turbonilla minuscula* Gabb: 197; pl. 16, fig. 1.
v. 1871*b* *Liris laqueata* Conrad: 194; pl. 10, fig. 3; pl. 11, fig. 8.
. 1878 *Turbonilla minuscula* Gabb; Boettger: 496; pl. 13, fig. 13.
. 1938 *Liris laqueata* Conrad; de Greve: 89; pl. 2, figs 10, 14–31; text-figs 6–11.
1966 *Tryonia laqueata* (Conrad) Taylor: 197 (*pars*).
1966 *Tryonia minuscula* (Gabb) Taylor: 197 (*pars*).
1969 *Liris laqueata* Conrad; Parodiz: 120.

LECTOTYPE of *Turbonilla minuscula* Gabb, 1869, ANSP 31397a, here selected. Late Caenozoic, Pebasian; Pebas, Peru (Orton Colln). ANSP 31397b (same information) is a paralectotype.

Lectotype of *Liris laqueata* Conrad, 1871, one of NYSM 9259, original of Fig. 126 herein, here selected. Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell Colln). Two other specimens registered under NYSM 9259 (same information), Figs 127–8, are paralectotypes.

OTHER MATERIAL STUDIED. G25288/1–4, Pichana, as above (Hauxwell Colln); GG19964–70, GG21639–49, Pichana (Hauxwell Colln, extracted from matrix 1982).



Figs 136–138 *Liris minuscula* (Gabb). Pebasian; Pichana, Peru; Hauxwell Colln. **136**, GG19966; a, front, × 40; b, same, × 66; c, oblique view of apex, × 150. **137**, GG21639; a, front, × 40; b, same, × 75. **138**, GG19968; side, × 40.

Further occurrences. Late Caenozoic, Pebasian; Pebas (Boettger 1878), Iquitos (de Greve 1938). No other records.

Diagnosis. *Liris* with low, well-rounded, sometimes obsolescent, axial folds; spiral sculpture mainly of very weak spiral threads; spire angle between 15° and 27°.

Description. The rather high, naticoid, apex is smooth and consists of 2–2½ whorls. Although rare individuals, including one of the paralectotypes of *L. laqueata* Conrad, lack axial folding, in most shells axial folding appears on the third whorl. The folds are slightly noded at the periphery for the next four whorls or so in a minority of specimens. The number of folds varies 12–16 per whorl and their strength also varies, not only from specimen to specimen, but also in any one individual: in some cases they may be virtually obsolete. The folds die away at the lower suture and are absent from the lower half of the body whorl. Spiral sculpture is visible only on exceptionally well-preserved individuals. It consists of extremely weak threads situated mainly, but not exclusively, on the upper half of the whorl. A weak carination, forming a shoulder, is rarely present. Another carination at the lower suture is seen in the majority of specimens. Weak spiral threads are also found on the neck of the body whorl. The spire angle varies considerably and is not constant in individuals, decreasing with growth to give a slightly pupiform appearance. The aperture is constricted, normally being under half the height of the last whorl. The peristome is markedly detached in some of the Iquitos shells figured by de Greve (1938), but is only slightly so in the specimens studied herein from both Pebas and Pichana.

Dimensions. In mm.	h	br	hap	h/br	sa
ANSP 31397a, lectotype of *Turbonilla minuscula*, Pebas.	3.7	1.4	0.8	2.8	22°
ANSP 31397b, paralectotype as above.	3.8	1.3	–	2.9	–
NYSM 9259a, lectotype of *Liris laqueata* Conrad, Pichana.	4.1	1.2	0.7	3.4	15°
GG19967, Pichana.	2.5	0.75	0.6e	3.3	18°
GG19964, Pichana.	2.15	0.8	0.4	2.7	27°
GG19965, Pichana.	1.9	0.6	0.4	3.2	15°
GG19966, Pichana.	1.4	0.5	0.3	2.8	15°

Remarks. Examination of the type material of *L. minuscula* and *L. laqueata* leaves no doubt that the two are conspecific.

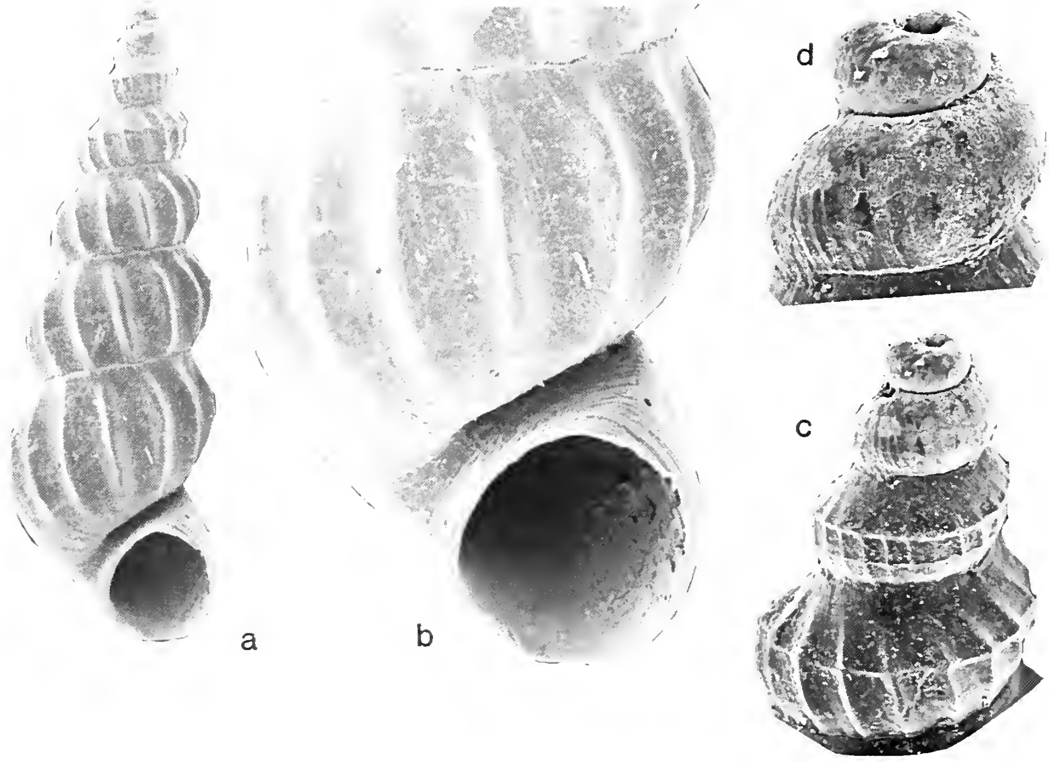


Fig. 139 *Liris scalarioides* (Etheridge). Pebasian; Puerto Nariño, Colombia; Weeda Colln. GG21560; a, front, × 20; b, body whorl and aperture, × 50; c, oblique view of early spire whorls, × 50; d, oblique view of apex, × 100. See also Fig. 456, p. 354.

Several records of these species are now included under *L. scalarioides* (Etheridge) (below), where comparisons between the two species are given.

Liris scalarioides (Etheridge, 1879) Figs 139–146, 456

*v 1879 *Melania scalarioides* Etheridge: 88; pl. 7, fig. 8.
. 1924 *Melania scalarioides* Etheridge; Roxo: 48.
. 1938 *Liris minuscula* (Gabb); de Greve: 92; pl. 1, figs 31–35; pl. 2, figs 1–9, 11–13; text-figs 12–18.
? 1966 *Tryonia minuscula* (Gabb); Taylor: 197 (*pars*).
. 1969 *Liris minuscula* (Gabb); Parodiz: 120.
. 1980 *Liris minuscula* (Gabb); Costa: 881; pl. 2, figs 1–4.
. 1981 *Liris minuscula* (Gabb); Costa: 643; pl. 1, figs 9, 10.

LECTOTYPE. GG22419, selected herein, the specimen figured by Etheridge, and the accompanying paralectotype GG22420 (both *ex* 97724); Late Caenozoic, Pebasian; Canamá, Peru; Barrington Brown Colln.

OTHER MATERIAL STUDIED. GG19852, GG19986–90, and GG21560–9 (over twenty shells), from Puerto Nariño, Colombia; Weeda Colln.

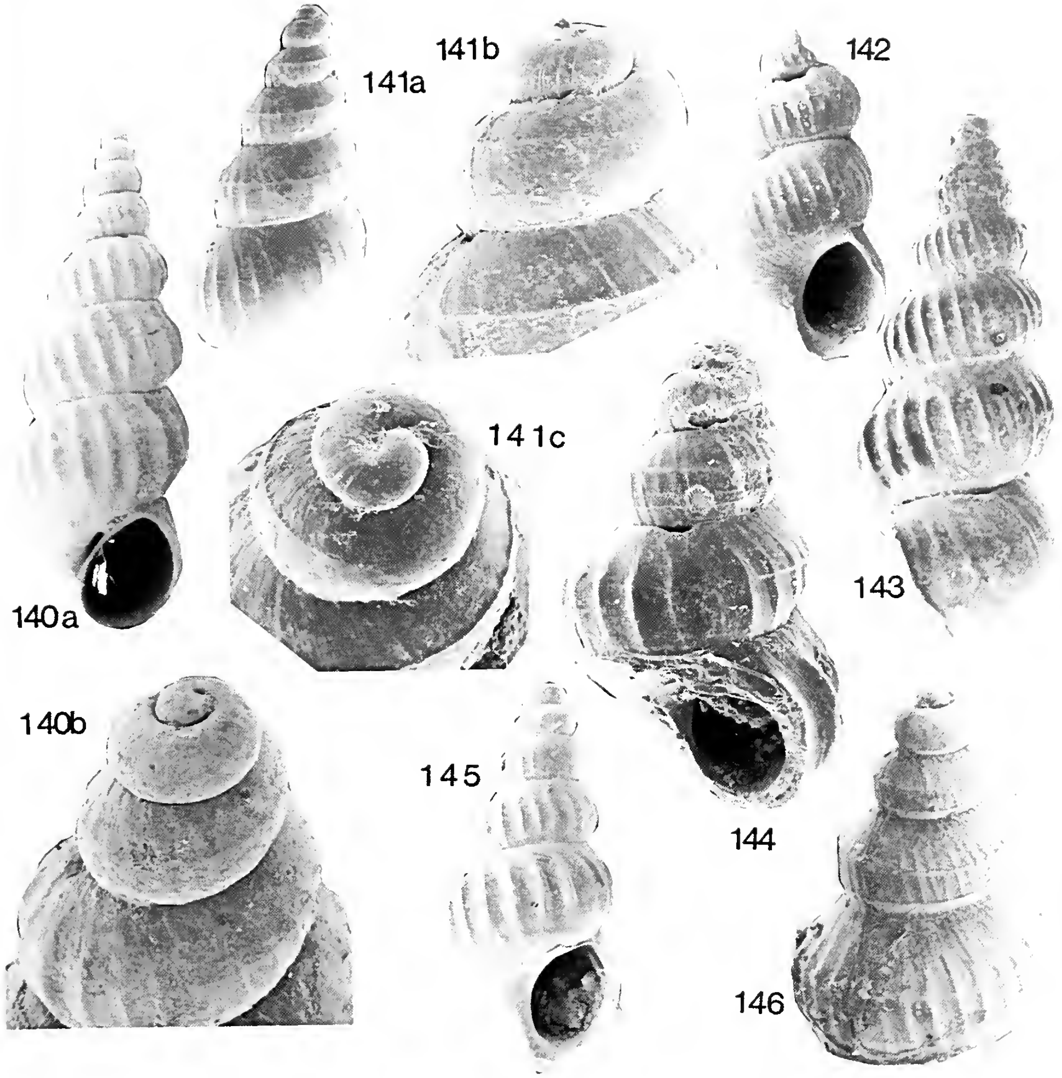
FURTHER OCCURRENCES. Late Caenozoic, Pebasian; Iquitos, Peru (de Greve 1938); ?Cachoero das Tracoas, Brazil (Roxo 1924); Três Unidos, Peru (Roxo 1924, Costa 1981); Afloramento em Atalaia do Norte and CPCAN 111, Sao Paulo de Olivença, Brazil (Costa 1980).

DIAGNOSIS. Large *Liris* with two or three carinate post-apical whorls; 14–25 sharply crested axial folds per whorl; spire angle 22°–32°.

DESCRIPTION. The apex is much larger than that of *L. minuscula*. The first whorl is disjunct and the second biconvex. Variation is shown in the development of the next three whorls or so. Usually a carina appears at mid whorl-height, with a straight, sloping, ramp above and a convex whorl side below. Below the carina, there are sometimes traces of weak spiral ribbing and also another carination coinciding with, and sometimes obscured by, the suture. All traces of spiral sculpture are lost thereafter for the remaining three to five whorls. The axial sculpture appears at the same time as the carina. At first, it is virtually confined to the lower half of the whorl and is sharply truncated by the sutural carina. There are 14–25 axial ribs per whorl, whose strength varies considerably, but all have narrow, slightly rounded crests, separated by wide concave interspaces. On the later spire whorls, some ribs stretch from suture to suture, but others do not touch the adapical suture. Ribs decrease in strength below the periphery and are absent, not only from the base of, but also often from the latter part of, the body

DIMENSIONS. In mm.	h	br	hap	h/br	sa
Lectotype GG22419.	4.1+	1.8	1.0	2.3	30°
GG21560.	4.4	1.4	0.7	3.1	22°
GG21561.	4.7	1.6	1.0	2.9	27°
GG21562.	2.7	1.1	0.8	2.5	32°
GG21563.	3.8	1.3	–	2.9	27°

All specimens from Puerto Nariño, except the lectotype (from Canamá). Greatest height for Iquitos specimens given by de Greve (1938: 95) was 6.0 mm.



Figs 140–146 *Liris scalarioides* (Etheridge). Pebasian; Puerto Nariño, Colombia; Weeda Colln. **140**, GG21561; a, front, × 15; b, oblique view of apex, × 50. **141**, GG21565; a, rear, × 20; b, oblique view of apex, × 50. **142**, GG19986; front, × 20. **143**, GG21563; side, × 20. **144**, GG21566; showing sculpture of early whorls, × 50. **145**, GG21562; front, × 20. **146**, GG21567; oblique view of early whorls, × 40. See also Fig. 456.

whorl approaching the aperture. The aperture is slightly constricted. In both Puerto Nariño and Iquitos shells, the peristome is sometimes detached.

REMARKS. The best specimens studied are those from Puerto Nariño. The lectotype is rather worn, and the paralectotype is incomplete. The diagnosis is sufficient to separate this species from *L. minuscula*. Costa's illustrations (particularly 1980: pl. 1, figs 1, 2), which show the carina typical of the young stages of *L. scalarioides*, confirm that not only her own records, but also that of Roxo (1924), should fall into the above synonymy. Further support for this redetermination is afforded by Costa's synonymy, which included references to the good figures quoted above of *L. minuscula* de Greve (1938), *non* Gabb, rather than de Greve's figures of '*L. laqueata*' which are, in fact, of *L. minuscula*: see p. 204.

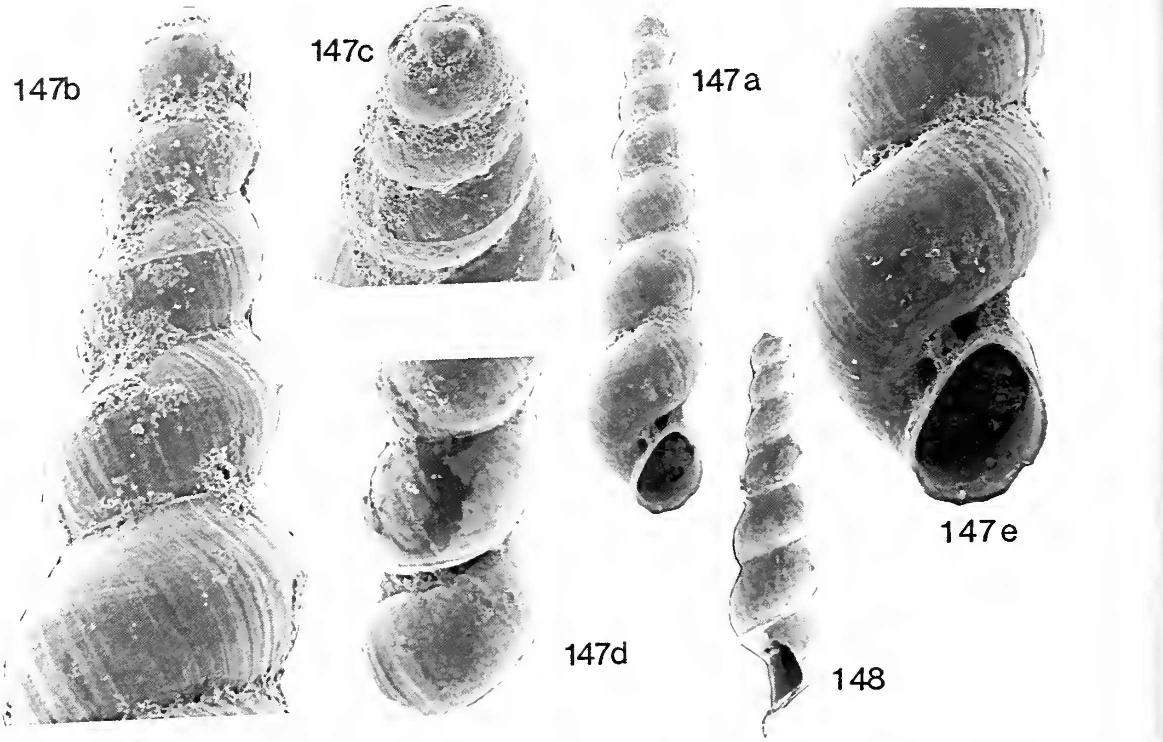
Liris acicularis sp. nov. Figs 147–148

HOLOTYPE. GG21666, Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell Colln, extracted 1982). GG21667–9, same details as holotype, are paratypes.

NAME. 'Sharply pointed'.

DIAGNOSIS. Pointed, straight-sided *Liris* with spire angle of about 11°; shell sculptured with extremely weak spiral threads, and weak carinae situated at periphery and lower suture; growth lines comparatively strong in relation to spiral threads.

DESCRIPTION. The first whorl is very small in relation to the bulbous second whorl. Subsequent whorls are distinctly less convex: their periphery is at mid-height and marked by a weak carina. A second carina occurs at, or just above, the



Figs 147–148 *Liris acicularis* sp. nov. Pebasian; Pichana, Peru; Hauxwell Colln. **147, holotype**, GG21666; a, front, × 30; b, early spire whorls, × 90; c, oblique view of apex, × 90; d, rear view of last whorls, × 50; e, body whorl and aperture, × 60. **148**, paratype, GG21667; × 30.

lower suture. Weak spiral threads are visible at magnifications of about × 30. The growth lines, in contrast, are comparatively strong; they are both opisthocline and prosocline, sloping backwards from the adapical suture. The peristome is markedly detached in the holotype, but less so in those paratypes in which the mouth is not damaged. The spire is virtually straight-sided from the second whorl to the ninth or body whorl.

DIMENSIONS. In mm.	h	br	hap	sa
Holotype, GG21666.	2.3	0.6	0.33	11°
Paratype, GG21667.	1.9	0.4	–	10°

REMARKS. These few specimens are described as a new species, which is assigned to *Liris* with some reservations. They do not appear to grade into *L. minuscula* (Gabb). They are noticeably sharply pointed, and are characterized by their very straight-sided spires, whilst both *L. minuscula* and *L. scalarioides* are definitely slightly pupiform. Rare specimens of *L. minuscula*, including one of the paratypes of *L. laqueata* Conrad and GG21460 (both also from Pichana) lack axial folding. However, they are much stouter shells and their growth lines are not strongly prosocline.

Dyris gracilis Conrad possesses a variable number of carinae: one shell from Pichana has only one carina, which, being situated at the periphery, corresponds with the weak carina of *L. acicularis*. The apertural features of the present species, in particular the detached peristome, are more reminiscent of *Liris* than *Dyris*, and consequently it is assigned to the former. Nevertheless, there must remain some doubt not only about its generic placing, but also the criteria used for separating the two genera.

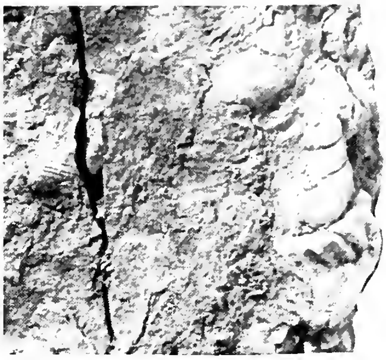
Liris sp. Figs 149–153

v. 1977 *Potamides* n. sp.; Bristow & Hoffstetter: 337.
v. 1982 *Liris* aff. *minuscula* (Gabb); Bristow & Parodiz: 5.
v. 1982 *Liris minuscula* (Gabb); Bristow & Parodiz: 6, 40.

MATERIAL STUDIED. Middle Tumbatú Formation, Chota Basin, Ecuador. GG19807/1–10, Loc. PH 1, 0° 29′ N, 78° 03′ W; GG19808/1–10, Loc. PH 2, 0° 28′ N, 78° 03′ W. No further occurrences.

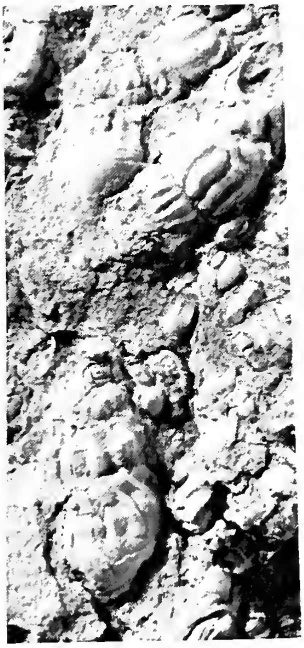
REMARKS. The material consists of thin – up to 20 mm thick – blocks of a buff-coloured shell conglomerate crowded with apparently unorientated and broken specimens. Bristow & Parodiz (1982: 5) refer to thin shell beds (10 to 20 cm thick) in the middle unit of the Tumbatú Formation. It is not known whether PH 1 and PH 2, which are very similar in appearance, represent both or only one of these beds. Bristow & Parodiz state (1982: 40) that some of the material they examined came from the San Cayetano Formation (? Upper Miocene) of the Loja Basin, Ecuador. They do not mention this species in the discussion of the fauna, flora and age of this formation (1982: 16), but do refer to *Dyris* cf. *gracilis* Conrad 'form' *tricarinata* (Boettger) occurring in BMPD samples (JW 424; Carrion Colln). The presence of *D. tricarinata* in the San Cayetano Formation is provisionally accepted herein. This material consists of well-bedded marl with internal moulds encrusted by some artefact rather resembling mud cracks. These could have been confused with the axial ribbing of *Liris*. No specimens referable to *Liris* from the San Cayetano Formation can be traced in BMPD.


149


151


152


150


153

igs 149–153 *Liris* sp. Neogene, Middle Tumbatu formation; Chota Basin, Ecuador; C. R. Bristow Colln. **149–150** both × 8, Loc. PH 2. **149**, GG19808/2. **150**, GG19808/1. **151–153** all × 5, Loc. PH 1. **151**, GG19807/1. **152**, GG19807/2. **153**, GG19807/3.

The specimens in samples PH 1 and PH 2 are rather large or *Liris*: it is estimated that, if undamaged, many would have xceeded 10 mm in height. Frequent fracture marks show that nany specimens are crushed. It is impossible to determine whether one or two species are present because of the variation in sculpture, not only on individual shells, but also between different specimens. All have strong axial folding: it is not possible to see whether the growth lines are truly parallel to the folds. Some whorls appear to lack all traces of spiral sculpture, others show weak spiral threads, whilst the remainder possess, in addition, a distinct but weak carinate shoulder. Some specimens appear to have early post-nuclear whorls which are much higher than broad: these are very unlike those of described species of *Liris*, at least at specific level. The rounded apertures and strong axial sculpture suggest, however, that many of them belong to a species with some resemblance to *Liris scalarioides* (Etheridge), which is, however, distinctly smaller. They clearly do not belong to *L. minuscula* (Gabb).

The only fossils known from the Tumbatú Formation, other than the present material, are plant fragments (Bristow & Parodiz 1982: 5, 6). The presence of *Liris* suggests some correlation with the Pebasian of the Upper Amazon Basin, and hence a probable Late Caenozoic age.

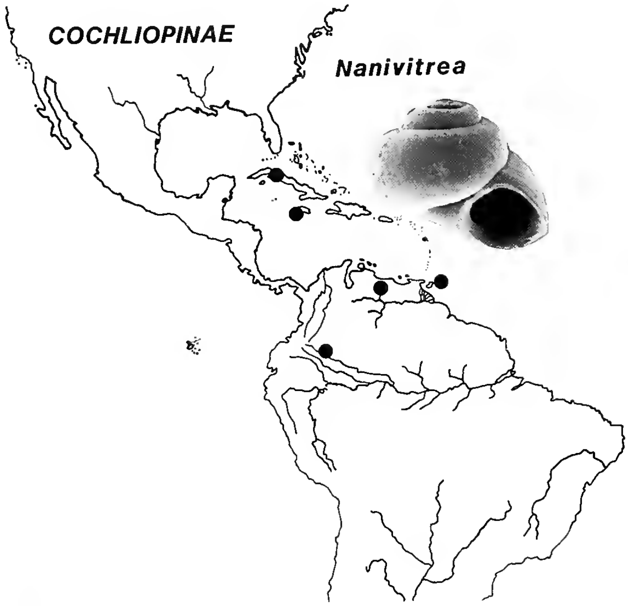


Fig. 154 Neogene and Recent distribution of Cochlopinae. ●, *Nanivitrea*; all records are Recent except those from La Tagua. Inset, *Nanivitrea colombiana* sp. nov.; La Tagua, Colombia.

Subfamily **COCHLIOPINAE** Tryon, 1866

[Tryon, 1866*a*, emended Taylor, 1966]

Taylor (1966: 173), as with the Littoridininae, proposed the Cochliopininae as a new subfamily: both had been established by earlier authors. His work, therefore, should be regarded only as an emendation and Tryon remains the author of the subfamily. Taylor (1966) also established three new tribes in the subfamily. One of these, the Cochliopini, belongs exclusively to the western hemisphere, mainly Central America and the Caribbean. Tribes are not formally recognized herein, but changes in the perceived relationships between various genera would now alter Taylor's classification. In his arrangement only two living species of Cochliopini were known from South America. One is *Cochliopina kugleri* (Forcart, 1948), originally described from Venezuela as *Valvata* and now transferred to *Nanivitrea*. The other is the monospecific genus *Limnothauma* Haas, 1955, which lives in Lake Titicaca, Peru, and is best placed in the Littoridininae.

The new species described here as *?Nanivitrea colombiana* belongs to a small group of genera including *Cochliopa* Stimpson (1865*a*), *Subcochliopa* Morrison (1946) and *Cochliopina* Morrison (1946). Morrison distinguished between his two genera on anatomical grounds, but they do not seem easy to separate on the shell characters that he also suggested were diagnostic. As Morrison ignored the little-known *Nanivitrea* entirely, his work may need revision and the taxonomy of the group is probably unstable. The distribution of *Amnicola rowelli* Tryon (1863), the type species of *Cochliopa*, had been disputed for a long time. Morrison, after comparing the type series with material that he had collected himself, concluded that it was Panamanian and not Californian as had been originally thought, and that the three species assigned to the genus were all from the Pacific drainage of Panama and the Pearl Islands.

The best illustrations of *Cochliopa* are those of Morrison's species: unfortunately he did not refigure *C. rowelli*. Tryon's original figures were inaccurate, but Binney (1865: 73, fig. 144) provided a better drawing. Wenz (1939: 575, fig. 1561) chose *Cochliopa riograndensis* Pilsbry & Ferris (1906) as his example of the genus: this is now the type species of *Cochliopina* Morrison.

Thiele (1929: 170, fig. 150) provided probably the first illustration of *Paludinella helicoides* Gundlach (*in* Poey, 1865: 70), the type species of *Nanivitrea*, and described it as translucent. Unfortunately, he gave no details authenticating his determination.

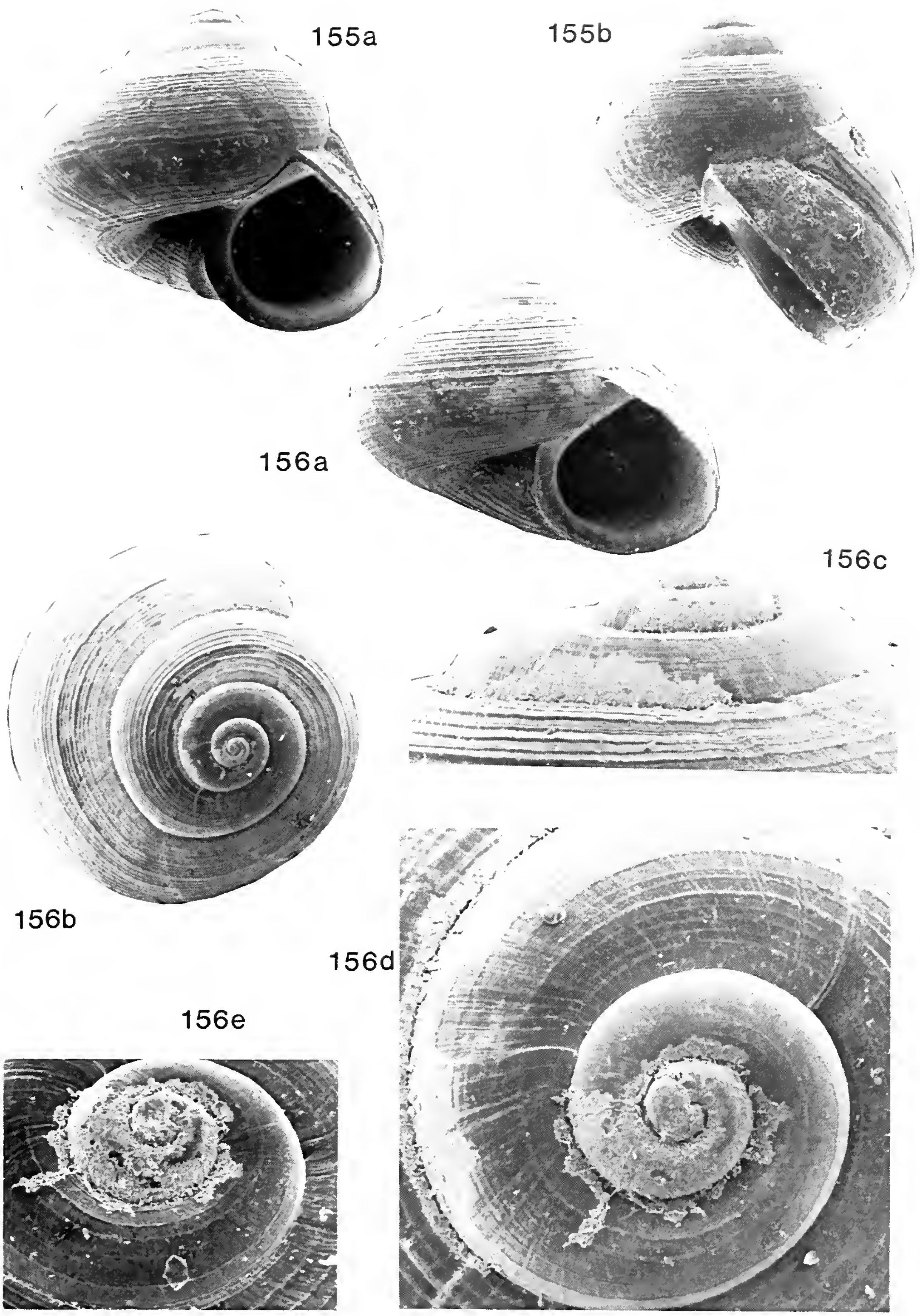
Insofar as it affects the generic assignment of the new Colombian fossil, an attempt is made below to distinguish on shell characters alone between the four genera under discussion. This is based partly on the views of both Morrison (1946) and Taylor (1966), and takes account of the features of the numerous species that they list.

Subcochliopa is restricted to shells with rather weak peripheral keeling and having slightly flattened bases. Shells are spirally lirate, sometimes with lirations obsolete on the base. The two Panamanian species described by Morrison are moderate-sized to very large, with shell heights of 3.5 mm and 7.5 mm respectively.

Cochliopa is best distinguished by its adpressed sutures, particularly between the body and penultimate whorls in adults. The shell can be smooth or finely striate and tends to be fairly large, with the height between 3.5 mm and 5.0 mm.

Nanivitrea has impressed sutures. Shells are smooth, normally translucent and small, with shell height less than 2.5 mm.

Cochliopina (Figs 155–157) is much the most widespread of these genera and is represented by about 20 species. It has impressed sutures and varies in shape between the almost planorbiform *C. hinkleyi* (Pilsbry, 1920) and the trochiform *C. izabel* (Pilsbry, 1920). The shell is normally striate, the striations being fine and of small amplitude in most species, but quite coarse in some such as *C. hinkleyi* and *C. miller* Taylor (1966). *C. izabel* is nearly smooth, but Pilsbry (1920) described a striate 'mutation' *perstriata*. The type species, *C. riograndensis* (Pilsbry & Ferris, 1906) is broadly heliciform and weakly striate and thus intermediate for these characters. In common with most other species assigned to the genus it i small, with a height of about 2.0 mm and a breadth of abou 2.7 mm. A few species, particularly some described by Morrison (1946) from Panama, are much larger, *C. wetmore*



Figs 155–156 *Cochliopina extremis* Morrison (1946). Recent; off San José Island, Pearl Islands, Panama (Pacific); paratypes, presented by nithsonian Institution. **155**, BMZD 1951.11.1.64; a, front, × 20; b, side, × 20. **156**, BMZD 1951.11.1.65; a, front, × 20; b, apical view, × 20; c, d, e, side, vertical and oblique views of apex, all × 100.

being the largest with height and breadth both about 6.0 mm. It seems possible that the species which have been assigned to *Cochliopina* may belong to more than one genus.

Ecological conclusions drawn from the presence of members of the Cochliopini can only be tentative. All except *Subcochliopa* are known to have reached islands. Morrison (1946: 19) noted that *Cochliopa* on San José Island ranged from tidal level almost to the source of streams, whilst *Cochliopina* was limited to a narrow zone of the stream a little above tidewater. Other *Cochliopina* are clearly fresh-water only, living far from the sea, with *C. riograndensis* favouring protected situations, such as under stones and among watercress, along edges of streams (Taylor, 1966).

Both Morrison (1946) and Taylor (1966) suggested that the more northerly species of *Cochliopina* lived in streams draining eastwards into the Gulf of Mexico and the Caribbean, whilst the more southerly species from Nicaragua to Panama occur only in the Pacific drainage system. Morrison (1946: 18) thought that this separation might have originated in the palaeobiological history of the region. However, the value of such observations is seriously reduced, both by doubts as to whether the genus is monophyletic and by considerable gaps in collecting of both fossil and Recent material. If Taylor's assignment of *Valvata kugleri* to *Cochliopina* were to be accepted, it would make it the only South American (Venezuelan) member of the northern group which lives in the Atlantic drainage system.

Genus ***NANIVITREA*** Thiele, 1927

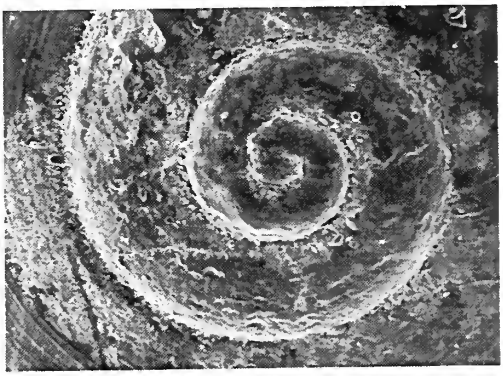
TYPE SPECIES. *Paludinella helicoides* Gundlach *in* Poey, 1865: 70. Recent, Cuba. By monotypy.

DIAGNOSIS. Like *Cochliopa* but with small, smooth and often translucent shell seldom exceeding 2.5 mm in height; sutures impressed.

OTHER SPECIES ASSIGNED. Recent: *Nanivitrea alcaldei* Jaume & Abbott (1948: 5), Cuba; *Valvata inconspicua* C. B. Adams (1851: 131), Jamaica; *Valvata pygmaea* C. B. Adams (1849: 42), Jamaica; *Valvata kugleri* Forcart (1948: 50), Venezuela. Fossil, first record herein, Late Caenozoic, La Tagua, Colombia: *Nanivitrea colombiana* sp. nov.

GENERIC DISTRIBUTION. Recent, Cuba, Jamaica, Venezuela. Late Caenozoic, Colombia.

157a



157b

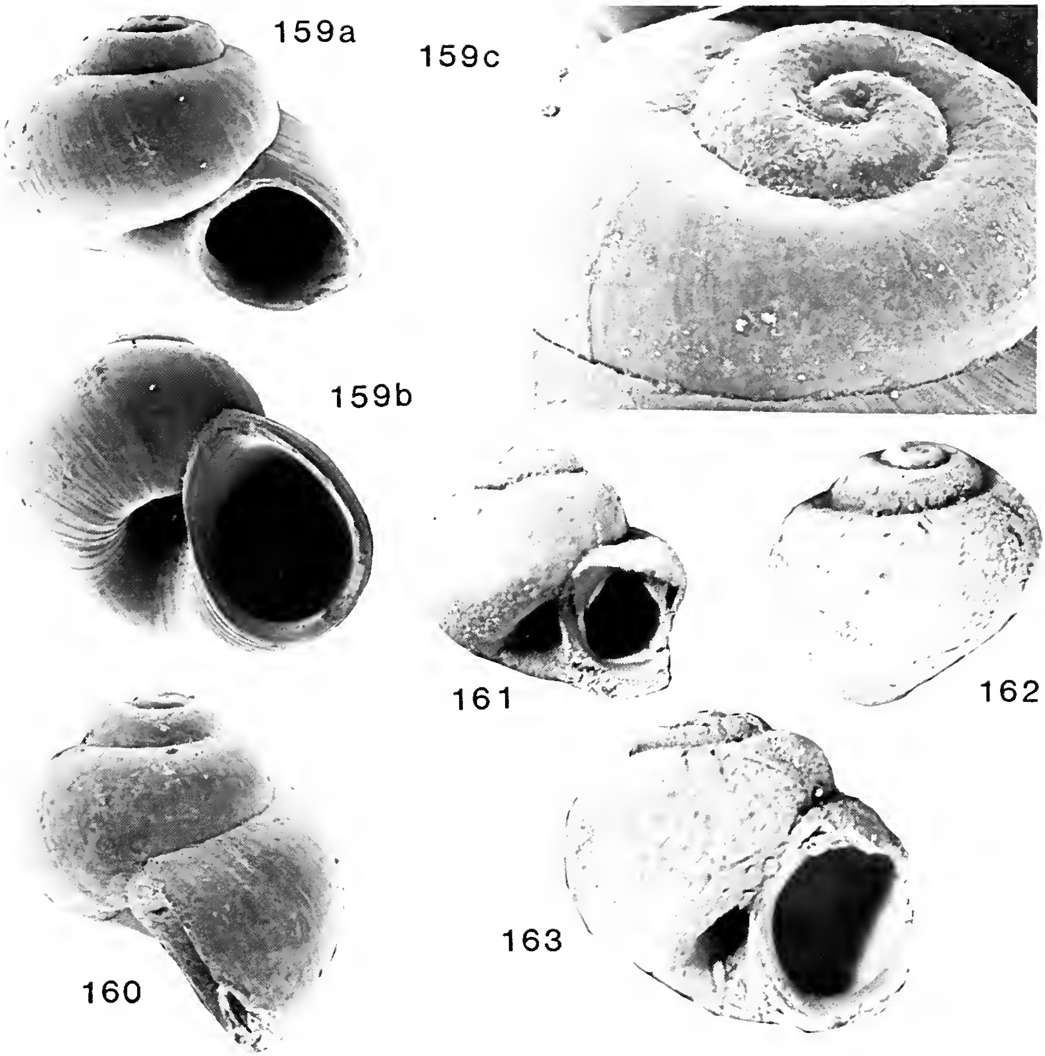
158a

158b

158c

Fig. 157 *Cochliopina diazensis* Morrison (1946). Recent; Panama; paratype, presented by Smithsonian Institution, BMZD 1951.11.1.81; a, front, × 20; b, vertical view of apex, × 100.

Fig. 158 *Nanivitrea colombiana* sp. nov. Neogene; 1.5 km upstream from La Tagua, Colombia; Weeda Colln. Paratype, GG19891; a, apical view, × 20; b, same, × 100; c, oblique view of apex, × 100.



Figs 159–163 *Nanivitrea colombiana* sp. nov. Late Caenozoic; La Tagua, Colombia. **159–160**, 1.5 km upstream from La Tagua, Weeda Colln. **159, holotype**, GG19887; a, front, × 25; b, obliquely from below, × 25; c, apical whorls, × 90. **160**, paratype, GG19889; side, × 25. **161–163**, Eden Colln. **161–162**, paratypes, Loc.33/480–560. **161**, GG19925/1; front, × 12.5. **162**, GG19925/2; rear, × 20. **163**, paratype, Loc. 54, GG19927/1; front, × 20.

REMARKS. Possible relationships with other cochliopinids are discussed above. *Valvata kugleri* was reassigned to *Cochliopina* by Taylor (1966) but, as it is both smooth-shelled and translucent, seems better placed in *Nanivitrea*. I agree with the views of Jaume & Abbott (1948), who commented on the similarity of *Cochliopina* to *Nanivitrea*. The new species is assigned to the latter because the majority of the specimens are completely smooth. It is, however, thick-shelled and would almost certainly not have been translucent. The known distribution of the genus is discontinuous, probably because such small shells have been overlooked. However, no specimens have been found among the other micromolluscs extracted from the Pichana and Puerto Nariño samples.

Nanivitrea colombiana sp. nov. Figs 158–163

HOLOTYPE. GG19887, Late Caenozoic, 1.5 km upstream from La Tagua on Rio Caqueta, Colombia (Weeda Colln). The following are paratypes: GG19888–91 (more than 30 shells), same details as holotype; GG19925–6, Loc. 33/480–560, La Tagua (Eden Colln); GG19927–8, Loc. 54, La Tagua (Eden Colln); GG21515, Loc. 44, La Tagua (Eden Colln).

NAME. 'Colombian'.

DIAGNOSIS. Heliciform, with breadth slightly greater than height; aperture rounded below and bluntly angled above; periphery at strongly impressed suture; umbilicus deep, but not wide enough in adult to show early whorls; shell smooth except for prosocline growth lines and rare spiral threads.

DESCRIPTION. The initial whorl is either flattened or even slightly sunken. For the next two whorls the suture lies below the highest point of the rather circular-sectioned whorls. That part of the shell nearest the suture slopes abapically with the result that young shells appear planorbiform. In later growth stages, the translation rate increases and the part of the whorl adjacent to the adapical suture slopes downwards, the shell assuming a more turbiniform shape. The later whorls remain strongly convex, with the periphery lying at the impressed suture. The shell in the apertural region is thick. The aperture is slightly higher than broad. It is rounded below and bluntly angled above, with the angulation lying at about its mid-width. The rim of the deep umbilicus is well rounded, with no trace of carination. The penultimate whorl is rarely visible from below except in juvenile specimens. The growth lines are strongly prosocline. Weak and randomly positioned spiral threads are visible only in a small proportion of specimens.

DIMENSIONS. In mm.	h	br	h/br
GG19887, holotype, 1.5 km upstream of La Tagua (Weeda Colln).	2.15	2.25	0.95
GG19888, paratype, same loc.	2.1	2.2	0.95
GG19925/1, paratype, Loc. 33/480–560, La Tagua (Eden Colln).	2.8	2.9	0.96
GG19927/1, paratype, Loc. 54, La Tagua (Eden Colln)	2.4	2.4	1.0

REMARKS. *N. kugleri* (Forcart) is similar, but relatively broader (h, 1.7 mm; br, 2.4 mm; h/br, 0.7; measurements from Forcart, 1948). In addition, its whorls are more evenly convex and have their periphery slightly higher, above, and not at, the suture. Its aperture is relatively broader with the adapical angulation well to the left of mid-breadth. Forcart described it as being translucent, and his type illustrations suggest that the shell is much thinner than that of *N. colombiana*.

Because of the planorbiform shape of the early whorls, broken juvenile stages of the present species strongly resemble *Coahuilix* D. W. Taylor, 1966. Without comparative material, it is not possible to say whether this similarity is a feature of all *Nanivitrea*.

Subfamily ?**LITHOGLYPHINAE** Thiele, 1929

[Tribus Lithoglypheae Thiele, 1929: 145, *nom. transl.* Wenz, 1939: 577]

The Pebasian *Eubora*, *Toxosoma* and *Tropidobora* are here doubtfully referred to the Lithoglyphinae of the Hydrobiidae.

Thiele (1929: 141–2) placed both *Potamolithus* Pilsbry (1896: 88) and *Littoridina* Souleyet (1852: 565) in his Tribus Littoridineae. This arrangement was followed by Wenz (1939). However, Davis & Pons da Silva (1984), following an earlier study (Pons da Silva & Davis, 1983), transferred *Potamolithus* to the Lithoglyphinae, their analysis of its anatomy suggesting a close relationship to the living European *Lithoglyphus* (Hartmann, 1821). Living members of the Lithoglyphinae are known from both Europe and North America. The fossil history of the subfamily appears to be poorly known, being confined mainly to Pleistocene records. Further investigation of this and its present distribution would be necessary to explain its occurence in the La Plata region satisfactorily. However, as the fossil *Eubora*, *Tropidobora* and possibly *Toxosoma* appear to be related to *Potamolithus* on shell characters, the three former are here placed provisionally in the Lithoglyphinae.

Taylor (1966) erected the Mexithaumatinae for his new species of Hydrobiidae, *Mexithauma quadripaludium*. The strong superficial resemblance of its shell to that of *Eubora bella* (Conrad) from the Pebasian of Pichana might suggest that they are closely related, but Hershler (1985: 112, fig. 52) convincingly argued that the siphonal notch of *Eubora* was unknown in living hydrobiids.

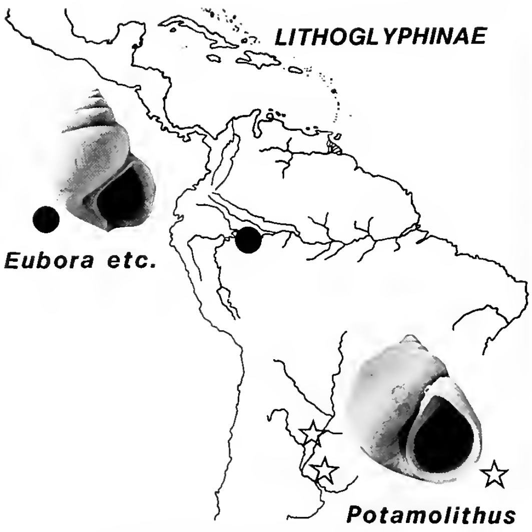


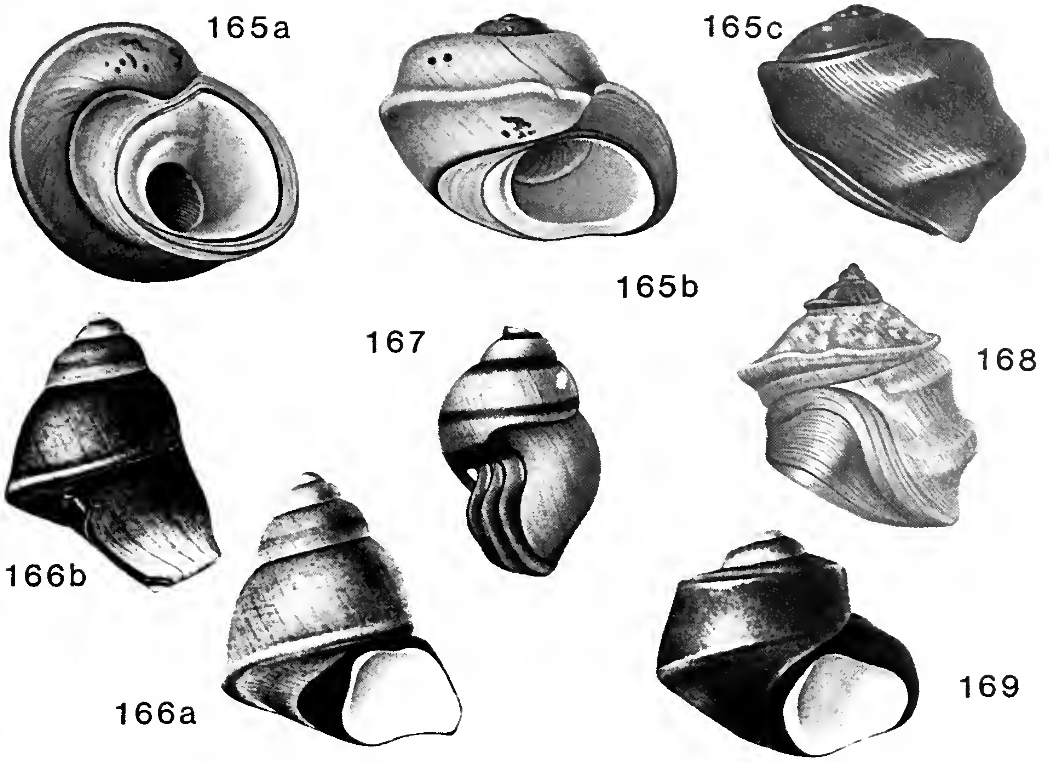
Fig. 164 Neogene and Recent distribution of Lithoglyphinae. ●, fossil *Eubora, Tropidobora* and *Toxosoma*; Pebasian Basin. ☆, Recent *Potamolithus*; Uruguay, northern Argentina and southern Brazil. Inset, *Eubora crassilabra* (Conrad), Pichana, Peru, × 2.5; *Potamolithus lapidum* (d'Orbigny), Uruguay, × 3.

Thompson (1964) assigned his living monotypic genus *Rachipteron* to the Amnicolidae (Rissoacea). His type species *R. philopelum* has some resemblance to *Eubora* in general shape, and like *E. bella*, is spirally ribbed. These ribs, however, are much more numerous and weaker than in the fossil. More importantly, *Rachipteron* also lacks the siphonal notch of *Eubora*.

Kadolsky (1980: 366) has proposed the new name *Eubora* for the preoccupied *Ebora* Conrad, 1871*b* and also decided that *Nesis* Conrad, 1871*b*, another preoccupied name, was not worthy of separation from *Eubora*. In dealing with *Toxosoma* Conrad, 1874*a*, Kadolsky concluded (1980: 372, 374) that it was closely related to *Eubora* and that both genera should, with some reservations, be placed in the Hydrobiidae, rather than regarded as related to *Lacuna* (Lacunidae of the Littorinacea) as suggested by de Greve (1938: 79).

Pilsbry (1944: 150–1, text-figs 2, 3a, b) erected *Tropidobora*, represented by a single species, *Pachytoma tertiana* Conrad, 1874*a*. He also redescribed and figured *Toxosoma* (1944: 151, text-figs 3a, b). He too had concluded that, in spite of its prominent columellar fold, *Toxosoma* was close to *Ebora*.

Both Pilsbry and Kadolsky had noted the resemblance between *Ebora*, *Tropidobora*, and the living *Potamolithus* Pilsbry (Figs 165–170), which is restricted to rivers of the Atlantic drainage system of Argentina, Uruguay and southern Brazil (Pilsbry 1911: 566–602; pls 38–41b; Parodiz 1969: 112, map 4). Pilsbry (1911) provided full and well-illustrated descriptions of numerous nominal living species from a small number of localities. His figures (1911: pl. 38, figs 1, 4) of the type species *P. rushi* Pilsbry, 1896 show the aperture to be subcircular and without any sinus or notch, except for a blunted angulation posteriorly where the inner and outer lips meet. The type material (in ANSP) came from Paysandú on



Figs 165–169 *Potamolithus*. Recent species from Uruguay also occurring in adjoining parts of Argentina. Illustrations copied from Pilsbry (1911). **165**a, b, c, *Potamolithus rushi* Pilsbry (1911: pl. 38, figs 1, 1a, 1b; type illustrations of type species of *Potamolithus* Pilsbry); Paysandú, Uruguay River; × 7.5. **166**a, b, *Potamolithus filiponei* von Ihering, figured Pilsbry (1911: pl. 41a, figs 8, 8a), Montevideo; × 8. **167**, *Potamolithus bisinuatus obsoletus* Pilsbry (1911: pl. 41, fig. 7a), gerontic paratype; Rio de la Plata, San Gabriel's Island, near Colonia, Uruguay; side view of outer lip, × 7.5. **168**, *Potamolithus microthauma* Pilsbry (1911: pl. 38, fig. 2b), a type illustration; Paysandú, Uruguay River; × 7.5. **169**, *Potamolithus quadratus* Pilsbry (1911: pl. 41a, fig. 6), a type illustration; Paysandú, Uruguay River; × 8.

the Uruguay River. Other species having apertures with broadly concave bases, but with no notch separating the columella from the base of the aperture, and with strongly sinuate outer lips, are illustrated by Pilsbry (1911). These include *P. bisinuatus obsoletus* Pilsbry (1911: 577; pl. 41, figs 3, 5) and *P. gracilis* with its subspecies *P. gracilis viridis* (1911: 577–8; pl. 41, figs 8, 9 respectively). *P. gracilis* s.str. also occurs at Paysandu, whilst both subspecies are found at San Gabriel's Island on Rio de la Plata, near Colonia, Fray Bentos, Uruguay.

Pilsbry (1911) also dealt with another group of species with broadly sinuate apertural bases, coupled with comparatively straight outer lips similar to that of the type species. These species have basal carinae which are much more strongly developed than in *P. rushi*, and are somewhat reminiscent of *Tropidobora* in general outline, though lacking the flattened base of the latter. Two of these, *P. carinifer* Pilsbry (see 1911: pl. 41A, fig. 5) and *P. quadratus* Pilsbry (1911: 592; pl. 41A, fig 6) also occur at Paysandú, the type locality of *P. rushi*. A third species, *P. filiponei* von Ihering (1910: 15) is known from Montevideo (Pilsbry 1911: 573; pl. 41A, figs 8, 8a).

It therefore seems that either the aperture of *Potamolithus* is highly variable or that the various species discussed above represent more than one genus. Their frequent co-occurrence suggests that the former explanation is the more likely, and indeed brings into question the necessity for recognizing so many species of *Potamolithus*. None of Pilsbry's excellent illustrations, nor the few largely unidentified samples of the genus in BMZD, have apertures particularly similar to those of the fossil genera under consideration. Although it seems reasonable to regard *Eubora* and *Tropidobora* as closely related, their general similarity to *Potamolithus* may be due to convergence and cannot be taken as strong evidence that all three might be grouped together.

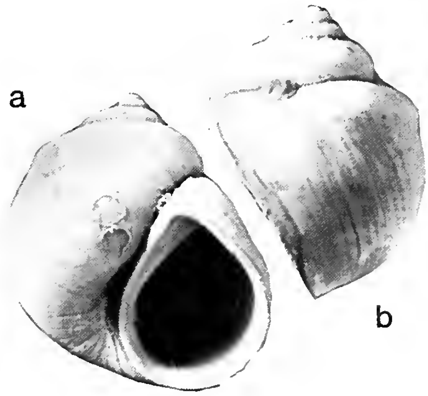


Fig. 170 *Potamolithus lapidum* (d'Orbigny), labelled as var. *supersulcatus* Pilsbry (1896: 88). Recent; San Gabriel's Island, Rio de la Plata, Uruguay (type locality); E. R. Sykes Colln, BMZD 97.2.19.1. a, front; b, side; both × 6.

As mentioned, Taylor (1966: 204) erected the monospecific subfamily Mexithaumatinae of the Hydrobiidae for his new genus and species *Mexithauma quadripaludium* Taylor (1966: 205; pl. 19, figs 58–63, text-fig. 22), which came from several fresh-water lagunas in the valley of Cuatro Cienegas, Coahuila, northern Mexico. Taylor did not compare it with either *Potamolithus* or any of the Amazon fossil genera, but its sculpture of spiral carinae is like that of *Eubora bella* (Conrad). The aperture is rounded below and pointed above. The inner lip is thickened as in *Eubora* and *Potamolithus*. Kadolsky (1980: 367), however, pointed out that it differs from *Eubora* in several important respects – having strictly prosocline growth lines, no basal apertural notch, a much less developed pseudumbilicus and no umbilical ridge. Nevertheless, as we have seen considerable variation occurs in the apertural characters of species assigned to *Potamolithus*. The presence of a columellar plait in *Toxosoma* clearly did not debar it from being considered to be closely related to *Eubora* by either Pilsbry (1944) or Kadolsky (1980). It seems, therefore, reasonable that such differences should not preclude a similarly close relationship between *Mexithauma* and the other genera under consideration. But a comparison of the anatomy of *Mexithauma*, *Lithoglyphus* and *Potamolithus* would be necessary before any firm conclusions could be drawn.

Ponder (1982) has reviewed the several Australasian and New Caledonian species of living *Hemistomia* Crosse (1872) occurring on Lord Howe Island. In the majority, the columella is simple, but in two species, columellar bulges of varying strength occur (Ponder 1982: figs 79, 80, 87). From the example of *Hemistomia* it may be argued that the columellar fold of *Toxosoma* does not preclude it from being fairly closely related to *Eubora*.

In summary, therefore, both the familial and subfamilial assignment of these Pebasian genera must remain undecided.

Genus ***EUBORA*** Kadolsky, 1980

[*nom. nov*. (Kadolsky, 1980: 366) pro *Ebora* Conrad, 1871*b*: 194, non Walker, 1867: 415.
= *Ebora (Nesis)* Conrad, 1871 (type species *Ebora (Nesis) bella* Conrad, 1871*b*: 194; Late Caenozoic, Pebasian; Pichana, Peru; by monotypy), non *Nesis* Mulsant, 1850: 67; nec Stäl, 1860: 67.]

Type species . *Ebora (Ebora) crassilabra* Conrad, 1871, Late Caenozoic, Pebasian; Pichana, Peru. By monotypy as type of *Ebora*.

Remarks. This genus is dealt with in detail by Kadolsky, 1980. Only five species so far have been assigned to it: *E. crassilabra* Conrad, *E. bella* (Conrad), *E. grevei* Kadolsky, 1980, *E. pygmaea* Kadolsky, 1980, *E. woodwardi* Kadolsky, 1980. All are confined to a few Pebasian localities of the upper Amazon Basin. No full treatment of them is warranted herein. Some new informtion and a few points not fully covered by Kadolsky are given below, and the opportunity is taken to publish photographic illustrations of some important specimens, in most cases for the first time. The taxonomic position of *Eubora* is discussed above (p. 214).

Eubora crassilabra (Conrad, 1871) Figs 171–172

*. 1871*b* *Ebora (Ebora) crassilabra* Conrad: 194; pl. 10, fig. 14.
v. 1871 *Ebora crassilabra* Conrad; Woodward: 102 (*pars*; *non* pl. 5, figs 1a, b, = *E. woodwardi* Kadolsky).
? 1874*a* *Ebora crassilabra* Conrad; Conrad: 32; pl. 1, fig. 9.
. 1878 *Lacuna (Ebora) crassilabris* (Conrad) Boettger: 494; pl.13, figs 12a–d.
. 1915 *Lacuna (Pseudocirsope) crassilabris* (Conrad); Cossmann: 102.
. 1980 *Eubora crassilabra* (Conrad) Kadolsky: 367; figs 3, 4 (*cum syn*).
1980 *Eubora* cf. *E. crassilabra* (Conrad) Kadolsky: fig. 5.
. 1980 *Lacuna (Ebora) crassilabris* (Conrad); Costa: 885; pl. 2, figs 7–10.

Holotype. NYSM 9194, Late Caenozoic, Pebasian; probably Pichana (Hauxwell Colln). Not studied herein.

Material studied. All from type locality and horizon (Hauxwell Colln), studied by Woodward (1871): G25297 (8 shells); GG19830/1-25 (GG19830/1 original of Kadolsky, 1980: fig. 4); GG19836, original of Kadolsky, 1980: fig. 5.

Further occurrences. Late Caenozoic, Pebasian, afloramento em Atalaia do Norte; CPCAN I, Tamanduá; CPCAN III, São Paulo de Olivença, Alto Amazonas, Brazil (Costa 1980: 885).

Dimensions. In mm.	h	br	hap	h/br	sa
GG19830/1 (Kadolsky 1980: fig. 4)	8.2	6.0	–	1.37	63°
GG19830/2	6.7	5.2	3.7	1.29	63°

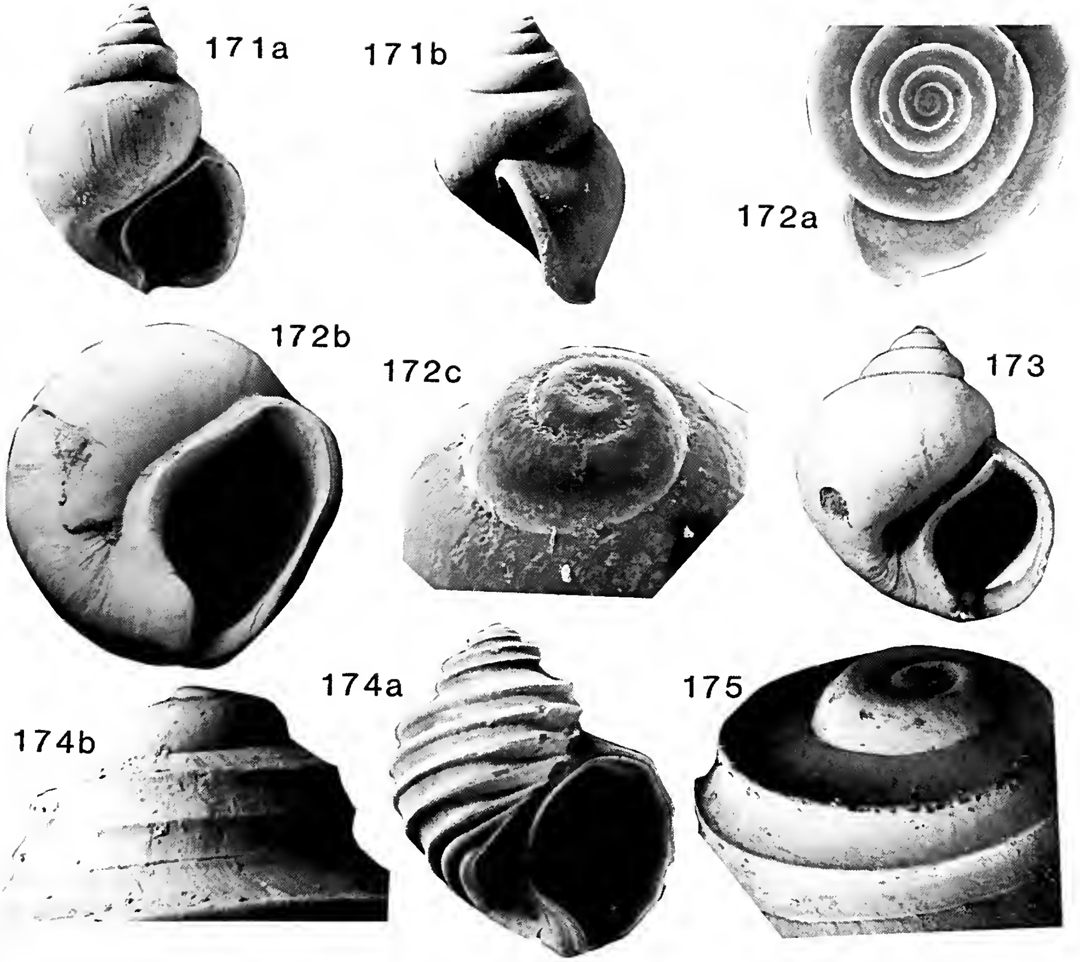
Remarks. The records of Costa (1980) are from new Pebasian localities lying to the east of the area from which the species was previously known, but they do not alter its known stratigraphical distribution. Costa later (1981) recorded and provided correctly identified figures of *E. woodwardi* from elsewhere (see below); her 1980 record of *E. crassilabris* can therefore be accepted with confidence. *E. crassilabris* is best distinguished from *E. woodwardi* by its less squat form and more vertical columella: that of the latter species is strongly curved to the right.

Eubora woodwardi Kadolsky, 1980 Fig. 173

v. 1871 *Ebora crassilabra* Conrad; Woodward: 102 (*pars*); pl. 5, fig. 1a, b.
. 1924 *Ebora crassilabra* Conrad; Roxo: 47.
*v 1980 *Eubora woodwardi* Kadolsky: 368, figs 6–8 (*cum syn*.).
. 1981 *Eubora woodwardi* Kadolsky; Costa: 641; pl. 1, figs 5, 6.

Holotype. GG19831/1, Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell Colln), the specimen figured both by Woodward (1871) and Kadolsky (1980): see also p. 355. Dimensions (mm): h, 7.6; br, 6.5; hap, 3.9; h/br, 1.17; sa, 84°. Four paratypes, GG19831/2–5, and six other shells, GG19831/6–11 not quoted by Kadolsky, were also studied. All from same horizon, locality and collection.

Further record. Late Caenozoic; Três Unidos, Peru (Roxo 1924, Costa 1981). Prior to the recognition of this species here by Costa (1981), it was believed (Kadolsky 1980) to be confined to Pichana and Iquitos.



Figs 171–175 Species of *Eubora*. All Pebasian; Pichana, Peru; Hauxwell Colln. **171–172**, *Eubora crassilabra* (Conrad). **171**, GG19830/1; a, front, × 5; b, side, × 5. **172**, GG19830/2; a, apical view, × 10; b, obliquely ventral view into aperture, × 12; c, oblique view of apex, × 50. **173**, *Eubora woodwardi* Kadolsky. GG19833/1, holotype, figured by Woodward (1871: pl. 5, figs 1a, b) as *Ebora crassilabra* Conrad and by Kadolsky (1980: fig. 6); front, × 6. **174–175**, *Eubora bella* (Conrad). **174**, GG19832/1; a, front, × 5; b, side view of apex, × 30. **175**, GG19832/2; oblique view of apex, × 50.

Eubora bella (Conrad, 1871) Figs 174–175

*. 1871*b* *Ebora (Nesis) bella* Conrad: 194; pl. 10, fig. 17.
v. 1871 *Ebora (Nesis) bella* Conrad; Woodward: 102; pl. 5, fig. 3.
. 1878 *Lacuna (Ebora) bella* (Conrad) Boettger: 494; pl. 13, fig. 3.
*. 1878 *Lacuna (Ebora) bella* (Conrad) var. *semisculpta* Boettger: 495; pl. 13, fig. 2.
. 1915 *Fossarus bellus* (Conrad) Cossman: 88.
. 1938 *Lacuna (Ebora) bella* (Conrad); de Greve: 72.
. 1980 *Eubora bella* (Conrad) Kadolsky: 369 (*cum syn.*), figs 9, 10.
. 1985 *Eubora bella* (Conrad); Hershler: fig. 52.

HOLOTYPE. NYSM 9193, Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell Colln). Not seen, studied by Kadolsky, 1980; efigured by Hershler, 1985.

MATERIAL STUDIED. GG19832/1–5 (*ex* G25475–80), also studied by Kadolsky (1980); Pichana, Peru (Hauxwell Colln). Dimensions (mm), GG19832/1: h, 8.7; br, 6.2; hap, 4.0; h/br, 1.40; sa, 85°.

DISTRIBUTION. Pichana (Conrad 1871*b*, Woodward 1871); ? Pebas (Boettger 1878).

REMARKS. Kadolsky (1980) studied all the previously figured specimens of this species (Conrad 1871*b*, Woodward 1871, Boettger 1878). He pointed out that Boettger's material had also been collected by Hauxwell and assumed that it therefore came from Pichana. Boettger, however, had stated that his specimens came from Pebas: for further discussion on the probable locality for Boettger's material see p. 323.

Woodward's figure was a copy of Conrad's. He stated that he possessed no specimens of this species, but five shells (GG19832/1–5) are present in BMPD.

E. bella bears a strong, probably superficial, resemblance to the living Mexican *Mexithauma quadripaludium* Taylor, 1966. The significance of this is dealt with in the discussion on possible generic relationships above, p. 216. The distinctions between the two are mainly in the apertural region. *E. bella* possesses a siphonal notch, which results in the formation of what Kadolsky refered to as the 'umbilical ridge', and it is falsely umbilicate. *E. grevei* Kadolsky is smaller and sculptured with weak axial ribs rather than carinae.

Eubora bella is very rare. In addition to those specimens quoted herein, Kadolsky mentioned only the two shells studied by Boettger (in Senckenburg Museum, Frankfurt). No further specimens were obtained from washings of Pichana matrix in BMPD.

Eubora grevei Kadolsky, 1980

. 1938 *Lacuna (Ebora) crassilabris* (Conrad); de Greve: 70 (*pars*); pl. 5, figs 19–21, 23 (not fig. 22).
*. 1980 *Eubora grevei* Kadolsky: 369, fig. 11.

This rare species is known only from the Late Caenozoic, Pebasian of Iquitos, Peru. A comparison with *E. bella* is given above. The holotype, PIMUZ J/4 (de Greve, no. 266), was not one of de Greve's figured specimens. Its height is 6.4 mm, and breadth 5.0 mm. Kadolsky assigned de Greve's fig. 22 to *E. woodwardi*.

Eubora pygmaea Kadolsky, 1980

. 1938 *Lacuna (Ebora) crassilabris* (Conrad); de Greve: 70 (*pars*).
*. 1980 *Eubora pygmaea* Kadolsky: 371, fig. 12.

The holotype, PIMUZ J/2 (de Greve, no. 249) is the only specimen known, and was not figured by de Greve. It is from the Late Caenozoic, Pebasian of Iquitos, Peru. Kadolsky pointed out that, although only half the size of *E. crassilabra* (h, 4.8 mm; br, 3.7 mm), the apertural characters of the genus are fully developed.

Genus ***TROPIDOBORA*** Pilsbry, 1944

TYPE SPECIES. *Pachytoma tertiana* Conrad, 1874*a*, Late Caenozoic, Pebasian; type locality uncertain, either Pebas, Old Pebas or Pichana. By original designation. No other assigned species.

DIAGNOSIS. Moderately thick-shelled, with four to six whorls; trochiform, conical, with basal carina and almost flat base of shell; aperture subrectangular with broad basal sinus; columella bent to the right; thick layer of shell present along inner lip, separating columella from aperture; inner and outer lips meeting adapically at rounded, rather obtuse, angulation, outer lip smooth within; not umbilicate, but slightly indented.

REMARKS. The apertural features of *Tropidobora* and *Eubora* are identical except for the profiles of their outer lips and bases. The two genera are here regarded as separate as no species with shell outlines between the conical *Tropidobora* and convex-whorled *Eubora* are yet known. The few species of Recent *Potamolithus* in BMZD lack the broad basal sinus of the two fossil genera. However, this character is present in other species originally assigned to *Potamolithus* by Pilsbry. It seems possible, as Kadolsky (1980: 367) suggested, that not all of these species are congeneric.

Parodiz (1969: 122) assigned *Tropidobora* to the Nymphophilinae (Taylor, 1966) after examining several hundred specimens of the living Mexican *Nymphophilus minckleyi* Taylor (1966: 199, figs 17–19), the only species then assigned to that subfamily which has, however, since been expanded to include North American genera (Thompson 1977, Hershler 1985). Taylor's figures show that there are important differences between the two, particularly in the aperture. *Nymphophilus* lacks the strong notch in the outer half of the basal lip which is so characteristic of *Tropidobora*. It is considered here that the two are not closely related, beyond both belonging to the Hydrobiidae.

Both *Brachypyrgulina* and *Limnothauma* Haas, 1955 (Recent, Lake Titicaca) have shells with some resemblance to *Tropidobora*. However, they lack its broad basal apertural notch and remain assigned to the Littoridininae.

Tropidobora tertiana (Conrad, 1874) Figs 176–178

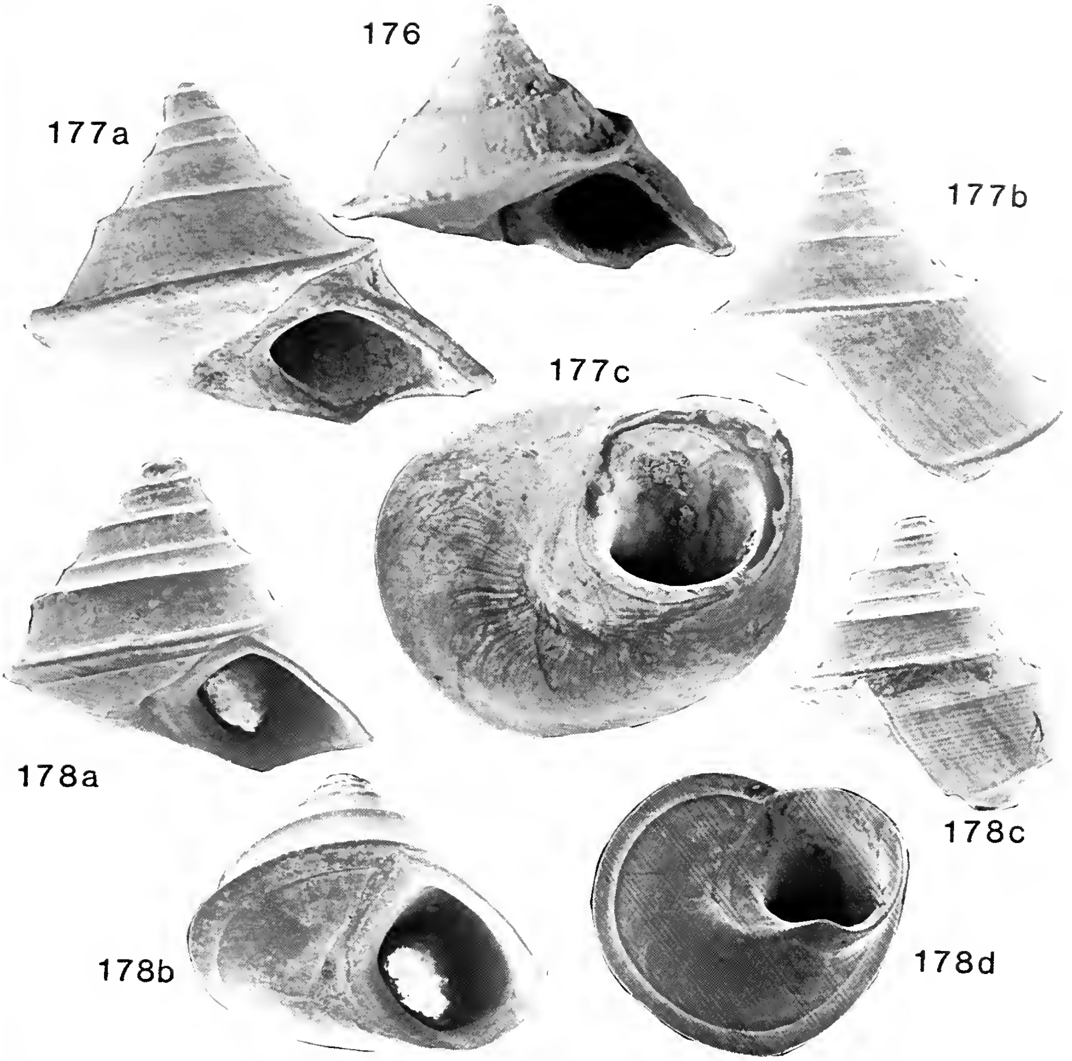
*v 1874*a* *Pachytoma tertiana* Conrad: 31; pl. 1, fig. 11.
. 1930 *Helicina? tertiana* (Conrad) Wenz: 3022.
. 1938 *Helicina? tertiana* (Conrad); de Greve: 68; pl. 4, figs 26–28, 31.
v 1944 *Tropidobora tertiana* (Conrad) Pilsbry: 150, text-fig. 2.
. 1969 *Tropidobora tertiana* (Conrad); Parodiz: 122.

HOLOTYPE. ANSP 16151, Late Caenozoic, Pebasian; either Pebas, Old Pebas or Pichana (Steere Colln).

OTHER MATERIAL STUDIED. G25294, G25295/1–3, GG21630 and also (extracted from washings, 1982) GG19995/1–4. All Late Caenozoic, Pebasian, Pichana (Hauxwell Colln). Also recorded from Iquitos (de Greve, 1938). Rare.

DIAGNOSIS. As for genus.

DESCRIPTION. There are between five and six whorls, including the apex. The first whorl is small and has a strongly convex profile. The second whorl is considerably larger and develops a high carinate shoulder, below which the whorl side is almost vertical, though the periphery lies at the lower suture. The carina rapidly drops to just above mid-whorl height during the next whorl and weakens considerably. By the penultimate (fourth or fifth) whorl this carina becomes obsolescent and by the final whorl it has disappeared altogether. On the early post-apical whorls the carina causes the whorl profile to be biconcave. The whorls are also carinate at both their upper and lower sutures, so that the later whorls have concave profiles. In contrast to the median carina, both the upper and lower sutural carinae increase in strength with growth of the shell and a flange is formed at the periphery of the final whorl. In G25294, an extra, weak, spiral thread is present on the side of the third whorl at about a third whorl height. It leaves no trace on later whorls though the mid-whorl carina persists as far as the aperture. A spiral thread is present on the base of the final whorl of this shell only. In all specimens the base of the shell is weakly convex. The apertural features are described in the generic diagnosis. The growth lines are weak. On the sides of the whorl, they are prosocline and virtually straight: as far as can be seen they are not deflected where they cross either the mid-whorl or sutural carinae. On the base of the shell, they are sigmoid, running parallel to the apertural margin, including the broad sinus. The inner margin of the basal sinus has a slightly angular junction with the base of the curved columella. This is the lowest portion of the shell and it forms a slightly angular ridge around the concavity at the axis of the shell.



igs **176–178** *Tropidobora tertiana* (Conrad). Pebasian; Peru. **176**, ANSP 16151, holotype (of *Pachytoma tertiana* Conrad) figured by Conrad (1874*a*: pl. 1, fig. 11) and by Pilsbry (1944: text-fig. 2); either Pebas, Old Pebas or Pichana; Steere Colln; front, × 10. **177**, GG21630; Pichana; Hauxwell Colln; a, front; b, side; c, base; all × 10. **178**, G25294; Pichana; Hauxwell Colln; a, front, × 10; b, oblique view of base, × 10; c, side view, × 8; d, base, × 8. (This specimen was unfortunately destroyed before figures c and d could be repeated).

IMENSIONS. In mm.	h	br	h/br	sa
olotype, ANSP 16151	4.5	5.7	0.79	80°
25294	5.0	5.2	0.96	65°
G21630	5.3	5.7	0.93	75°

ote. Because the peripheral flange increases in relative strength ith growth, the spire angle becomes more obtuse with growth. The gures given are the maximum.

EMARKS. This rare species cannot be confused with any ther South American Caenozoic or Recent gastropod. Dif- erences between it and some species of the living *Potamo- thus* are discussed above (p. 215).

Genus ***TOXOSOMA*** Conrad, 1874*a*

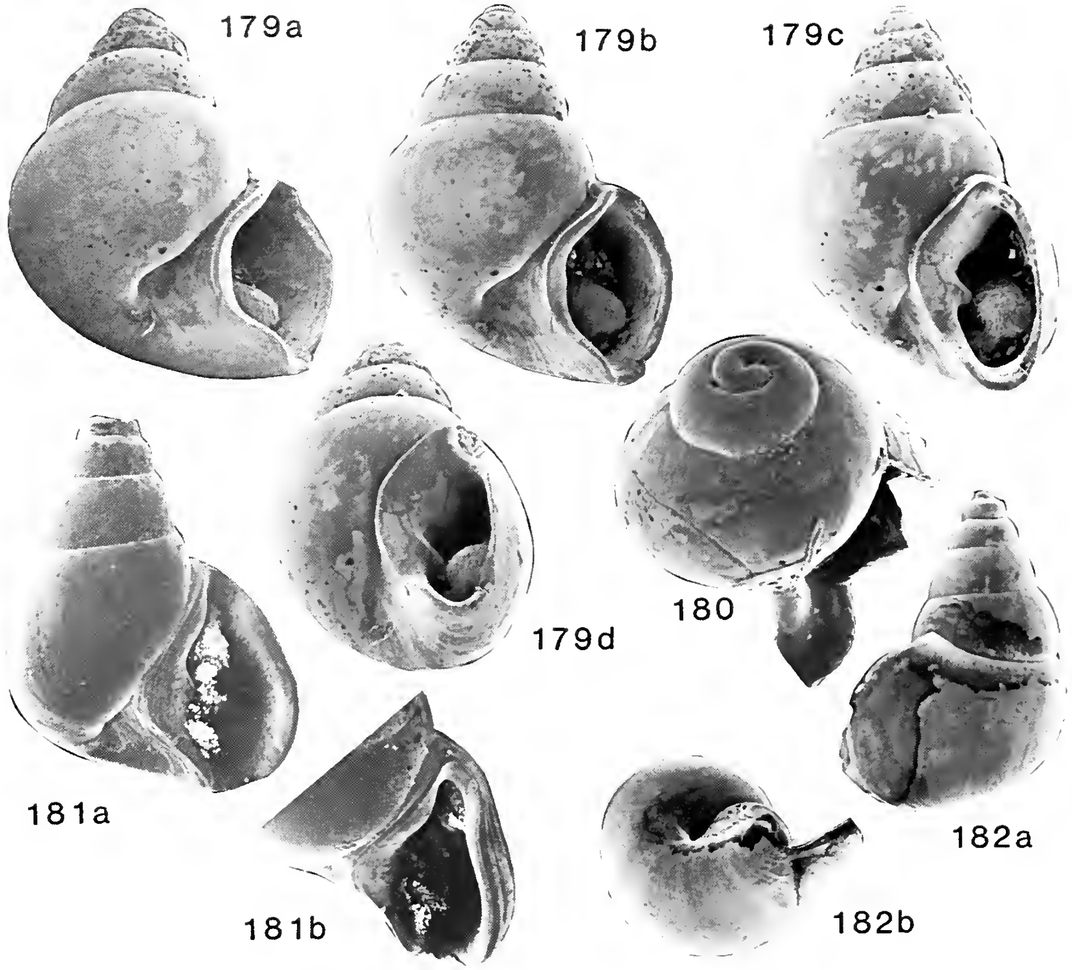
= *Liosoma* Conrad, 1874*a*: 31 (type species *Liosoma curta* onrad, 1874*a*: 31; Pebasian; Pebas, Old Pebas or Pichana. By monotypy); = *Pseudolacuna* Boettger, 1878: 495 (type species *Pseudolacuna macroptera* Boettger, 1878: 496; Pebas. By monotypy); = *Alycaeodonta* Etheridge, 1879: 85 (footnote), a *nomen nudum*, and acknowledged as a synonym of *Pseudolacuna* by Etheridge himself.]

TYPE SPECIES. *Toxosoma eboreum* Conrad, 1874*a*: 31; Late Caenozoic, Pebasian; Pebas, Old Pebas or Pichana. By monotypy, no other species assigned.

Confined to Late Caenozoic, Pebasian, of the Upper Amazon Basin. The suprageneric position of *Toxosoma* is discussed on p. 216 under Lithoglyphinae.

Toxosoma eborea Conrad, 1874*a* Figs 179–184

*. 1874*a* *Toxosoma eborea* Conrad: 31; pl. 1, fig. 7.
*. 1874*a* *Liosoma curta* Conrad: 31; pl. 1, fig. 8.
*. 1878 *Pseudolacuna macroptera* Boettger: 416; pl. 13, figs 14, 15.



Figs 179–182 *Toxosoma eborea* Conrad. Pebasian; Peru. **179–180**, Pichana; Hauxwell Colln. **179**, GG19835; a–d, four views to show details of apertural region, all × 15. **180**, GG21636; oblique view of apex of juvenile shell, × 50. **181–182**, Canamá; Barrington Brown Colln (these shells were not figured by Etheridge, 1879). **181**, GG19834/3; a, front view; b, oblique view into aperture; both × 12. **182**, GG19834/2; a, rear; b, base; both × 10.

v. 1879 *Pseudolacuna macroptera* Boettger; Etheridge: 85; pl. 7, fig. 12.
. 1915 *Pseudolacuna macroptera* Boettger; Cossmann: 107; pl. 12, figs 27–30.
. 1924 *Pseudolacuna macroptera* Boettger; Roxo: 47.
. 1938 *Pseudolacuna macroptera* Boettger; de Greve: 74; pl. 5, figs 17, 18, 24–29, 31–36.
. 1944 *Toxosoma eborea* Conrad; Pilsbry: 151, figs 3a, b.
. 1969 *Toxosoma eborea* Conrad; Parodiz: 121.
. 1980 *Toxosoma eborea* Conrad; Kadolsky: 373, figs 15–17 (v fig. 16)
. 1980 *Pseudolacuna macroptera* Boettger; Costa: 886; pl. 3, figs 1–6.
. 1981 *Toxosoma eborea* Conrad; Costa: 642; pl. 1, figs 7, 8.

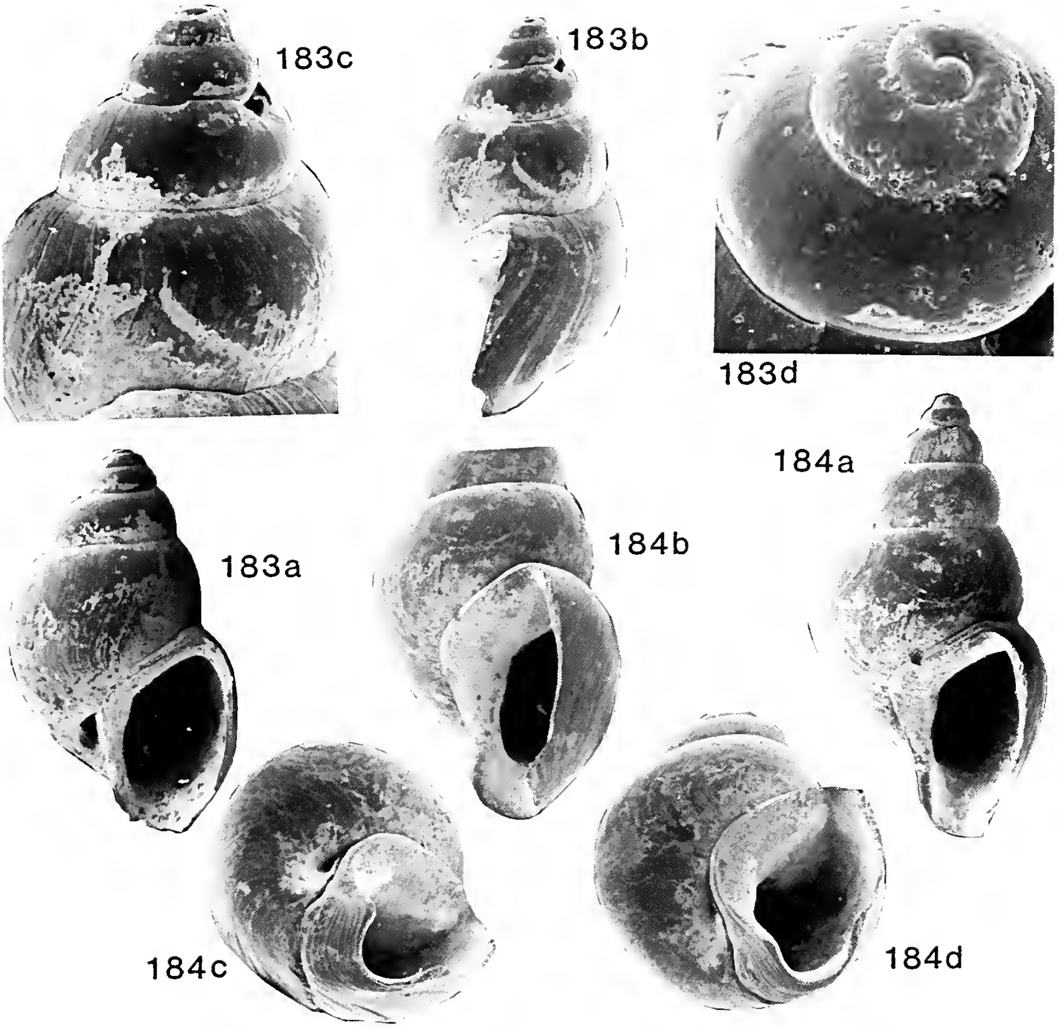
HOLOTYPE of *Toxosoma eborea* Conrad, ANSP 161152, Late Caenozoic, Pebasian; Pebas, Old Pebas or Pichana (Steere Colln), redescribed and refigured by Pilsbry (1944).

Holotype of *Liosoma curta* Conrad, same locality details as *Toxosoma eborea*, presumed lost, not listed as present in ANSP by Richards (1968).

Holotype of *Pseudolacuna macroptera* Boettger, Collection de Paléontologie, Université de Paris, 15485; Late Caenozoic, Pebasian; probably Pichana (Hauxwell Colln), refigured by Cossmann (1915) and Kadolsky (1980); not studied.

MATERIAL STUDIED. Late Caenozoic, Pebasian; GG19834/1, figured both by Etheridge (1879: pl. 7, fig. 12) and Kadolsky (1980: fig. 16) and two accompanying, unfigured shells, GG19834/2, 3, Canamá (C. B. Brown Colln, *ex* BMPD 97727); GG21513, Canamá (C. B. Brown Colln, extracted from matrix 1984); GG19853/1–6, G25481–6, Pichana (Hauxwell Colln) and GG19956/1–6, GG21635–8, Pichana (Hauxwell Colln, extracted 1982); GG19990–9, numerous specimens, Puerto Nariño, Colombia (Weeda Colln).

FURTHER OCCURENCES. All late Caenozoic, Pebasian: Três Unidos (Roxo 1924, Costa 1981); Iquitos (de Greve 1938); Rio Napo at mouth of Rio Mazan, about 30 km N of Iquitos (Willard 1966); CPCAN I, Tamandui, CPCAN III, Afloramento em Atalaia do Norte (Costa 1980). The record from the Neogene of the Cuenca Basin, Ecuador (Bristow & Parodiz 1982) is not accepted. Late Caenozoic, Pebasian; Upper Amazon Basin only.



Figs 183–184 *Toxosoma eborea* Conrad. Pebasian; Puerto Nariño, Colombia; Weeda Colln. **183**, GG19990; a, front, × 10; b, side, × 10; c, upper spire from side, × 20; d, oblique view of apex, × 50. **184**, GG19991; a, front, × 10; b, side, × 10; c, base, × 12.5; d, oblique view of base, × 12.5.

Dimensions. In mm.	h	br	hap	sa
GG19835/1, Pichana.	4.1	(2.9)	2.0	53°
GG21635, Pichana.	3.8	2.2	–	–
GG21636, Pichana.	1.2	–	–	–
GG19834/1, Canamá (fig'd Etheridge, 1879: pl.1, fig. 7).	4.7	(3.7)	2.6	48°
GG19834/2, Canamá.	4.5+	(3.5)	2.5	45°
GG19834/3, Canamá.	4.3+	(3.3)	2.4	40°
GG19990, Puerto Nariño.	5.5	3.2	2.9	50°
GG19991, Puerto Nariño.	6.0	3.6	3.1	50°

Note. Breadth measurements in brackets include the apertural wing. Height to breadth ratios of this species are not given because the wing introduces a variable factor.

Remarks. Kadolsky (1980) has redescribed this species in detail, but gave no dimensions. The illustrations in Costa (1981) confirm Roxo's earlier (1924) record from Três Unidos. The numerous specimens obtained from Puerto Nariño tend to be relatively large and also have rather convex whorl profiles and comparatively weak columellar folds. Unfortunately the wing-like outer lip of these shells is invariably broken. Nevertheless, they appear to be close enough in all essential features to be considered as belonging to the same species as the shells from Pichana in BMPD. In specimens from both Pichana and Puerto Nariño, the growth lines are extremely sinuous, particularly on the last whorl during growth of which the outer lip becomes increasingly produced. An umbilicus is present even in comparatively large immature specimens: it becomes plugged only in the late growth stages. The columellar plait dies away just before it reaches the inner lip, and is therefore often rather difficult to see in mature specimens with strongly produced outer lips. Broken specimens reveal that the columellar plait is present on earlier whorls and is not resorbed as growth proceeds.

Kadolsky (1980) appears to be correct in regarding *Liosoma curta* Conrad, 1874*a*, as a member of this species which is not fully grown.

The specimen GG19816 (Fig. 185), from the Miocene of the Cuenca Basin, Ecuador, identified as this species by

Fig. 185 Indeterminate gastropod, figured as *Toxosoma eboreum* by Bristow & Parodiz (1982: 42, fig. 16). Miocene, Mangán Formation; Loc. CRB 36, Cuenca Basin, Ecuador; GG19816, × 10.

Parodiz (*in* Bristow & Parodiz, 1982: 41, fig. 16) is not a *Toxosoma*. It has moderately coarse axial ribbing and indistinct traces of spiral threads. Both it and GG19815 come from the Mangán Formation at Loc. 36b, not 26b as quoted by Parodiz. G43325–6 (Carrion Colln), from the San Cayetano Formation of the Loja Basin, Ecuador, were labelled by Parodiz as belonging to this species, but were not mentioned in Bristow & Parodiz (1982). The material consists of blocks of well-bedded buff marl rich in moulds of small gastropods which resemble this species in shape. They are, however, considerably smaller, with a maximum height of 2 mm, and have much smaller whorls. Unfortunately neither the shape of their growth lines nor the presence or absence of a columellar plait can be made out. Although these specimens might be *Toxosoma*, they are much more likely to be very young 'post-spat' of the smooth-spired *Heleobia*, which is common at certain horizons in the Ecuadorian non-marine Neogene.

Family **VITRINELLIDAE** Bush, 1897

I am indebted to Dr W. F. Ponder (Australian Museum, Sidney) for the suggestion that the Pebasian fossil taxa dealt with below are best assigned to the otherwise fully marine family Vitrinellidae (Bush 1897: 122) rather than, as I had originally thought, to the fresh-water genus *Coahuilix* (Hydrobiidae). These fossil species, not necessarily congeneric at first sight, also bear some resemblance to the basommatophoran Superfamily Glaciodorbacea. In addition, earlier references in the literature to Pebasian species of *Planorbis* refer, at least in part, to the fossil taxa under consideration. The presence of small, virtually planorbiform, shells in several major groups means that correct familial, and even superfamilial, assignment is often indeterminate. Such shells tend to show comparatively few diagnostic features and the anatomy of many of the living taxa has not been fully investigated.

Several genera normally assigned to the Vitrinellidae are best referred to the Trochacea. N. J. Morris (BMPD) states (personal communication) that preliminary examination has shown the presence of nacre in some of these taxa: on these grounds alone, they cannot belong to the Rissoacea. This adds to the difficulties of interpreting both the living and fossil representatives of the family.

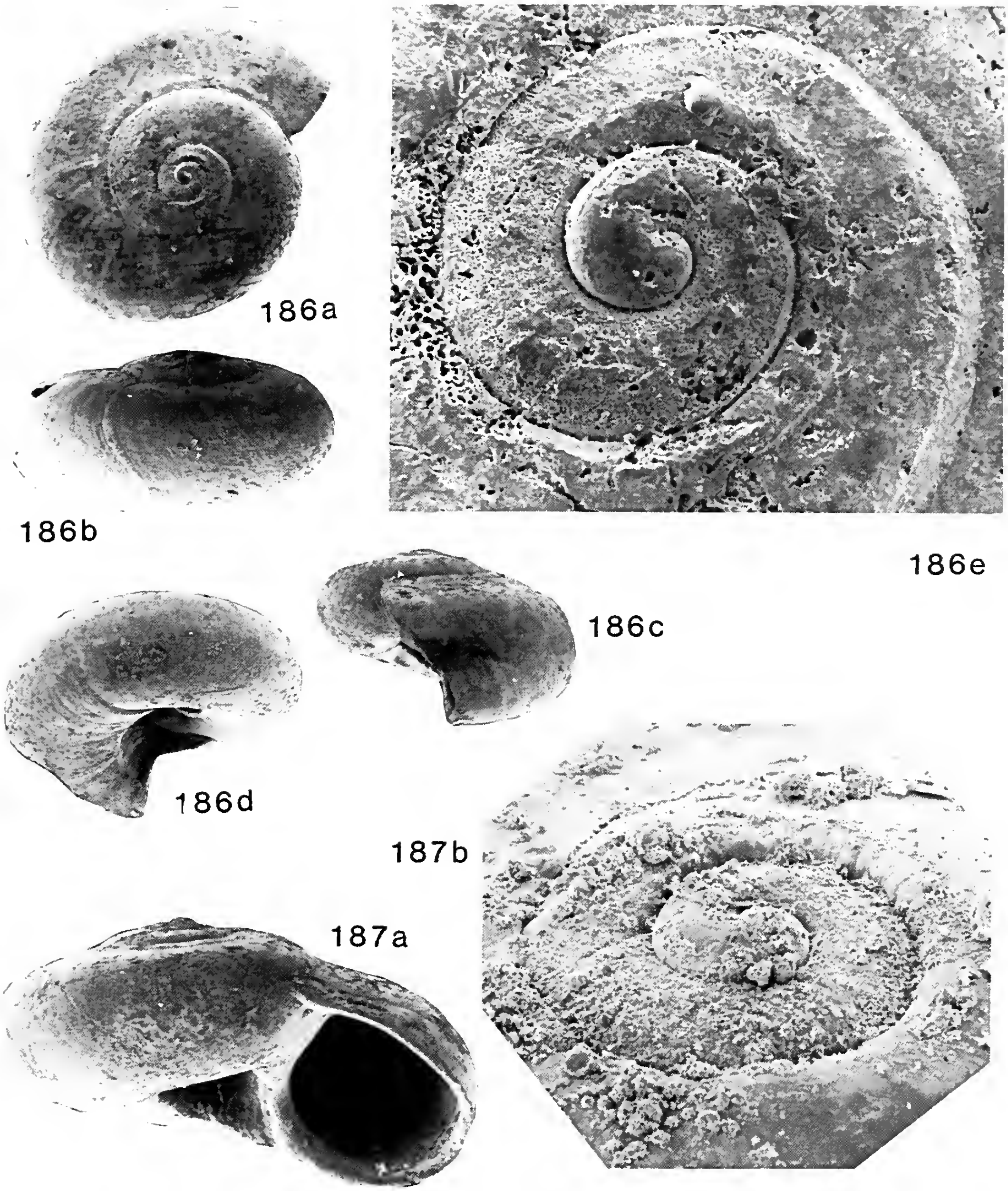
The Pebasian species are fairly similar to *Vitrinella* itself. The discussion below deals briefly first with similar supra-generic taxa, secondly with the nominal genera of Vitrinellidae which the fossils resemble, and concludes with a review of the fossil and living record of similar taxa.

Coahuilix hubbsi (Hydrobiidae, Cochliopinae) was newly described by Taylor (1966: 180, text-figs 8–13) from fresh-water pools in Coahuila Province, northern Mexico. Taylor assigned this single western hemisphere species to his new tribe Horatiini, in which he included the living fresh-water Balkan genera *Horatia* and *Hauffenia*. It is perhaps questionable that such geographically widely-separated genera should be so closely related. However, *Valvata micra micra* and *V. micra nugax*, both of Pilsbry & Ferris (1906: 172–3; pl. 9, figs 7–13) from Texas might well be placed closer to *Coahuilix*, rather than to *Horatia (Hauffenia)* as was suggested by Taylor (1966: 179). Hubricht (1940) recorded but did not figure *Horatia* from Texas and an artesian well in Alabama.

Taylor also suggested (1966: 179) that the three Pebasian species under consideration herein, *Planorbis bourguyi* Roxo (1924: 50, fig. E) from Três Unidos, *Planorbis* sp. of de Greve (1938: 107; pl. 4, figs 29, 30) from Iquitos and the unfigured *Planorbis pebasana* (Conrad, 1874*a*: 30) from either Pichana, Pebas or Old Pebas, were Cochliopinae (Cochliopini) *incertae sedis*. De Greve's specimen is redescribed here. The type material of *P. pebasana* is apparently lost, being absent both from ANSP (Richards 1968) and NYSM (Clarke 1906). Roxo's specimen has not been re-examined by me. He figured only the dorsal view, from which no family assignment is possible. The illustration shows a diameter of 5.2 mm, but the actual size of the specimen is unknown as no scale was given. The suggestion by Parodiz (1969: 166) that *P. pebasana* and *P. bourguyi* might be synonymous cannot be checked.

From Taylor's (1966) description and pen-and-ink type illustrations, it would appear that *Coahuilix hubbsi* (diameter 0.96–1.08 mm) might be distinguished from the similarly-sized *Vitrinella hauxwelli* sp. nov. (p. 226) from Pichana in having only 2¼ as opposed to 3½ whorls. The larger initial hemisphere of *C. hubbsi* has a diameter of about 0.1 mm, as against 0.04 mm in the fossil species. Taylor stated that the embryonic shell of his genus was of one whorl, but gave no description either of its surface or of any changes which separated it from the succeeding teleoconch, other than that the post-embryonic shell was sculptured with raised (collabral) riblets. From the type illustration, these appear to be in addition to the growth lines and are strong enough to make the outline of the shell distinctly rugose in dorsal view. This feature is particularly distinct in the illustrations of Taylor's paratype (1966: figs 12, 13), in which the lower margin of the body whorl also appears to be rugose in front view. The Pebasian fossils lack such riblets. In *C. hubbsi*, European Horatiinae and *V. hauxwelli* the apertures are entire. In mature *C. hubbsi* alone, it is strongly flared: there is no trace of flaring in the similarly-sized *V. hauxwelli*.

The fresh-water basommatophoran Superfamily Glacidorbacea (Ponder 1986: 53) is based on the living Australian *Glacidorbis* Iredale (1943). Ponder at the same time erected *Gondwanorbis* as a subgenus of *Glacidorbis* for the living Chilean species *Glacidorbis magellanicus* Meier-Brook & Smith (1976). This, to date, is the known distribution of the superfamily. *Glacidorbis* and *V. hauxwelli* are of almost identical planorbiform shape and have similar entire apertures. Ponder's description, however, is of a shell which is distinctly larger. *Glacidorbis* attains a diameter of 2.3 mm at 2½ whorls, whilst *V. hauxwelli* has 3½ whorls at a diameter of 1.0 mm. Ponder describes the 'protoconch' of *Glacidorbis* as not being clearly separable from the teleoconch. His illustrations clearly show its granular surface and that the diameter of the initial hemisphere of the shell is about 0.15 mm.

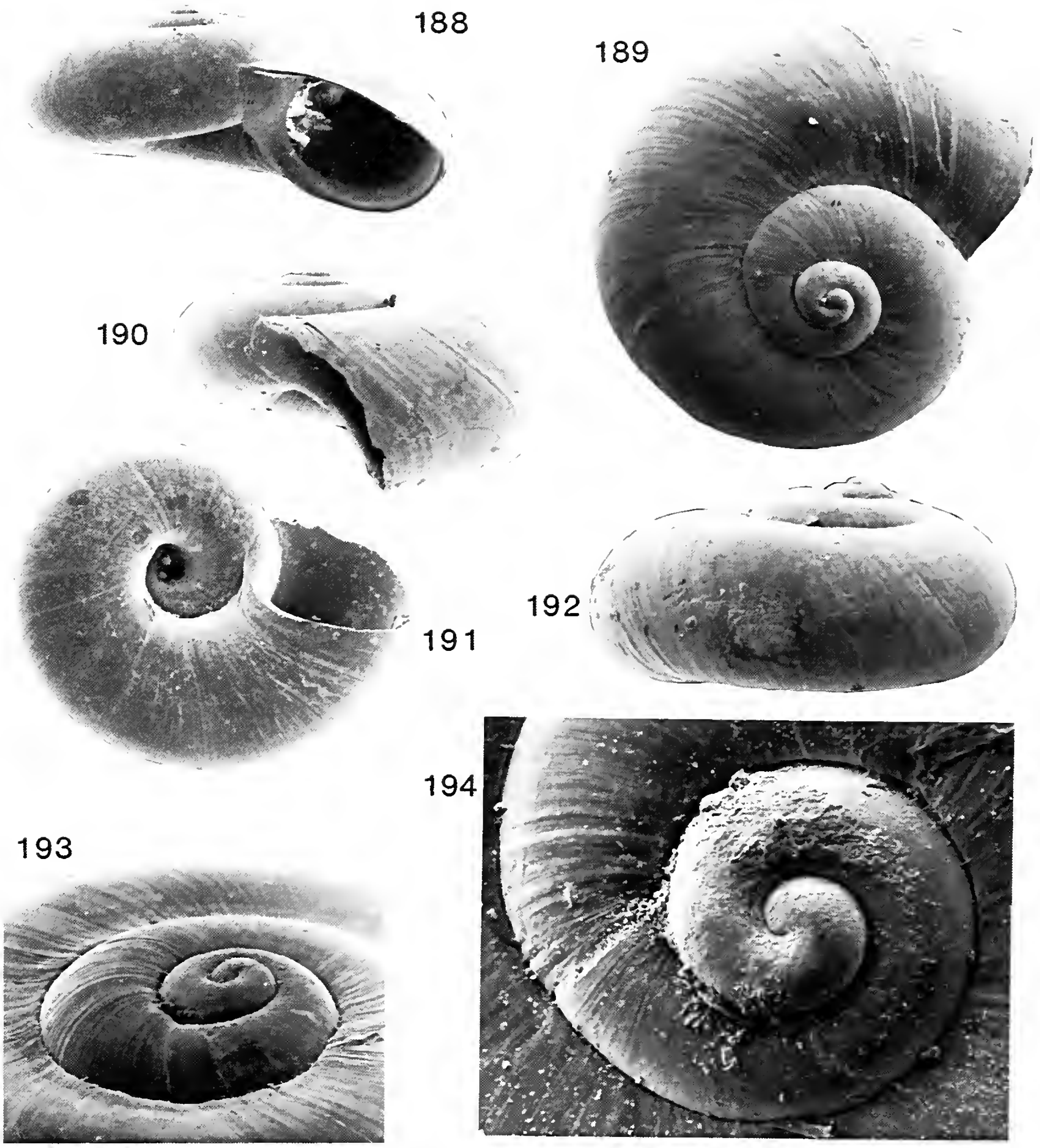


Figs 186–187 *Vitrinella helicoidea* C. B. Adams, type species of *Vitrinella* (s.str.). Recent beach drift; Miami, Florida; presented and identified by D. R. Moore; BMZD 1984240 (2 shells from sample). **186**; a, b, c, d, respectively apical, rear, side and (to show umbilical ridge) obliquely ventral views, all × 25; e, apex, showing aperture of larval shell at about ten o'clock, × 200. **187**; a, front, × 40; b, oblique view of apex showing larval aperture at about eight o'clock, × 200.

The Pebasian fossil material is almost certainly not so well preserved as Ponder's specimens of *Glacidorbis*, but the embryonic shell of *V. hauxwelli* shows no trace of any granular surface. It is much smaller, and is clearly delineated from the teleoconch by a very strong growth line. The growth lines in *Glacidorbis* appear to be virtually orthocline and almost straight, whilst those of the fossils are more prosocline and markedly sinuous.

Vitrinellidae with which the Pebasian fossils should be compared are *Vitrinella* s.str., *V. (Vitrinellops)*, *V. (Striovitrinella)*, *Cochliolepis* and *C. (Tylaxis)*. Doubt must remain about the value of some of the distinctions between these taxa, which seem to be both arbitrary and unnecessary. Neither *Vitrinella* nor its type species were figured in their original descriptions (C. B. Adams 1850). The true identity of *Cochliolepis* is uncertain, as the type specimens of the type species were destroyed. There is no uniformity of opinion as to its correct identification, as the original illustrations (Stimpson 1858) lacked detail.

Vitrinella C. B. Adams (1850: 3) has as type species *Vitrinella helicoidea* C. B. Adams (1850: 9), by subsequent designation of Bush (1897: 122): living, Jamaica, probably



Figs 188–194 *Vitrinella (Vitrinellops) floridana* (Pilsbry & McGinty). Recent; spoil bank of canal SE of Rockport, Texas; presented and determined by D. R. Moore; BMZD 1984241 (7 shells from sample). **188–192**; respectively front, apical, side, basal and rear views, all × 50. **193**; oblique view of apex, followed by rapid expansion in whorl diameter, × 100. **194**; apex with larval aperture at eight o'clock, × 200. (Note, in particular, general similarities in whorl profile between Fig. 193 and Figs 197a, b of *V. (V.) hauxwelli* sp. nov., p. 227).

from beach sand in cove near Port Royal (C. B. Adams 1850: 4). The only specimens available for study are three somewhat worn shells from a beach drift, Miami, Florida (BMZD 1984.240), presented and identified by D. R. Moore (Figs 186, 187). These agree with the description and illustrations in Pilsbry & McGinty (1946: 13; pl. 2, figs 3, 3a, b). The shell has 3–4 whorls in all, and is smooth except for growth lines and a few, apparently random, growth halts. The spire is very low, with an angle of about 150°. Later whorls are rather more convex and the suture lies at the periphery. Growth lines are strongly prosocline and curved, so that the most forward point of the aperture, when viewed from above, lies half-way between the periphery and the suture with the previous whorl. The embryonic shell appears to consist of 1¼–1½ whorls, reaching a diameter of 0.25 mm. Its initial hemisphere appears to be slightly sunken in the spire and has a diameter of about 0.05 mm. The boundary with the teleoconch is marked by a strong growth line, and a rugose ridge almost immediately develops adjacent to the suture on the upper surface of the first teleoconch whorl. The aperture is almost entire except for a slight concavity where it is adpressed to the previous whorl. The inner lip is thickened. The umbilicus is deep and bordered by a well-marked spiral cord.

Vitrinellops was erected as a subgenus of *Vitrinella* by Pilsbry & Olsson (1952: 73). Its type species is *V. zonitoides*

Pilsbry & Olsson (1952: 73; pl. 13, figs 2, 2a, b): Recent, San Miguel Island, Pearl Islands, off the Pacific coast of Panama. They defined their new subgenus as being similar to *Vitrinella* s.str., but lacking the keel bordering the umbilicus. They pointed out (1952: 71) that comparatively few species belonged to *Vitrinella* s.str. (three Pacific species listed, p. 84) whilst the majority (16 Pacific species listed), which could be either smooth or sculptured with minute spiral striae, were assigned to *Vitrinellops*. Their lists were copied by Keen (1971: 373–4). However, *Striovitrinella* (Olsson & McGinty, 1958: 31) was proposed for their newly described striate living Caribbean species, *V. (S.) elegans* (1958: 31; pl. 3, figs 1, 1a–d). The similar Pacific species are now best assigned to this subgenus.

The remarks below on *Vitrinellops* are based on the only good sample of the subgenus available for study. The living *Vitrinella floridana* Pilsbry & McGinty (1946: 16; pl. 2, figs 4, 4a) described from Florida is here reassigned to *Vitrinellops*. Sample BMZD1984241, collected by W. H. Rice from a spoil bank of a canal SE of Rockport, Texas, was specifically determined and presented by D. R. Moore, and contains several well-preserved specimens (Figs 188–194) of 3 – 3½ whorls, with diameter 1.1 – 1.5 mm. The embryonic shell has 1½ – 1¾ whorls with a diameter of about 0.37 mm. In some individuals it is set at a slight angle to the post-embryonic shell. Its initial hemisphere has a diameter of 0.048 – 0.060 mm. Growth lines may be made out on the latter part of the embryonic shell, which is separated from the post-embryonic shell by a very marked, orthocline, growth halt. For a short period the shell then appears to expand more rapidly than the embryonic shell, sometimes giving this stage a rather flared appearance. *V. (Vitrinellops) floridana*, in common with the type species of the subgenus and the majority of the other Pacific species assigned to it by Pilsbry & Olsson (1952), has a low but distinct spire. Only two species dealt with by them approach the planorbiform condition: these are *V. (V.) subquadrata* Carpenter (1856) (1952: 76; pl. 11, figs 5, 5a, b), which has a slightly raised spire, and their own species *V. (V.) margarita* (1952: 74; pl. 13, figs 5, 5a, b), which is planorbiform and was described as having excessively minute spiral striations. This last feature suggests a connection with *Striovitrinella*, whilst its very broad aperture is reminiscent of the otherwise Caribbean–Atlantic *Cochliolepis*. At least one species presently assigned to *Cochliolepis, C. striata* Dall (1889), is spirally striate (see Pilsbry, 1953: 432; pl. 52, fig. 2).

Among the living Pacific species now transferred to *V. (Striovitrinella)* from *V. (Vitrinellops)* is *V. ponceliana* (de Folin 1867), whose syntypes (BMZD 196458, from the Pearl Islands, Pacific coast of Panama) possess an embryonic shell very similar to that of *Vitrinellops*. The post-embryonic shell, which is low-spired with an almost entire aperture and an umbilicus lacking a spiral ridge, differs from typical *Vitrinellops* only in being spirally striate. Although both Pilsbry & Olsson (1952) and Keen (1971) listed the spirally striate and low-spired *Cyclostremella dalli* Bartsch (1911) under *Vitrinellops*, both papers entirely ignored the planispiral, but otherwise very similar, *Cyclostremella californica* Bartsch (1907: 232; pl. 40, figs 10–12). The inclusion of planispiral and almost planispiral species in subgenera of *Vitrinella* suggests that the Pebasian *V. hauxwelli* might also be accommodated within this group.

Among the Pebasian fossils, The single Iquitos shell described by de Greve (1938) as *Planorbis* sp. is the most readily acceptable as a member of the Vitrinellidae, with strong similarities to a number of species normally assigned to *Cochliolepis*. Unlike the apparently more widespread group of *Vitrinella* and its subgenera, the name *Cochliolepis* appears not to have been used for species from the western Pacific, but only for those from the Caribbean and Atlantic. The presence of *V. margarita* suggests, however, that species with *Cochliolepis*-like characters do occur in the Pacific. According to Pilsbry (1953: 433), the type specimen of its type species *Cochliolepis parasitica* Stimpson (1858: 307), collected live from the harbour of Charleston, South Carolina, was destroyed in the Chicago fire of 1871. Pilsbry selected a neotype, USNM 87142, without either describing or figuring it or giving locality details. Pilsbry indicated (1953: 431–3), however, that several authors had misidentified this species, including Gardner (1948: 194; pl. 25, fig. 1). I therefore know of no correctly identified illustration of this species showing its shell characters. Neither the genus nor its subgenus *Tylaxis* is represented in BMZD collections. *Cochliolepis (Tylaxis)* Pilsbry (1953: 434), type species *T. virginica* (Pilsbry 1953: 434; pl. 52, figs 4, 4a, b), Miocene, Virginia, differs from *Cochliolepis* (s.str.) only in having a more thickened columellar and parietal callus and flattened, gently sloping walls of the rather wide umbilicus, and in other, perhaps rather superficial, details.

Typical species of *Cochliolepis* are not unlike *Vitrinellops* except that they tend to be rather large, ranging 2.0 – 6.5 mm in diameter, and are more involute, with the result that the sutures on the upper surface are almost tangential, thus producing a rather flush-sided, low spire. The aperture is entire, or nearly so, and is rather broad. None of the species illustrated in Gardner (1948: pl. 25) nor in Pilsbry (1953: pl. 52) could be confused with the Iquitos fossil. The living *Cochliolepis surinamensis* Altena (1966: 235, figs 2a–d; 1975: 18, figs 8a–d) from a shell ridge near Paramaribo, Surinam, differs from this fossil in that its spire is slightly concave and its aperture not entire, but crescentic, the inner lip strongly embracing the penultimate whorl as in Planorbidae. Furthermore, it seems to be larger at all stages. The holotype has a diameter of 2.7 mm at 2¾ whorls, and from the type illustration the initial hemisphere of the larval shell would appear to have a diameter of 0.08 mm.

The problem whether the new species *V. hauxwelli* from Pichana and *V. degrevei* from Iquitos should be regarded as congeneric cannot be satisfactorily answered for several reasons. The strong growth halt occuring after half a whorl in *V. hauxwelli* is here interpreted as representing the change from embryonic to post-embryonic shell, and would suggest lecithotrophic development, a reasonable assumption as this development type appears to be a common response to reduced salinities in groups whose marine members normally have free-swimming veliger larvae. Unfortunately the single specimen of *V. degrevei* is not sufficiently well preserved to show where its embryonic shell ended. However, in *V. hauxwelli* and *V. degrevei* the initial hemispheres are of similar size and subsequent whorls develop at similar rates, taking account of the fact that the latter species is much more involute than the former. On balance, it seems more likely that one, rather than two similar, genera of marine Vitrinellidae invaded the Pebasian Basin. These fossil species are therefore both assigned, with some reservations, to *Vitrinellops* in spite of the differences in their adult shells, and in spite of the fact that the embryonic shell of *V. hauxwelli* differs so markedly from that of typical marine *Vitrinellops*. Comparisons of Figs 193 and 197a, b, showing their early whorls, clearly demonstrate their general similarity. Disregarding these considerations, however, it could be argued that *V. hauxwelli* belonged to *Vitrinellops* and *V. degrevei* to *Cochliolepis*. But the above discussion on the available genus-group taxa suggests that the boundaries between them are possibly arbitrary, as well as ill-defined, not only because of lack of knowledge of their soft-part anatomy and other biological information, but also because their type-species are not fully understood.

Members of the genera discussed above are mainly tropical in distribution, living on the Pacific coast from California to northern Peru (Pilsbry & Olsson 1945, 1952; Keen 1968, 1971), in the Caribbean (C. B. Adams 1850; Olsson & McGinty 1958), southern United States, including its Atlantic coast (Pilsbry & McGinty 1945–50; Moore 1972) and also the Atlantic coast of South America as far south as Brazil (Altena 1966, 1975; Rios 1985). None of these living species can be confused with the Pebasian fossils.

The same genera occur in Neogene deposits of the south-eastern United States (Gardner 1948; Pilsbry 1953), Venezuela (Weisbord 1962) and Trinidad (Jung 1969). Surprisingly, the rich molluscan faunas from the Canal Zone of Panama, although containing several Vitrinellidae described by Woodring (1957) from the fine-grained sediments of the Gatun Formation, have not yet yielded any similar to those under consideration. No Vitrinellidae have been described from the Neogene deposits of the Pacific coastal strips of Colombia, Ecuador and northern Peru.

Both Gardner (1948: 193) and Woodring (1957: 69) drew attention to the difficulties of vitrinellid classification owing to the paucity of information about living members of the family. Moore (1972) provided a most useful and readable account of the shell morphology and anatomy characteristic of the family, as well as geographical distribution and habitat. He concluded that most vitrinellids were herbivores, with most species living in quite shallow water under rocks, or in grass beds such as those occurring in marine bays and lagoons. All the shells of living vitrinellids that I have been able to examine have embryonic shells characteristic of free-swimming larvae. As far as is known, the present records of the family are the first from a reduced salinity habitat and also the first description of what is interpreted as an embryonic shell of only half a whorl, suggesting lecithotrophic development.

Genus ***VITRINELLA*** C. B. Adams, 1850

TYPE SPECIES. *Vitrinella helicoidea* C. B. Adams (1850: 9). Living, Jamaica; by subsequent designation of Bush (1897: 122).

Subgenus ***VITRINELLOPS*** Pilsbry & Olsson, 1952

TYPE SPECIES. *Vitrinella (Vitrinellops) zonitoides* Pilsbry & Olsson (1952: 73; pl. 13, figs 2, 2a), by original designation.

Vitrinella (Vitrinellops) hauxwelli sp. nov. Figs 195–197

HOLOTYPE. BMPD GG19952, Late Caenozoic, Pebas Beds; Pichana, Peru; Hauxwell Colln, 1870, extracted from matrix, 1980. GG19953–4, GG21516, and GG21517/1–3 (same details as holotype) are paratypes.

NAME. From Juan Hauxwell's collection, purchased by the British Museum in 1870.

DIAGNOSIS. Planorbiform *Vitrinellops* with slightly sunken spire; embryonic shell of half a whorl, terminating with strong growth line; shell smooth except for growth lines; aperture entire, almost circular, but slightly broader than high; sutures very deeply impressed; umbilicus broad.

DESCRIPTION. The shell has three whorls. Adapically, it is almost planispiral, but the minute initial whorl is slightly sunken and deviated. A strong growth line, marking the aperture of the apparently smooth embryonic shell, can be seen in the holotype, and more clearly in paratype GG19953. In both specimens the initial hemisphere has a diameter of 0.04 mm and the maximum diameter of the embryonic shell is 0.08 mm. Close-set growth lines may be seen on the adapical surface of the post-embryonic shell immediately following the embryonic aperture. By the third whorl, the translation rate has increased so that the initial whorl is just visible in side view, except where it is obscured by the last half whorl, whose whorl expansion rate is rather greater than that of earlier whorls. The aperture is nearly circular, slightly wider than high, and is strongly opisthocline, leaning at about 20° from the vertical. The growth lines are clearly visible, slightly sinuous, and fairly regular both in strength and frequency. The umbilicus is deep. The nearly circular form of the aperture, coupled with the rather evolute mode of growth, results in both the upper and lower sutures being deeply impressed.

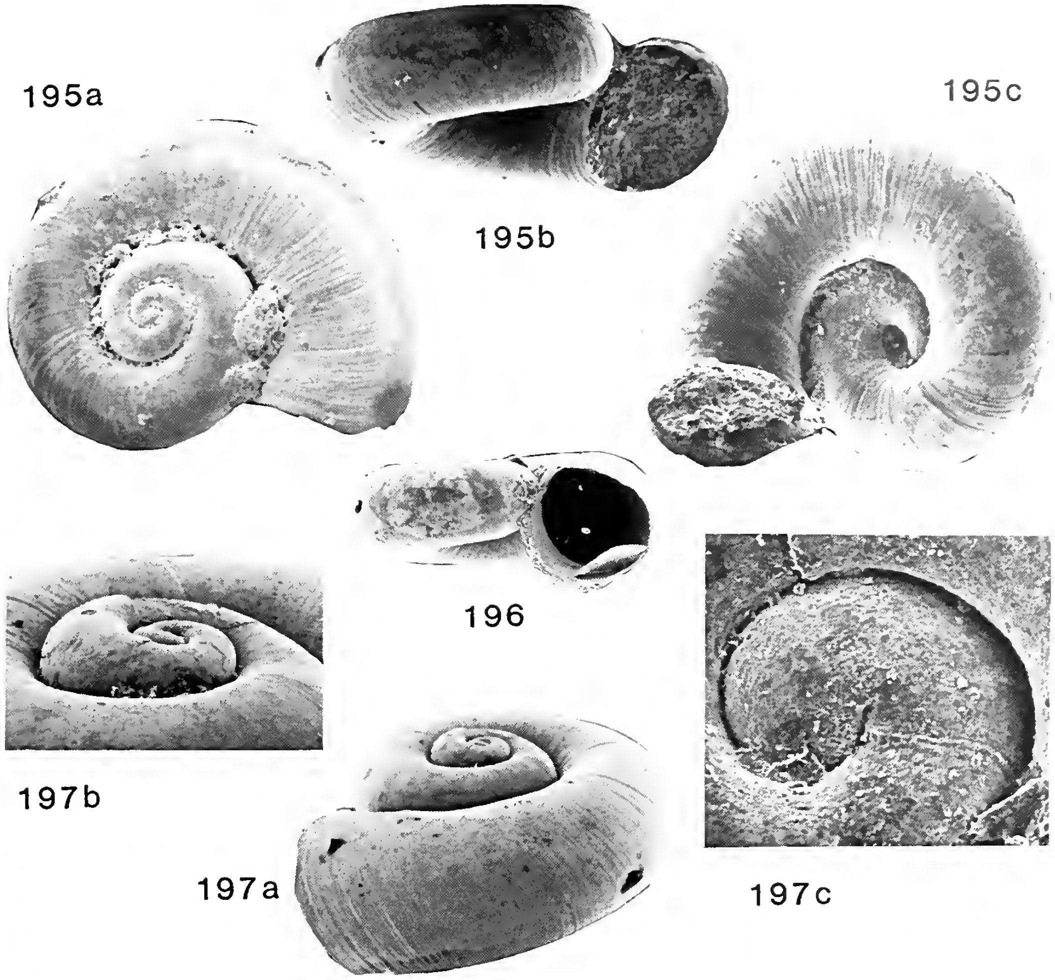
DIMENSIONS. In mm.	d	h	hap	brap
GG19952, holotype, Pichana, (Hauxwell Colln).	1.15	0.57	0.40	0.43
GG19953, paratype.	1.25	–	–	–
GG19554, paratype.	0.85	0.40	0.32	0.35

REMARKS. The half-whorled embryonic shell immediately distinguishes this species from all living *Vitrinellops* which I have examined. Most *Vitrinellops* also have a slightly raised spire. The planorbiform *V. (V.) margarita* Pilsbry & Olsson (1952: 74; pl. 13, figs 5a, b; Recent, Pearl Islands off the Pacific coast of Panama) is larger (d, 2.2 mm) and relatively lower. Its aperture is much broader and is crescentic, embracing the previous whorl. Illustrations (Pilsbry & Olsson 1952: 76; pl. 11, figs 5, 5a, b) show that the planorbiform *V. (V.) subquadrata* Carpenter (1856; Recent, Mazatlan) develops marked columellar and parietal callus by the time it reaches a diameter of 0.85 – 1.0 mm. From above, the growth lines appear to be much more convexly curved than in *V. (V.) hauxwelli*. *Cochliolepis pluscula* Jung (1969: 430; pl. 43, figs 21–23) from the Upper Miocene Melajo Clay of Trinidad might be better referred to *Vitrinellops*. Its rounded aperture is similar to that of the Pebasian species, but it has a distinct spire and a less open umbilicus. It is also slightly larger (d, 1.6 mm).

Vitrinella (Vitrinellops) degrevei sp. nov. Fig. 198

v. 1938 *Planorbis* sp. de Greve: 107; pl. 4, figs 29, 30.

HOLOTYPE. PIMUZ no. 2531. Late Caenozoic, Pebasian; Iquitos, Peru (Peyer Colln). No other material.



Figs **195–197** *Vitrinella (Vitrinellops) hauxwelli* sp. nov. Pebasian; Pichana, Peru; Hauxwell Colln. **195**, **holotype**, GG19952; a, dorsal view; b, front; c, ventral view; all × 50. **196**, paratype, GG19954; front, × 50. **197**, paratype, GG19953; a, slightly oblique side view, × 50; b, view of early whorls, × 120; c, dorsal view of protoconch and first growth lines, × 500. Compare Fig. 193.

Name. For L. de Greve, who described and figured the pecimen in 1938.

Diagnosis. Comparatively large, involute *Vitrinellops* with ow spire; adapical surface of whorls weakly convex and utures only slightly incised; aperture broad; umbilicus narrow.

Description. The unique shell is rather involute in both dorsal and ventral views. There are about 3½ whorls, and in he later growth stages the expansion rate increases slightly. Traces of two rather strong growth halts just prior to the perture suggest that full size is being reached. The early whorls strongly resemble those of the preceding species in ize and shape, but neither growth lines nor a growth halt ndicating the transition from embryonic to post-embryonic hell are visible at the half-whorl stage. At 1½ whorls, owever, some almost orthocline, slightly forwardly-bowed rowth lines can be observed with difficulty, but they are not lear enough to be identified as representing the embryonic perture. The upper surface of the shell is slightly domed and he sutures of the weakly convex whorls are not deeply mpressed. The lower surface is considerably more convex nd the umbilicus is narrow: although infilled with immovable matrix, it is unlikely that whorls preceding the body whorl would be visible. The aperture is much broader than high and its periphery is rather below half whorl height. The inner lip is almost straight and vertical, but its upper left portion is slightly indented by the previous whorl. The growth lines are markedly opisthocline, being inclined strongly from the vertical. From above, they appear bowed forward, whilst from below, the bowing is reversed.

Dimensions. In mm.	d	br	hap	brap
Holotype. PIMUZ 2531.	1.93	1.13	0.76	0.90

Remarks. This species may easily be distinguished from the preceding one by its raised spire and involute form. In shape it somewhat resembles the Recent Surinam *Cochliolepis surinamensis* Altena (1966). The distinctions between the two and the reasons for assigning the fossil to *Vitrinellops* rather than *Cochliolepis* are given above in the remarks on the family (p. 225).

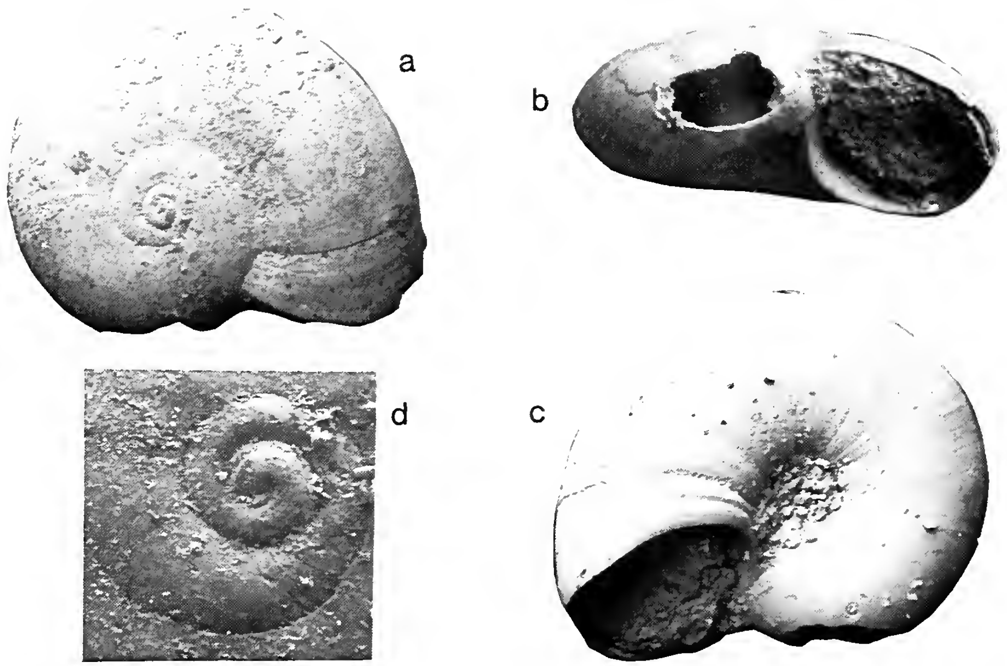


Fig. 198 *Vitrinella (Vitrinellops) degrevei* sp. nov. **Holotype**. Pebasian; Iquitos, Peru; Peyer Colln, PIMUZ no. 2531. a, dorsal view, × 30; b, front, × 30; c, ventral view, showing almost orthocline growth lines, × 30; d, dorsal view of early whorls, × 100.

Fig. 199 *Vitrinella (Vitrinellops)* sp. Pebasian; Pichana, Peru; Hauxwell Colln. GG19950; a, dorsal view, × 50; b, side, × 50; c, front, × 50; d, ventral view, showing sigmoid growth lines, × 90.

Vitrinella (Vitrinellops) sp. Fig. 199

MATERIAL. GG19950, Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell Colln, 1870, extracted 1980). No further material.

REMARKS. This single planorbiform shell, whose upper surface is partly obscured by immovable matrix, does not merit naming as a new species. There are about 2¾ whorls. As far as can be seen, the early whorls are similar to those of the two preceding species. It is, however, clearly separable from the relatively common *V. (V.) hauxwelli* found with it at Pichana by its more involute form, and by the absence of slightly sunken early whorls. Its round aperture, which is similar to that found in *hauxwelli*, immediately distinguishes it from the distinctly spired and involute *V. (V.) degrevei*, which it greatly resembles in ventral view. In dorsal view, the growth lines are very strongly bowed forwards.

Superfamily **CERITHIACEA** Fleming, 1822

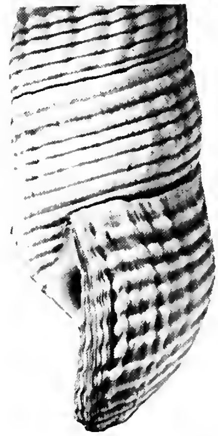
[*nom. transl.* Cossmann, 1906: 1, *ex* Cerithiadae Fleming, 1822: 491.]

201

200a

202

200c



200b

ig. 200 *Doryssa atra* (Bruguière). BMZD 1984202. Recent; Guyana; Cuming Coll. **Lectotoype** (herein selected) of *Melania nicotiana* Reeve, figured by Reeve (1860: pl. 30, fig. 202). a, front, × 2; b, side, × 2; c, oblique view into aperture, showing growth lines on neck of whorl, × 3.
ig. 201 *Doryssa consolidata* (Bruguière). BMZD 1984203. Recent; Brazil; Cuming Colln. Specimen figured by Reeve (1860: pl, 1, fig. 3). × 2.
ig. 202 *Doryssa pernambucensis* (Reeve). BMZD 1984204. Recent; Brazil; Cuming Colln. One of the syntypes of *Melania pernambucensis* Reeve, specimen figured by Reeve (1861: pl. 1, fig. 3). × 2.

Morrison (1954: 357) advanced the supposition that freshwater melanians (i.e. approximately Thiaridae *sensu* Wenz 939) were polyphyletic, having been derived from several different families of marine Cerithiacea. Although Parodiz 1969) used the families Pleuroceridae and Thiaridae *sensu* Morrison, this classification has not gained general acceptance.

Few palaeontologists would dispute that the Thiaridae *sensu* Wenz) were almost certainly derived from more than one source, and as Morrison himself pointed out, his work should help in elucidating the zoogeographical story of these nails.

Morrison's classification is followed here, as far as is possible. The Pleuroceridae are dioecious and include *Doryssa* nd *Pachychilus*. The Thiaridae dealt with herein are all members of the Hemisininae. They are parthenogenetic and nclude *Aylacostoma*, *Hemisinus*, *Longiverena*, *Verena* and *Basistoma*, all of which have living type species. The extinct enus *Sheppardiconcha* is also placed in the Hemisininae, on the grounds that it is similar to other members of the family, in particular *Basistoma*.

Morrison's synonymy was accepted by Parodiz (1969: 134; Parodiz *in* Bristow & Parodiz 1982: 43). Because of this controversy, the Pleuroceridae and *Doryssa* are briefly discussed below even though neither appear to be present in the faunas under consideration. Morrison's work is difficult to interpret because of the almost total lack of illustrations and because he names so few species. In discussing *Aylacostoma* (s.str.) he described it as having prominent spiral sculpture, and referred to *Aylacostoma ruginosum* (Morelet) from Central America. This species is spirally striate and has no close resemblance to the comparatively smooth Brazilian type species of *Aylacostoma*. This example, coupled with that of *Doryssa* (below), suggests Morrison's often important and interesting conclusions must always be thoroughly checked. Correct classification of these fossils is not easy when they lack salient diagnostic features such as operculae. The crucially differing modes of reproduction can, in dead specimens, only be revealed by the presence of embryonic shells. Embryonic shells are formed in the parthenogenetic Hemisininae, but, so far, I have not found them in the dioecious Pleuroceridae.

Family **PLEUROCERIDAE** Thiele, 1929

[*emend. et nom. transl.* Morrison, 1954: 357–8, *ex* Pleurocerinae Thiele, 1929: 192 (subfamily)]

Subfamily **PLEUROCERINAE** Thiele, 1929

[*emend.* Morrison, 1954]

Pleurocerinae, *sensu* Morrison, embraces several genera such as *Pachychilus* and *Doryssa* included in Melanatriinae (Thiele 1928: 399) by Thiele (1929: 189) and Wenz (1939: 684–6).

Genus ***DORYSSA*** H. & A. Adams, 1854
(Figs 200–202)

Type species. *Bulimus ater* Bruguière, 1792*a*, Recent, north-western South America. By subsequent designation of Brot (1874: 8).

Diagnosis. Medium to large Thiaridae with spire angle between 20° and 30°; aperture well rounded except for posterior angulation where inner and outer lips meet adapically; neck of body whorl meeting left-most part of inner lip well to the left of shell axis, with lowermost part of shell well to the right of and below that position, where the rounded abapical junction of inner and outer lips occur; lower part of aperture jutting forward strongly; sculpture of spiral ribbing sometimes developing elongate tubercles; opisthocyrt collabral sculptural elements of very variable strength. Operculum circular, multispiral. Dioeceous.

Other species assigned. Recent: seventeen species (Brot, 1877) including *D. consolidata* (Bruguière) and *D. pernambucensis* (Reeve); additional species described and listed later (von Ihering 1902: 659–665; Pilsbry *in* Baker 1914); all from Atlantic drainage system, Brazil to Venezuela. Fossil: the living *D. devians* Brot, Quaternary, Surinam (Schepman 1887).

Distribution. Quaternary and Recent, South America (as above).

Remarks. It is probable that none of the four fossil species assigned to *Doryssa* by Parodiz (1969) belong to that genus: the only fossil record accepted is given above. *Sheppardiconcha* is herein regarded as a separate genus unrelated to *Doryssa. Hemisinus (Basistoma) corrosensis* Pilsbry & Olsson 1935 proves on examination of the holotype (ANSP 13092) to belong to *Hemisinus* (s.lat.) and not, as suggested by Parodiz, to *Doryssa*.

Doryssa atra (Bruguière, 1792) Fig. 200

* 1792*a* *Bulimus ater* Bruguière (*ex* Richard MS): 126.
* 1822 *Melania truncata* Lamarck: 164.
. 1859 *Melania truncata* Lamarck; Chenu: 291, fig. 1989.
*v 1860 *Melania nicotiana* Reeve: pl. 30, fig. 202.
. 1870 *Doryssa atra* (Richard) Brot: 304 (*cum syn.*).
. 1872 *Melania truncata* Lamarck [= *Bulimus ater* Richard]; Brot: 8; pl. 1, fig. 1.
. 1874 *Doryssa atra* (Richard); Brot: 342; pl. 35, fig. 7.
. 1902 *Doryssa atra* (Richard); von Ihering: 661.
. 1939 *Doryssa atra* (Richard); Wenz: 686, fig. 1971.
. 1956 *Melania truncata* Lamarck; Mermod: 66, fig. 127.
. 1956 *Doryssa atra* (Bruguière); Pain: 96, figs 3a–c.
. 1980 *Doryssa atra* (Bruguière); Tillier: 14; pl. 1, fig. 1.

Material studied. Lectotype (selected herein) of *Melania nicotiana* Reeve, the specimen figured by Reeve (1860: pl. 30, fig. 202) and two accompanying unfigured paralectotypes; Guyana, Cuming Colln, BMZD 1984202.

Remarks. Tillier (1980) discusses the original collections of Richard and Leblond from which the material named by Bruguière came. Both Brot (1872) and Mermod (1952) examined the Lamarck collection in the Geneva N.H.M. Both *M. truncata* Lamarck and *M. nicotiana* Reeve are synonyms of *D. atra*. The species figured by Reeve (1860: pl. 30, fig. 195) as *Melania atra* Richard was misidentified and subsequently renamed as *Doryssa lamarckiana* by Brot (see Brot, 1874: 344; pl. 35, figs 1, 1a). The species lives in rivers of the Guyanas and north-eastern Brazil (Tillier 1980: 15). The above specific synonymy is not exhaustive.

Family **THIARIDAE** Wenz, 1929

[*emend.* Morrison, 1954: 357–8, 374]

Wenz (1929: 2517) established the Thiaridae as a family. His classification was set out in detail (1939): the family was divided into several subfamilies including Pleurocerinae and Thiarinae (1939: 712). Thiaridae *sensu* Morrison (1954) more or less corresponds with Thiarinae of Wenz (1939).

Subfamily **HEMISININAE** Thiele, 1928

[*nom. transl.* herein, = Semisininae Cossmann, 1909: 125 (subfamily), = Hemisinuseae Thiele, 1928: 401 (tribus), = Hemisinuieae Thiele, 1929: 201 (tribus), = Semisinuinae Wenz, 1929: 2561 (subfamily), = Hemisinuieae Wenz, 1939: 717 (tribus), = Aylacostominae Parodiz, 1969; 141 (subfamily)]

Under Art. 11 (f)(i)(1) of the International Code (ICZN 1985: 25) a family group name must, when first published, be based on the name then valid for a contained genus. This provision is first met by Thiele, 1929. Swainson's (1840) genus was *Hemisinus*. Suprageneric taxa based on the unjustified replacement name *Semisinus* Fischer, 1885 are not valid. Parodiz (1969) based Aylacostominae on Hemisinuieae 'Wenz'. However, in the same work (1969: 143), he used *Hemisinus* Swainson as a subgenus of *Aylacostoma* Spix, 1827, thereby acknowledging that they were not exactly synonymous.

Embryonic shells of up to *c.* 5–6 whorls have been obtained by syringing out the apertures of adult shells of Recent Hemisininae in BMZD dry collections (no spirit material being available). The extent of this study has been severely restricted owing to lack of suitable material. At the most two, but usually only one, embryonic shell has been obtained per adult. Many adults have yielded no embryonic shells, but it is not clear whether this is because none of the soft parts were

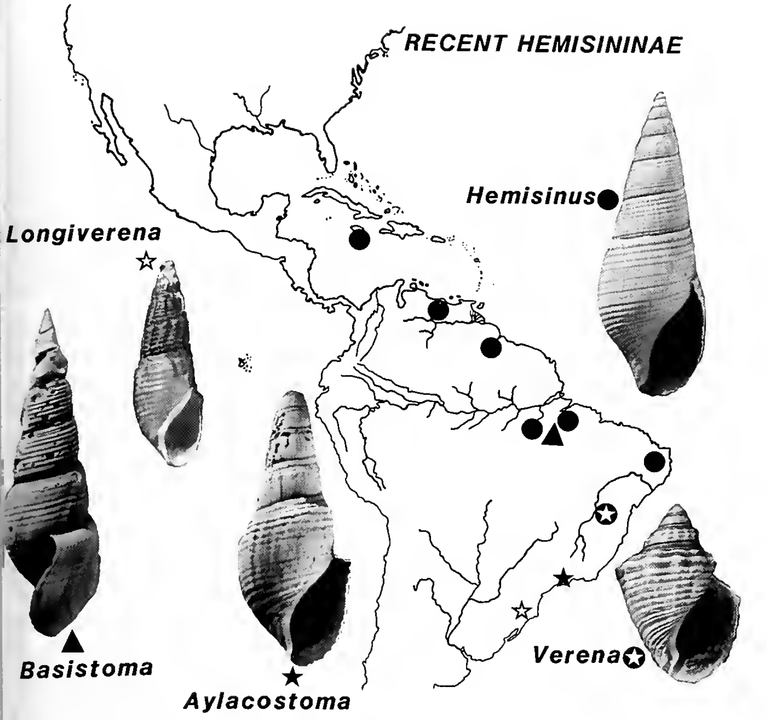


Fig. 203 Recent distribution of Hemisininae: map based on very few authenticated records. ●, *Hemisinus*; ★, *Aylacostoma*; ▲, *Basistoma*; ☆ *Longiverena*; ✪, *Verena*. Inset: *H. brasiliensis* (S. Moricand), × 1; *A. glabrum* Spix, × 1; *B. edwardsi* Lea, × 0.75; *L. tuberculata* (Spix), × 0.75; *V. crenocarina* (S. Moricand), × 0.75; all Brazil.

preserved or whether no embryonic shells were ever present in these particular individuals.

Specimens examined have included representatives of the type species of four genera, *Hemisinus lineolatus* (Wood), *Verena crenocarina* (Moricand), *Longiverena tuberculata* (Spix) and *Basistoma edwardsi* Lea. Embryonic shells of one other living species, *Hemisinus globosus* Reeve, here placed in the synonymy of *H. kochi* (Bernardi), and two young juveniles of fossil *Verena browni* (Etheridge) obtained from washings from the Puerto Nariño deposit have also been studied. All the embryonic shells so far examined have features in common. The shell has a hemispherical, cup-like, origin and is, for the first whorl or so, virtually planorbiform. After this, the whorl translation rate increases rapidly so that the embryonic shell takes on a form increasingly reminiscent of shells mature enough to have enjoyed a free existence. In all the examples studied, the sculpture typical of the early teleoconch soon appears. This varies considerably in the taxa examined. For example, the later embryonic whorls of *H. lineolatus* are virtually smooth, whilst those of *Basistoma edwardsi* are strongly carinate.

Genus *BASISTOMA* Lea, 1852

Type species. *Basistoma edwardsi* Lea, 1852: 296; pl. 30, fig. 1, by original designation. Recent, Rio Tocatins, eastern Brazil. No other assigned species.

Diagnosis. Turritelliform Hemisininae with numerous whorls; spiral sculpture of numerous ribs on early whorls, reducing in strength on later whorls, eventually dying away altogether; no collabral sculpture except strongly reverse sigmoid growth lines giving rise to pronounced sinus at shoulder height or apertural notch; aperture about quarter shell height; outer lip produced forwards below periphery; wide basal notch present; columella weakly callused. Operculum not seen. Embryonic shell with spiral ribbing.

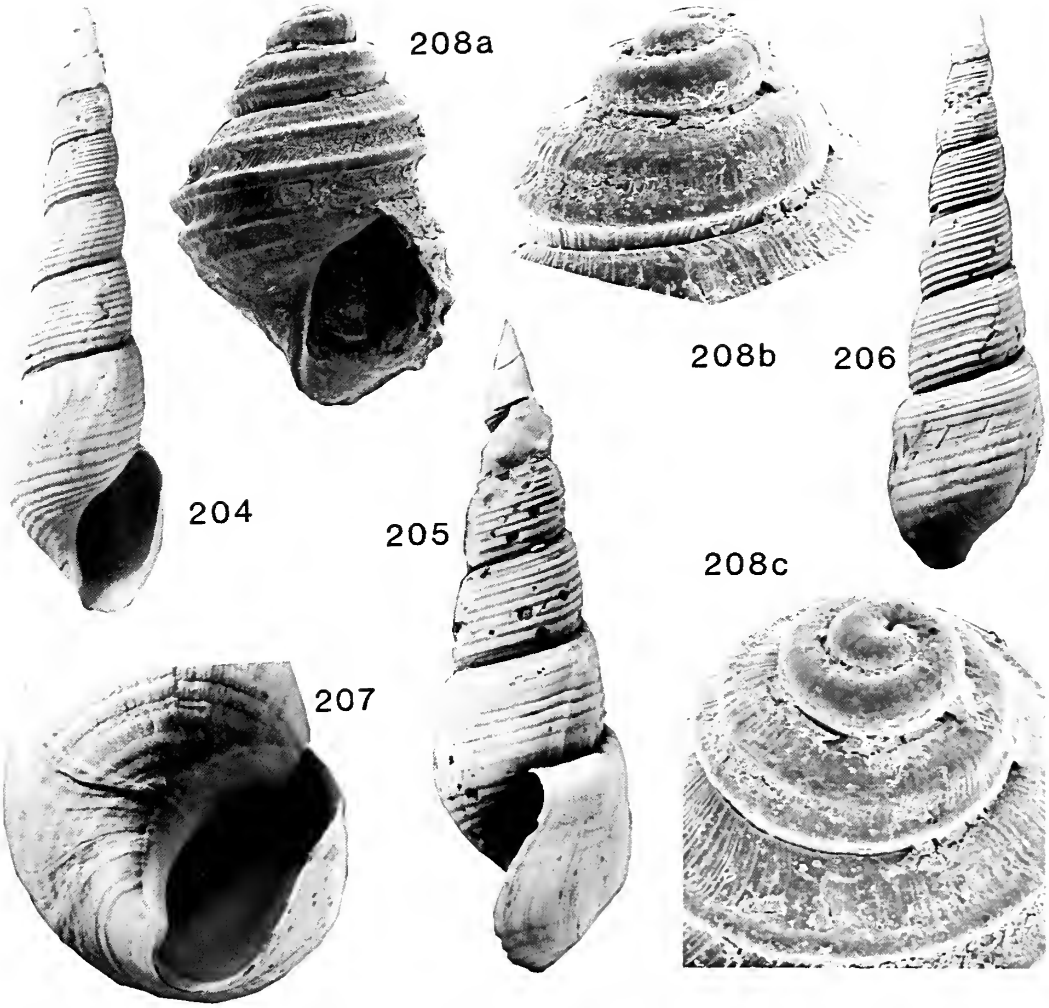
Remarks. The above diagnosis is based on four shells of *B. edwardsi*, one of which yielded an embryo, from Para, Brazil (BMZD). The spires are all eroded. The embryonic shell is spirally ribbed, suggesting that this type of ribbing persists more or less unchanged for the first six whorls or so, before gradually changing into grooves on the later whorls, whilst spiral sculpture becomes obsolete on the last whorl except on the neck region.

No additional information on this taxon is given in later works (Reeve 1860 – *Hemisinus*; Brot 1874: 397; von Ihering 1902: 672). Wenz (1939: 718, fig. 2076) gives the range of *Basistoma* as from the Palaeocene onwards from Europe as well as from south and central America and the West Indies. This pattern of distribution is rejected here. Morrison (1954: 376) wrote that *Basistoma* was the exact equivalent of *Aylacostoma*, being based on the same type of shell. This synonymy is not upheld but helps to explain Morrison's rather broad view of what *Aylacostoma* contained. Comparisons with *Sheppardiconcha* are given under the latter, below.

Genus *SHEPPARDICONCHA* Marshall & Bowles, 1932

Type species. *Sheppardiconcha bibliana* Marshall & Bowles, 1932: 3, by original designation. Miocene, Cuenca Basin, Ecuador.

Diagnosis. Hemisininae resembling *Basistoma*, but with early whorls smooth or sculptured with sharp spiral ribs; sculpture on later whorls variable; spiral sculpture often



Figs 204–208 *Basistoma edwardsi* Lea. Recent; Para, Brazil. **204**, BMZD 49.1.5.48; front, × 2. **205**, BMZD 49.5.16.13; side, × 2. **206**, BMZD 49.55.16.14; rear, × 2. **207**, BMZD 49.5.16.15; oblique view of aperture and neck of body whorl, × 3. **208**, BMZD 1984205, embryonic shell washed from adult in above sample. a, front, × 25; b, slightly tilted view of early whorls, × 50; c, oblique view of apex, × 50.

Fig. 209 Distribution of the extinct genus *Sheppardiconcha*. Key as for Fig. 6 (p. 177), with the addition of: A, Siquire Formation, Venezuela (Macsotay 1968). Inset: *S. bibliana* Marshall & Bowles, × 1.25; Miocene; Cuenca Basin, Ecuador.

tuberculate and dominant over collabral; growth lines strongly reverse sigmoid with apex of sinus high on whorl profile; aperture rounded posteriorly, notched below.

OTHER SPECIES ASSIGNED. *Hemisinus tuberculiferus* Conrad, 1874*b*, Late Caenozoic, Pebasian; Iquitos. *Cerithium coronatum* Etheridge, 1879, Late Caenozoic, Pebasian; Canamá, Três Unidos, Iquitos. *Sheppardiconcha lataguensis* sp. nov., Late Caenozoic; La Tagua. *Hemisinus (Sheppardiconcha) picardi* Macsotay, 1968, Miocene, Siquire Formation; northern Venezuela.

DISTRIBUTION. Neogene only; Ecuador, Colombia, Peru, Brazil, Venezuela. Unknown living.

REMARKS. *Sheppardiconcha* and *Basistoma* are compared herein for the first time. The main distinction is the character of the sculpture. *Basistoma* lacks collabral ribbing and its spiral sculpture is simple, bearing no trace either of tubercles or any other modifications. Unfortunately, neither the earliest whorls nor the apertural features of *Sheppardiconcha*, and in particular its type species *S. bibliana*, are sufficiently well known for careful comparisons to be made. It is difficult to assess whether the differences seen between the two genera are really of generic or merely of specific importance.

Marshall & Bowles (1932: 3) suggested that *Hemisinus tuberculiferus* Conrad (1874*b*) also belonged to their new genus *Sheppardiconcha*: this assignment is accepted here.

Morrison (1954: 367) regarded *Sheppardiconcha* as a synonym of *Doryssa* of the Pleuroceridae because of its similar shell characters: this arrangement was followed by Parodiz (1969: 134; *in* Bristow & Parodiz 1982: 43). In poorly preserved or incomplete specimens it is very difficult to separate these two genera belonging to different families. In *Doryssa* the base of the aperture is not notched. Other genera ncluding *Aylacostoma* and *Sheppardiconcha* possess a basal notch. This is seen rarely in the usually damaged specimens of *Sheppardiconcha* (Palmer, *in* Liddle & Palmer 1941: pl. 6, figs 11, 12; *S. bibliana*), and in material of *S. lataguensis*, *S. coronata* and *S. tuberculifera* (PIMUZ) examined herein. As he base of the aperture is frequently damaged, examination of the growth lines on the base of the shell is essential in order o determine whether a basal notch is present. About the last quarter whorl of the outer lip is frequently broken away, and one must orientate the shell by revolving it about its long axis o allow for this.

In practice, the genera may usually be separated by the growth lines, which are strong enough to be clearly interpreted even on many badly damaged specimens. Growth lines n *Sheppardiconcha* are strongly reverse sigmoid with a well-developed sinus or invagination high on the whorl side, at houlder level, when present. In contrast, those of *Doryssa* re more gently opisthocyrt with the most backward point occuring at about mid-whorl height. In *Aylacostoma* their form is rather like those of *Doryssa*, whilst in *Longiverena* hey are somewhat variable in form but never so strongly urved as in *Sheppardiconcha*. In *Longiverena* the collabral sculpture is considerably more important than in *Sheppardiconcha*, whilst *Aylacostoma* is much smoother altogether.

Sheppardiconcha bibliana Marshall & Bowles, 1932

Figs 210–214

1932 *Sheppardiconcha bibliana* Marshall & Bowles: 3; pl. 1, fig. 6.
. 1939 *Hemisinus (Sheppardiconcha) bibliana* (Marshall & Bowles) Wenz: 718, fig. 2077.
. 1941 *Hemisinus (Sheppardiconcha) biblianus* (Marshall & Bowles); Palmer, *in* Liddle & Palmer: 400 = 44; pl. 6, figs 1–12.
. 1969 *Doryssa bibliana* (Marshall & Bowles) Parodiz: 134; pl. 15, fig. 12; pl. 16, figs 6, 8, 12.
v 1982 *Doryssa bibliana* (Marshall & Bowles); Bristow & Parodiz: 8, 10, 44, fig. 18.

HOLOTYPE.: USNM 372837, Miocene (given as probably Pliocene, Marshall & Bowles 1932: 2); Biblián, Cuenca Basin (Sheppard Colln). Paratypes are USNM 372838 (several specimens), as above; USNM 372839, Miocene; Paccha, Cuenca Basin (many specimens) (all Sheppard Colln). Type material not studied.

MATERIAL STUDIED. All from Miocene, Cuenca Basin, Ecuador. GG55394–6 (20 specimens) and GG21770–4 from type locality, Biblián (Sheppard Colln); GG19872/1–12, CRB 5; GG19871–6, CRB 8, both top Biblián Formation, near El Valle (Bristow & Parodiz 1982: 8). From the Loyola Formation, numerous specimens including GG19874, GG19875/1–5, CRB 17; GG14364, GG19877/1–10, CRB 14; GG19878/1–2, CRB 2; GG19879/1–5, CRB 28; GG19869, GG19880/1–5, CRB 18; GG19873/1–20, GG21775–6, CRB 61 (see Bristow & Parodiz, 1982: 8, 10, 15 for locality lists).

FURTHER RECORDS. PRI, numerous specimens from several localities, Miocene, Cuenca Basin (Liddle Colln; Olsson Colln) (Liddle & Palmer 1941: 45). CM 46791, Bristow & Parodiz 1982: 44, fig. 18, said to be from the Mangán Formation, Cuenca Basin. Parodiz *in* Bristow & Parodiz (1982: 44) stated that this species is common in BMPD collections from CRB 36a of the Mangán Formation: this may be a clerical error as no specimens of *S. bibliana* from the Mangán Formation are present in BMPD. The specimen figured by Parodiz may have come from the Loyola Formation at CRB 61, a locality from which he did not list the species.

DISTRIBUTION. Miocene, top Biblián Formation, Loyola Formation and ? Mangán Formation, Cuenca Basin, Ecuador (as above).

DIAGNOSIS. *Sheppardiconcha* with apical angle of about 22°; sutures very incised, the adaptical suture channelled; early whorls otherwise straight-sided, later whorls becoming more convex; form of apex unknown; spiral sculpture of about six ribs on succeeding spire whorls, developing into a mixture of broad bands separated by grooves and ribs on later whorls; collabral sculpture of sigmoid growth lines and, on later whorls, low amplitude folds which produce tubercles on adapical spiral ribs.

DESCRIPTION. All the material is damaged. All but two specimens have lost their early whorls and no complete apertures are known. The collections studied suggest that some differential size sorting has occured. At the type locality and CRB 17, the largest shells are less than 25 mm long and 10 mm broad. At other localities most specimens are larger, achieving a maximum length (by reconstruction) of about 50 mm and a breadth of up to 17 mm. A complete specimen of this size would have had about eleven whorls: few have more than five preserved. As the sculpture and whorl profile changes with growth, it appears at first sight that two species might be present. Some specimens with the middle growth

213



214


210

211


212


Figs 210–214 *Sheppardiconcha bibliana* Marshall & Bowles. Miocene; Cuenca Basin, Ecuador. **210–211**, type locality, Biblián, Canar Prov.; Sheppard Colln. **210**, GG21770; × 3. **211**, GG21771; × 3. **212–214**, Loyola Formation, Bristow Colln. **212**, GG19874; Loc. CRB 17, × 4. **213**, GG14364; Loc. CRB 14, × 4. **214**, GG21775; Loc. CRB 61, × 2.5.

stages preserved, however, form the link necessary to show that only one species is present. The earliest whorls appear to be small and biconvex. Their sculpture is not known but the rather simple spiral ribs and sigmoid growth lines typical of the early whorls are present by the third or fourth whorls, and often persist to the seventh whorl, by which a shell height of 20 mm has been attained. Both the spiral and collabral sculpture of later whorls are very variable. A feature in common with the earlier whorls is the tendency for the spiral rib or band nearest the upper suture to be prominent whilst a rather sharp rib is developed just above the lower suture. On the final whorl up to six spiral ribs can be made out with difficulty on a few specimens. The aperture is fairly broad and the callus pad stands proud of the general shell surface.

GG14364 (Fig. 213) from CRB 14, and GG21775 (Fig. 214) from CRB 61, illustrate the two extremes of variation. In GG14364 the whorl profile is very similar to that of young shells from CRB 17. The sutures are rather incised. There are four fairly evenly spaced strong spiral ribs, the uppermost bearing about twenty elongate tubercles per whorl. The other ribs are non-tuberculate. The shell surface is otherwise smooth except for clearly visible growth lines. This specimen is very like *S. tuberculifera* from Iquitos, but the latter has much more angular spiral ribs. In contrast, GG21775 has about ten close-set spiral bands. The uppermost forms a rounded ramp just below the suture and also bears about twenty tubercles on each whorl. The growth lines are bunched to form strong, sinuous rugae.

DIMENSIONS. In mm.	h	br	hap	sa
Holotype, USNM 372837 (from Marshall & Bowles 1932, both text and type illustration)	20	8.5	6	20°
GG21775, CRB 61, Loyola Formation	*26.2 (eh = 39)	12.8	–	21°
GG21776, as above	*31.5 (eh = 43)	16.2	–	–

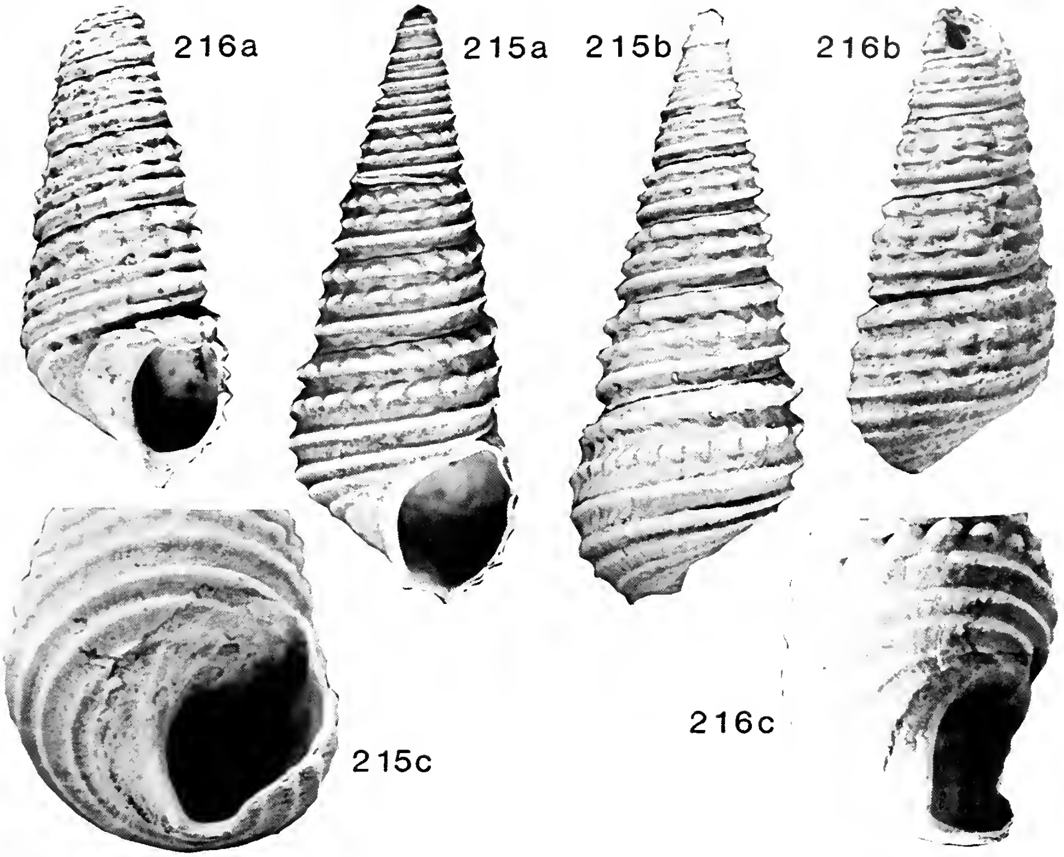
(* = decollated or damaged).

REMARKS. Comparisons with the rather similar *S. lataguensis* sp. nov. are given under the latter, p. 238. *S. bibliana* is easily distinguished from *S. tuberculifera* (Conrad) and *S. coronata* (Etheridge), both of which are essentially smooth except for spiral ribbing bearing strong tubercles. *S. bibliana* is far more common in collections (BMPD, USNM, PRI, and Carnegie Museum, Pittsburgh) than other *Sheppardiconcha*.

Sheppardiconcha tuberculifera (Conrad, 1874*b*)

Figs 215–216

*	1874*b*	*Hemisinus tuberculiferus* Conrad: 83; pl. 12, fig. 4.
.	1932	*Sheppardiconcha tuberculifera* (Conrad) Marshall & Bowles: 3.
v	1938	*Semisinus tuberculiferus* (Conrad) de Greve: 104; pl. 4, figs 1–6, 12.
.	1966	*Hemisinus (Sheppardiconcha) tuberculiferus* (Conrad); Willard: 66–68; pl. 63, figs 6–8.



Figs 215–216 *Sheppardiconcha tuberculifera* (Conrad). Pebasian; Iquitos, Peru; Peyer Colln. **215**, PIMUZ 330; figured by de Greve (1938: pl. 4, fig. 1). a, front, × 4; b, back, × 4; c, aperture and neck of body whorl obliquely from below, showing anterior notch, × 6. **216**, PIMUZ 351; figured by de Greve (1938: pl. 4, fig. 12). a, b, c, same views and magnifications.

. 1969 *Aylacostoma (Hemisinus) tuberculifera* (Conrad) Parodiz: 143.

TYPE MATERIAL. ANSP, Late Caenozoic; Iquitos (Conrad 1874*b*) (not seen).

MATERIAL STUDIED. PIMUZ 330, figured by de Greve, 1938: pl. 4, fig. 1; PIMUZ 351, de Greve, 1938: pl. 4, fig. 12; Late Caenozoic, Iquitos.

FURTHER OCCURENCES. All late Caenozoic. Negro Urca, 200 km NW from Iquitos (Willard 1944: 66); Rumi Tuni Valley of Napo River, 225 km north from Iquitos (Willard 1944: 67, 58).

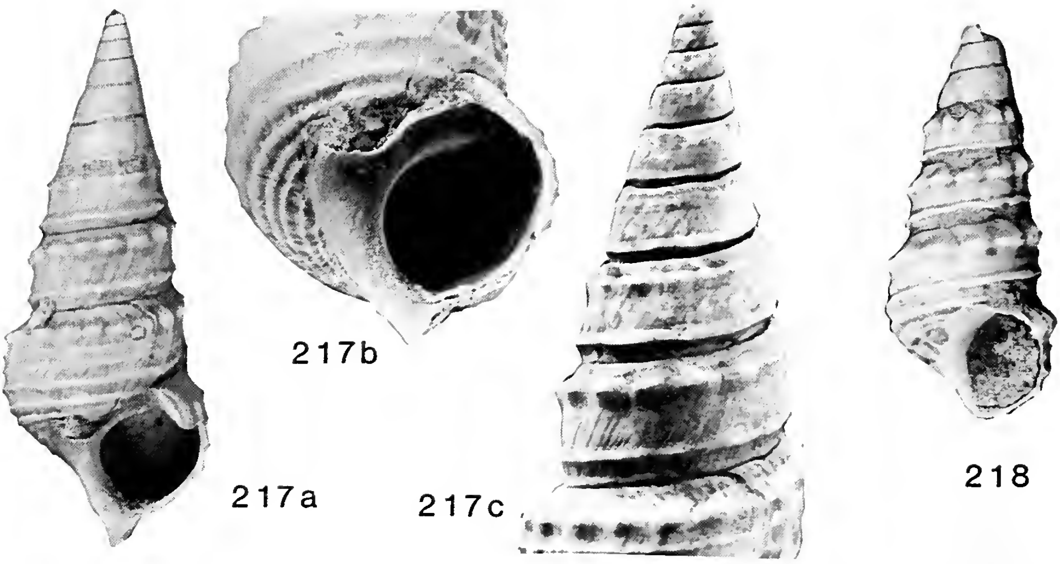
DISTRIBUTION. Late Caenozoic, Pebasian; Iquitos and district, Peru (as above).

DIAGNOSIS. *Sheppardiconcha* with 3–5 angular spiral ribs on pire whorls; upper spiral ribs strongly tuberculate, lower nes less so; collabral ribbing absent.

DESCRIPTION. The apex is not preserved in any of the specinens examined. If complete, adult shells would have had bout twelve whorls. PIMUZ 330 has a damaged apex and a otal of nine whorls preserved. The first three of these are ndoubtedly post-nuclear. They are pagodiform, with a definte carina developed not far above the lower suture. By the hird whorl present, two further spiral ribs have appeared on he ramp, above the carina. On the following whorl, the first sign of tuberculation manifests itself as irregular interruptions of the spiral ribbing. By the fifth or sixth whorl present, the adult sculpture is fully developed. It consists of 7 – 12 spirally elongate tubercles per whorl on the upper two spiral ribs, whilst the lower rib (the continuation of the original carina) is intermittently constricted and almost tuberculate. A fourth smooth rib marks the lower suture on these later whorls. The sculpture of PIMUZ 351 differs mainly in that there are five spiral ribs, the upper three being tuberculate. In addition, the lowest spiral rib gradually moves upwards away from the lower suture as growth proceeds, with the result that the form of the suture is inconstant. On the neck of the body whorl there are either three or four spiral ribs. In this species the collabral sculptural elements consist of the basically spiral tuberculations, which however are arranged collabrally, and also the strongly opithocyrt growth lines.

DIMENSIONS. In mm.	h	br	sa
PIMUZ 330	20.8	8.3	27°
PIMUZ 351	16.4	7.3	24°
PIMUZ 348 (from de Greve 1938: 104)	33.9	11.6	28°
Type illustration (from Conrad, 1874*b*: pl. 11, fig. 4)	–	–	26°

Note. Conrad gave no scale. His illustration was 38 mm high and was of a front view. Pilsbry (1944) stated that his specimen was 35 mm high; his figure was of a back view.



Figs 217–218 *Sheppardiconcha coronata* (Etheridge). Pebasian; Canamá, Peru; Barrington Brown Colln. **217**, GG21223 (*ex* 97722); **lectotype** (herein selected), figured by Etheridge (1879: pl. 7, fig. 5). a, shell with broken outer lip, orientated almost in side view, × 2.5; b, aperture obliquely from below, × 4; c, early spire whorls, × 4. **218**, GG21224; paralectotype, front view, × 2.5.

Remarks. No lectotype selection is made because, without studying the relevant material, there is no way of telling whether Conrad (1874*b*) and Pilsbry (1944) figured the same specimen or not: Conrad (1874*b*: 82) had stated that the species occurred crowded in the clay. No detailed diagnosis and description is given here either, as only two shells were studied, to decide on the generic determination and to compare with *S. coronata* (Etheridge). Conrad (1874*b*: 82) gave the type locality as 'Iquitos, about 100 miles West of Pebas'. This locality was misquoted as 'Pebas' by both Pilsbry (1944) and Parodiz (1969); there are no other records of the species from Pebas. Conrad's illustration is probably partly a reconstruction for he stated (1874*b*: 83) that the labrum was broken in every specimen. In contrast, the aperture he illustrates appears to be undamaged.

S. tuberculifera is similar to *S. coronata* (Etheridge) in enough features to suggest a fairly close relationship. The ribbing of both consists of rather sharp angular spiral carinae. In addition, in *S. tuberculifera* there are 3 – 5 spiral ribs on later whorls and all but the most abapical bear tubercles very similar to those present on *S. coronata*. However, the early whorls of *S. tuberculifera* are pagodiform, not straight-sided: they bear two, and later three, spiral ribs, the lowest of which forms the carina. However, the pagodiform early whorls of *S. tuberculifera* serve to distinguish it from *S. coronata*, whose early whorls are straight-sided. In *S. bibliana* the early whorls have strongly incised sutures, whilst the central part of the whorl is straight-sided.

Sheppardiconcha coronata (Etheridge, 1879)

Figs 217–218

*v 1879 *Cerithium coronatum* Etheridge: 87; pl. 7, fig. 5.
. 1924 *Cerithium coronatum* Etheridge; Roxo: 46.
. 1938 *Cerithium(?) coronatum* Etheridge; de Greve: 106; pl. 3, figs 13–16, 20.
. 1967 *Aylacostoma (Longiverena) coronatum* (Etheridge) Santos & Castro: 413, figs 4–6.
1981 *Aylacostoma (Longiverena) coronatum* (Etheridge); Costa: 645; pl. 1, figs 13–14.

Lectotype (selected herein). GG21223, specimen described and figured by Etheridge (1879); Late Caenozoic, Pebasian; Canamá, Brazil (Barrington Brown Colln). GG21224, as above (not figured by Etheridge) is a paralectotype.

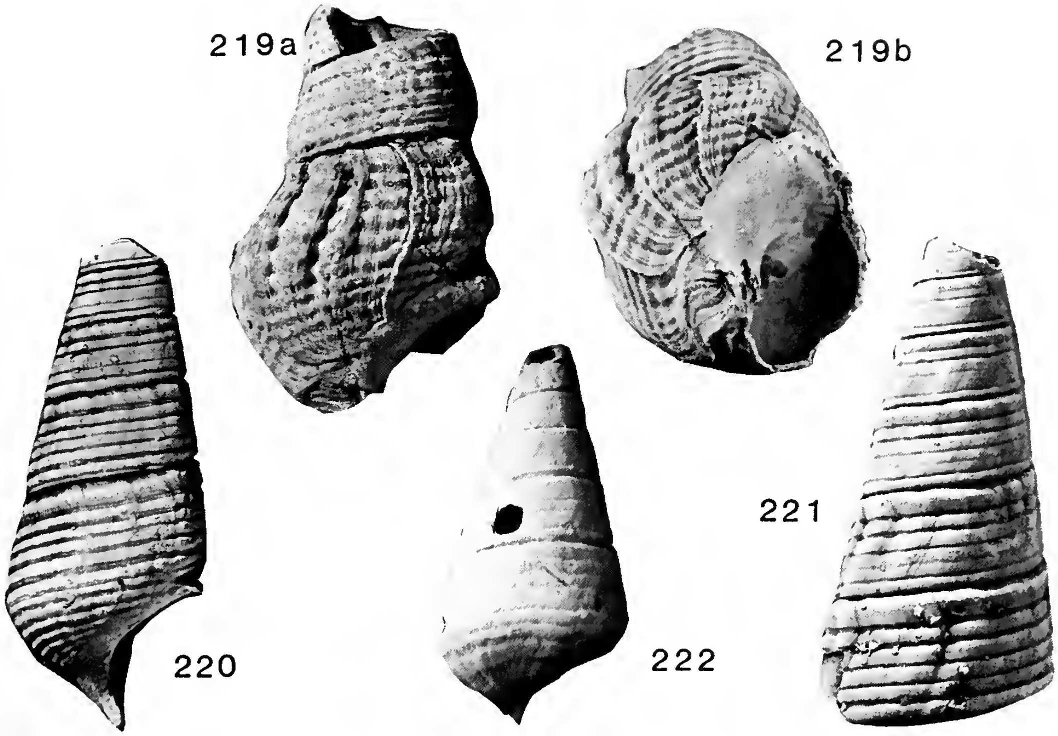
Further material studied. GG21511, Canamá, juvenile shell extracted from matrix of Barrington Brown Colln in 1984.

Further occurrences. Late Caenozoic: Três Unidos, Brazil (Roxo 1924, Santos & Castro 1967, Costa 1981); Iquitos, Peru (de Greve 1938).

Distribution. Late Caenozoic, Pebasian; Upper Amazon Basin, Brazil and Peru.

Diagnosis. Small acute-spired *Sheppardiconcha* with apical angle of about 30°; early whorls smooth, straight-sided with incised sutures; later whorls bicarinate; one or two spiral ribs developed between carinae on last whorl or so; body whorl with up to eight spiral ribs below periphery; collabral sculpture, confined to last three whorls, of folds producing coronate shoulder and dying out on flank of whorl.

Description. The apex is unknown, but examination of the lectotype – on which ten whorls are present – shows that the earliest whorls would have been very small. The first four preserved whorls are very weakly convex. They are virtually unsculptured, but the presence of strongly opisthocyrt growth lines shows that they are well preserved and not worn smooth. A carina is developed low down on the fourth whorl, making the suture incised and the flank of the whorl increasingly straight-sided. Two whorls later the second carina develops at the shoulder, and within a further whorl becomes coronate. Two or three extra, rather angular, spiral ribs are developed between the two carinae. On the final whorl up to eight spiral ribs are developed below the periphery, the rib



Figs 219–222 *Sheppardiconcha lataguensis* sp. nov. Late Caenozoic; 1.5 km upstream from La Tagua, Colombia; Weeda colln. **219**, GG19856, **holotype**. a, orientated with broken aperture facing front, × 3; b, obliquely from below, showing aperture and growth lines on neck region of body whorl, × 3. **220**, GG19857, paratype, orientation same as Fig. 219a, × 3. **221**, GG19858, paratype, × 3. **222**, GG19859, paratype, × 8.

lying in line with the adapical suture being particularly strong. The collabral sculpture is confined to later whorls only and consists of 12 – 20 folds per whorl. These are strongest at the shoulder where they form the coronae, and die out both above on the ramp and below on the flank of the whorl, sometimes just affecting the lower carina. The outer lips are broken in both specimens. The inner lip on the lectotype is callused from the base of the columella upwards but is broken away in the parietal region. The callus is arched away from the surface of the columella, leaving a space between the two. The growth lines show no sign of a basal apertural notch.

Dimensions. In mm.	h	br	h/br	sa
GG21223, lectotype, Canamá.	29.5	11.5	2.57	29°
GG21224, paralectotype, Canamá.	20.8	9.7	–	27°
de Greve 1938, Iquitos.	27.4 (max)	–	–	28°–32°
Santos & Castro 1967, Três Unidos.	29 (max)	–	–	23°–30°
Costa 1981, Três Unidos.	33	–	–	27°

Note. Dimensions from de Greve, Santos & Castro and Costa taken rom their text, except for spire angles, which are taken from their llustrations.

Remarks. This species is fairly close to *S. tuberculifera* (Conrad), with which it occurs at Iquitos, and also to *S. ataguensis* sp. nov. (below). Comparisons are given under hese species.

Sheppardiconcha lataguensis sp. nov. Figs 219–222

Holotype. GG19856, 1.5 km upstream from La Tagua (Weeda Colln). GG19857–9 and GG19885–6, information as above, are paratypes.

Name. From locality of La Tagua.

Diagnosis. Moderate-sized with little or no collabral sculpture; early whorls smooth; sculpture on later whorls consisting of 5–7 increasingly strong spiral grooves separated by broad, flat-topped interspaces; sutures incised; whorls almost straight-sided, but becoming biconvex on last whorl or so.

Description. All the specimens are broken. Undamaged apices and apertures are unknown, and the narrowest whorl preserved has a diameter of about 1 mm. Fully grown shells would have had 12–14 post-apical whorls and the total height is estimated as about 45 mm. Traces of spiral sculpture first appear on the third whorl present and consist of a shelf-like rib just above the incised lower suture; after about the eighth whorl this loses its relative prominence, merging into the general sculptural pattern. A very weak spiral groove may sometimes be seen at about mid-height of the third whorl; other grooves are soon added so that the full complement of five or six, but rarely seven, are present by the sixth whorl, reaching about full strength three whorls later. On the penultimate and final whorls the grooves become nearly as broad as the intervening ribs. Collabral sculpture is absent except for very weak and irregular folds. The growth lines are strongly curved and a combination of opisthocline–opisthocyrt. On the last whorl or so, there may be growth halts, giving a rugose appearance. The full growth lines are seen on

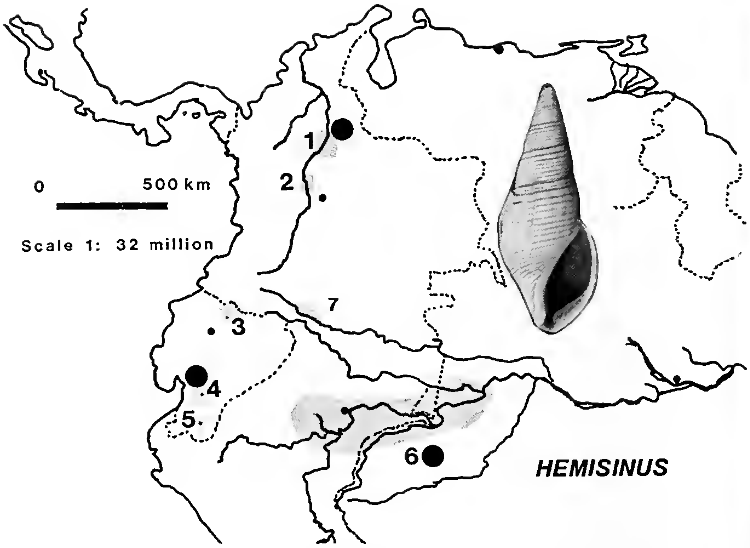


Fig. 223 Tertiary distribution of *Hemisinus*. Key as for Fig. 6 (p. 177). Inset: *H. sulcatus* Conrad, × 1.25; Pichana, Peru.

the last whorl: they are reverse sigmoid and strongly recurved at the base, indicating that the outer lip and basal notch would have had a typical *Sheppardiconcha* shape in unbroken specimens. The inner lip is not strongly callused even in fully grown shells. The earlier whorls are very straight-sided, with the apical angle between 20° and 24°; they form an acute cone, broken only by the slightly incised suture and the rather swollen bands adjacent to it. The last two whorls, however, are increasingly biconvex, with the periphery fairly low down.

Dimensions. In mm.	h	eh	br	sa
Holotype, GG19856	19.0	45	13.5	–
Paratype, GG19857	22.1	30	9.7	21°

(Both specimens decollated and otherwise damaged)

Remarks. This species is distinguished from other fossil *Sheppardiconcha* by the almost complete lack of collabral sculpture. *S. bibliana* Marshall & Bowles is fairly similar, having a last whorl more convex than the preceding ones and sculpture mainly of spiral grooving. However, its whorls are always less straight-sided and the sutures more impressed. Its spiral grooves are more numerous and less regularly spaced, and it always has some collabral folding. *S. coronata* (Etheridge), like *S. lataguensis*, has smooth, straight-sided early whorls; it is easily distinguished by its later whorls which bear sculpture of sharp spiral ribs, the one on the shoulder being strongly coronate.

The northern Venezuelan Miocene species originally described as *Hemisinus (Sheppardiconcha) picardi* Macsotay (1968: 302; pl. 1, figs 1, 5, 8) is similar to *S. lataguensis* in having predominantly spiral sculpture. It may be distinguished from the latter by its strong subsutural cord.

Genus ***HEMISINUS*** Swainson, 1840

[= *Semisinus* Fischer, 1885: 701, unjustified emendment of *Hemisinus* Swainson, 1840: 199, 341]

Type species. *Melania lineolata* Wood, 1828: 42; = *Hemisinus buccinoides* Reeve, 1860: pl. 1, fig. 3. Recent, Jamaica. By monotypy.

Diagnosis. Relatively high-spired Thiaridae with aperture about two-fifths shell height; columella separated from outer lip by anterior notch; shell smooth or with weak spiral sculpture; collabral sculpture absent; whorls weakly convex, nearly straight-sided, lacking ramp and shoulder; operculum rapidly expanding, paucispiral, auriculate.

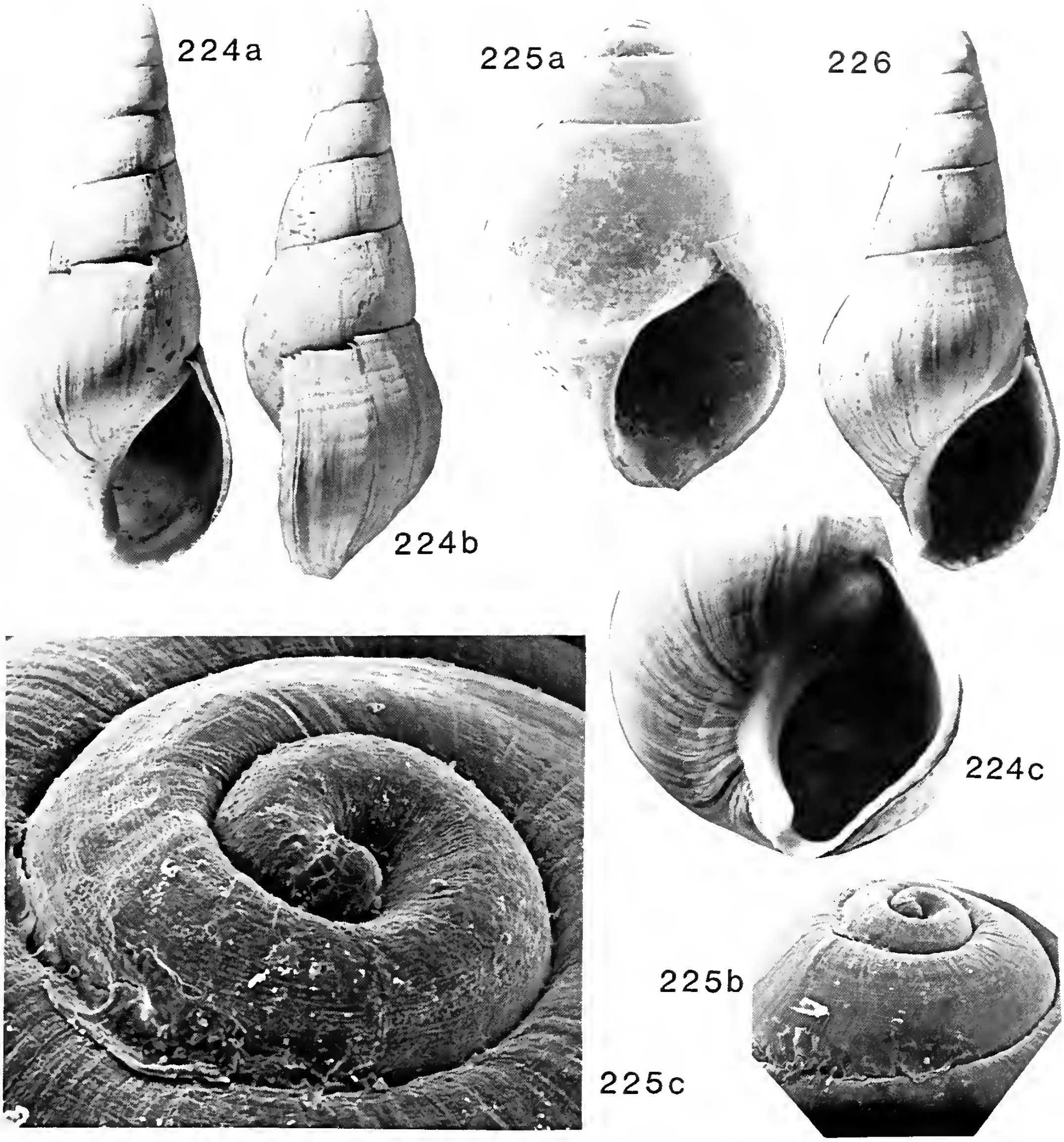
Species assigned. Fossil: *Hemisinus corrosensis* Pilsbry & Olsson, 1935; Tertiary, Los Corros Formation; Colombia. *Hemisinus sigmachilus* Pilsbry & Olsson, 1935; Tertiary, Mugrosa Formation; Colombia. *Hemisinus* sp. indet., = *H. sulcatus* Parodiz *in* Bristow & Parodiz, 1982: 47 (*pars*), *non* Conrad; Miocene, Mangán Formation; Ecuador (see p. 246). For *Hemisinus sulcatus* Conrad, 1871*b*; Pebasian; Pichana, Peru, see under *H. brasiliensis* (Moricand, 1838) (p. 244). For *H. sulcatus* de Greve, 1938; Pebasian; Iquitos, see under *H. kochi* Bernardi, 1856 (p. 240).

Recent: Several species from northeastern South America and the Caribbean, described in monographs by Reeve (1860) and Brot (1878) are assigned to *Hemisinus*. Some species described from other parts of South America and elsewhere do not appear to be congeneric.

Distribution. ? Palaeogene, Neogene and Recent northern and eastern South America and Caribbean.

Remarks. The evidence (Pilsbry & Olsson 1935, Wheeler 1935) for the Los Corros and Mugrosa Formations being Eocene and Oligocene respectively is far from conclusive and is discussed in the section dealing with the Magdalena Valley, p. 333. The fossil occurences of living species described below are, however, definitely in Neogene strata. Many of the nominal living species are based on small and often poorly localized samples: a thorough taxonomic study would almost certainly reduce their number considerably.

Neither *Melanella karsteni* Anderson, 1928 (Fig. 447, p. 335) from the Tertiary of Colombia, tentatively placed in *Hemisinus* by Pilsbry & Olsson (1935: 12), nor *H. gracillimus* Pilsbry & Olsson 1935 from the La Cira Formation of



igs 224–226 *Hemisinus lineolatus* (Wood). Recent, ? Caribbean only. **224**, BMZD 1984206; **lectotype** (herein selected) of *Strombus lineolatus* Wood, figured by Wood (1828: pl. 4 [*Strombus*], fig. 11) and by Gray (1834: pl. 13, fig. 4); locality unknown; Gray Colln. a, front, × 2; b, side, × 2; c, aperture and neck of body whorl obliquely from below, × 3. **225**, embryonic shell syringed out of adult, unlocalized, dried specimen of *H. lineolatus*, BMZD 1984207; a, front, × 15; b, oblique view of apex, × 15; c, apex, × 200. **226**, BMZD 1984208; holotype of *Hemisinus buccinoides* Reeve, figured by Reeve (1860: pl. 1, fig. 3), labelled 'Jamaica?'; Cuming Colln; front, × 2.

olombia, nor *H. pictus* Pilsbry, 1944, from the supposed ligocene of the Pachitea River, Peru, are well enough reserved for generic assignment. The last, as Pilsbry pointed ut, has spirally arranged dashes of colour characteristic of *emisinus*.

Gray (*in* Griffith & Pidgeon 1834: 598) is frequently redited with authoriship of *Melania lineolata*, but Wood's arlier work, in which the species is figured, is clearly valid.

emisinus lineolatus (Wood, 1828) Figs 224–226

v 1828 *Strombus lineolatus* Wood: 13; pl. 4 (Strombus), fig. 11.
v 1828 *Melania* (ex *Strombus*) *lineolatus* Wood: 42 (index).
. 1834 *Melania lineolata* Gray, *in* Griffith & Pidgeon: 598; pl. 13, fig. 4.
. 1840 *Hemisinus lineolatus* (Gray) Swainson: 341.
. 1847 *Hemisinus lineolatus* (Gray); Gray: 153.
. 1854 *Hemisinus lineolatus* (Wood); H. & A. Adams: 302.
. 1858 *Hemisinus lineolatus* (Wood); H. & A. Adams: pl. 32, figs 2, 2a, b.
. 1859 *Hemisinus lineolatus* (Gray); Chenu: 291, fig. 1995.
v. 1860 *Hemisinus lineolatus* (Gray); Reeve: pl. 1, figs 4a, b.
*v 1860 *Hemisinus buccinoides* Reeve: pl. 1, fig. 3.
. 1878 *Hemisinus lineolatus* (Gray); Brot: 373 (*pars*); pl. 38, figs 6, 6a–c.

. 1885 *Semisinus lineolatus* (Gray) Fischer: 701.
. 1902 *Hemisinus lineolatus* (Gray); von Ihering: 672.
? 1914 *Hemisinus lineolatus* (Gray); Vernhout: 36.
. 1939 *Hemisinus (Hemisinus) lineolatus* (Gray); Wenz: 718, fig. 2075.
. 1954 *Aylacostoma (Hemisinus) lineolata* (Gray) Morrison: 377.
? 1956 *Hemisinus lineolatus* (Gray); Pain: 103 (*pars*), figs 11a, b.

LECTOTYPE of *Strombus lineolatus* Wood (selected herein), the largest of four unlocalized Recent shells, Gray Colln, BMZD 1984206; the remaining shells are paralectotypes. The holotype of *Hemisinus buccinoides* Reeve (Recent, Jamaica; Cuming Colln) is BMZD 1984208.

OTHER MATERIAL STUDIED (All BMZD, Recent). Three shells, Venezuela (Cuming Colln); four shells (E. Chitty Colln), four shells (Mrs Longstaff Colln), 12 shells (Trechmann Colln), all Jamaica; several unlocalized shells, no history, including embryonic shell BMZD 1984207.

FURTHER RECORDS. All Recent. Distribution: Venezuela, Pernambuco (Reeve 1860); Brazil, Venezuela, the Guianas and Jamaica (Pain 1956: 103–105, table). Unknown fossil.

DIAGNOSIS. Almost smooth *Hemisinus*; spire angle 30°; spiral sculpture of faint grooving not covering all of shell; growth lines except on earliest whorls very weakly curved; whorls barely convex, waisted below suture; last whorl slightly swollen; earliest whorls smooth except for markedly opisthocline growth lines; colour patterning of brown spiral lines or dashes on offwhite to pale brown or grey background. Operculum as for genus. Parthenogenetic.

DESCRIPTION. The apex is present in several specimens including the lectotype, and is well preserved in one of the accompanying paratypes, as well as in shells from Jamaica and Venezuela (Chitty and Cuming Collns, respectively). It is absent in the holotype of *H. buccinoides*. The first whorl is virtually flush with the apex; the second is embraced by the succeeding whorl above the periphery but the suture drops away steeply so that more of the third whorl is visible, with the suture eventually lying below its periphery. The opisthocline growth lines are strong but no spiral sculpture is present. In these early whorls the shell is semi-transparent and three or four septa plugging the earlier-formed parts of the spire may be seen. The later shell surface is fairly smooth except for the growth lines and indications of weak grooving, mainly confined to the last whorl or so, and not persisting onto the neck region of the body whorl. The whorls are only weakly convex in profile, later ones being both more strongly convex and also waisted below the suture. In larger shells the outer lip is slightly flared; evidence of several previous apertures may be found on the last whorl, but no proper varices are formed. In both the lectotype and the holotype of *H. buccinoides* the callus high on the inner lip is swollen into a weak ridge, constricting the adapical extremity of the aperture. An embryonic shell (BMZD 1984207) extracted from an unlocalized specimen has five whorls and a height of 4.6 mm.

DIMENSIONS. In mm.	h	br	hap	h/br	sa
Lectotype of *H. lineolatus*	39.8	16.2	15.0	2.65	30°
Holotype of *H. buccinoides*	37.1 (eh = 40)	17.2	15.3	2.42	32°

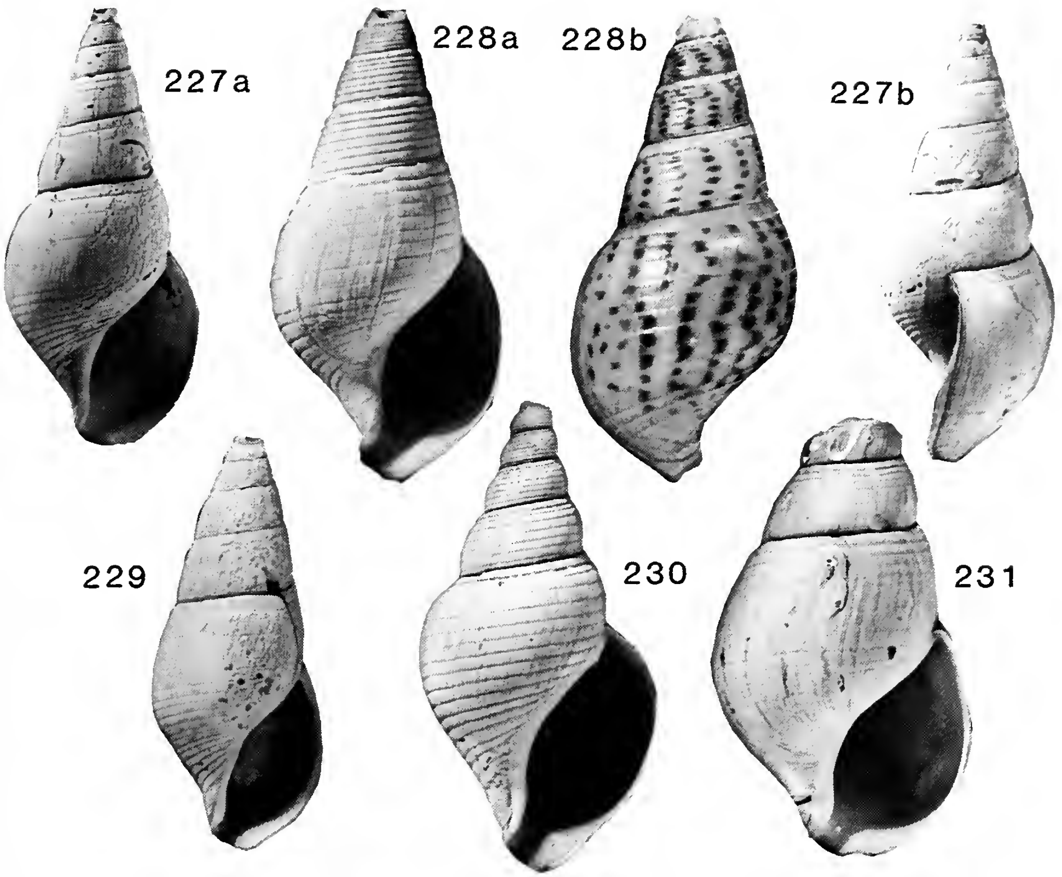
REMARKS. Wood's (1828) illustration is reduced but it is marked (a +), thus indicating a shell size of about 1½″ (38 mm). Only the specimen selected here as lectotype is of about this size: the three paralectotypes are 24–28 mm high, and would thus have fallen into the 'one inch' bracket in the notation adopted by Wood.

This species is distinguished from the very similar *H. brasiliensis* by its lack of a properly developed pattern of spiral grooving. More importantly the earliest whorls – which correspond to the embryonic shell – of the two species may also be distinguished on a similar basis. *H. lineolatus* is smooth except for growth lines whilst *H. brasiliensis* is spirally ridged from the earliest stages. Both Brot (1878) and Pain (1956) include *H. punctatus* Reeve in the synonymy of *H. lineolatus*. The two appear similar in early illustrations (Wood 1828, Reeve 1860, Brot 1878) showing the orange-brown spiral colour patterning, the differences in sculpture not being apparent. *H. punctatus* is spirally striate: unfortunately its apical whorls are unknown. Pain remarked (1956: 104) that *H. lineolatus* was known from the Black River in Jamaica, but was otherwise unknown in the West Indies; he suggested that the Guiana occurrence might be an introduction by man from Jamaica. There is no evidence for this, nor for the opposite and equally plausible supposition that the species was introduced to Jamaica from South America. The distribution data is both suspect and anomolous. The fact that several BMZD samples give the locality as Jamaica suggests that the species does occur on that island. The similarities in shape, size and coloration between *H. lineolatus* and *H. brasiliensis* (Moricand), which occurs in Venezuela, brings into question the accuracy of some earlier reports: the habit of adding locality data to unlocalized specimens on the basis that they had been described from a particular locality was all too prevalent.

Hemisinus kochi (Bernardi, 1856) Figs 227–242

* 1856 *Melania kochi* Bernardi: 83; pl. 3, fig. 6.
v. 1860 *Hemisinus kochi* (Bernardi) Reeve: pl. 5, fig. 21a–d.
*v 1860 *Hemisinus punctatus* Reeve: pl. 1, figs 1a, b.
*v 1860 *Hemisinus pulcher* Reeve: pl. 4, figs 15a, b.
*v 1860 *Hemisinus zebra* Reeve: pl. 4, figs 15c, d.
*v 1860 *Hemisinus obesus* Reeve: pl. 4, figs 17a, b.
*v 1860 *Hemisinus globosus* Reeve: pl. 6, fig. 26.
. 1878 *Hemisinus lineolatus* (Gray); Brot: 374 (*pars*).
. 1878 *Hemisinus pulcher* Reeve; Brot: 387; pl. 40, figs 6a, b.
. 1878 *Hemisinus globosus* Reeve; Brot: 388; pl. 40, fig. 3
. 1878 *Hemisinus zebra* Reeve; Brot: 389; pl. 40, figs 11, 11a.
v. 1878 *Hemisinus obesus* Reeve; Brot: 389; pl. 40, fig. 7.
. 1902 *Hemisinus zebra* Reeve; von Ihering: 670, 680.
. 1902 *Hemisinus obesus* Reeve; von Ihering: 670.
. 1902 *Hemisinus pulcher* Reeve; von Ihering: 671, 680.
. 1902 *Hemisinus globosus* Reeve; von Ihering: 671, 680.
. 1902 *Hemisinus kochi* (Bernardi); von Ihering: 671.
v. 1938 *Semisinus sulcatus* (Conrad) de Greve: 99, text-fig. 23; pl. 4, figs 17–19, 21–25.
. 1969 *Aylacostoma sulcatus* (Conrad) Parodiz: 141 (*pars*), not pl. 14, figs 6, 7.

MATERIAL STUDIED. For convenience, due to the number of syntypic series examined, this is divided into (a) type



Figs 227–231 *Hemisinus kochi* (Bernardi). Recent, Brazil. **227**, BMZD 1984209/1; **lectotype** (selected herein) of *Hemisinus punctatus* Reeve, figured by Reeve (1860: pl. 1, figs 1, 1a); 'Pernambuco' = Recife, Brazil; Cuming Colln. a, front, × 2; b, side, × 2. **228**, BMZD 1984209/2; previously unfigured paralectotype of *H. punctatus*; same details as lectotype. a, front, × 2; b, side, × 2. **229**, BMZD 1984209/3; previously unfigured paralectotype of *H. punctatus*; same details as lectotype; front, × 2.5. **230**, BMZD 1984210; specimen figured by Reeve (1860: pl. 5, fig. 21) as *H. kochi* (Bernardi); Brazil; Cuming Colln; front, × 2. **231**, BMZD 49.1.5.36; **lectotype** (selected herein) of *Hemisinus obesus* Reeve, figured by Reeve (1860: pl. 4, fig. 17); Para, Brazil; front, × 2.

designations and (b) further material studied. Many of the igures given in Reeve (1860) are not the same size as the specimens and details of the colour patterning are often naccurate. Some of the data given was also muddled. Specinens of *Melania* from Para, Brazil, were bought at Stevens' sale and registered in 1849 as BMZD 1849.1.5.28–40. Numbers 36–40 are the syntypes of *H. obesus* Reeve, which Reeve stated were in the Cuming Collection, bought by BM in 1866. Numbers 28–31 and 32–35 are *H. globosus* Reeve and *H. pulcher* Reeve, respectively. It seems possible that these pecimens might also be syntypic material.

TYPE DESIGNATIONS. Lectotype (selected herein) of *Hemisinus punctatus* Reeve. Shell figured Reeve (1860: pl. 1, figs 1a, b) nd two unfigured paralectotypes. Recent, 'Pernambuco' = Recife, Brazil; Cuming Colln, BMZD 1984209.

Lectotype (selected herein) of *Hemisinus obesus* Reeve, BMZD 49.1.5.36, shell figured Reeve (1860: pl. 4, fig. 17) nd four paralectotypes, BMZD 49.1.5.37–40. Recent, Para, Brazil.

Lectotype (selected herein) of *Hemisinus pulcher* Reeve. hell figured Reeve (1860: pl. 4, figs 15a, b) and two nfigured paralectotypes. Recent, Pernambuco; Cuming Colln, BMZD 1984211.

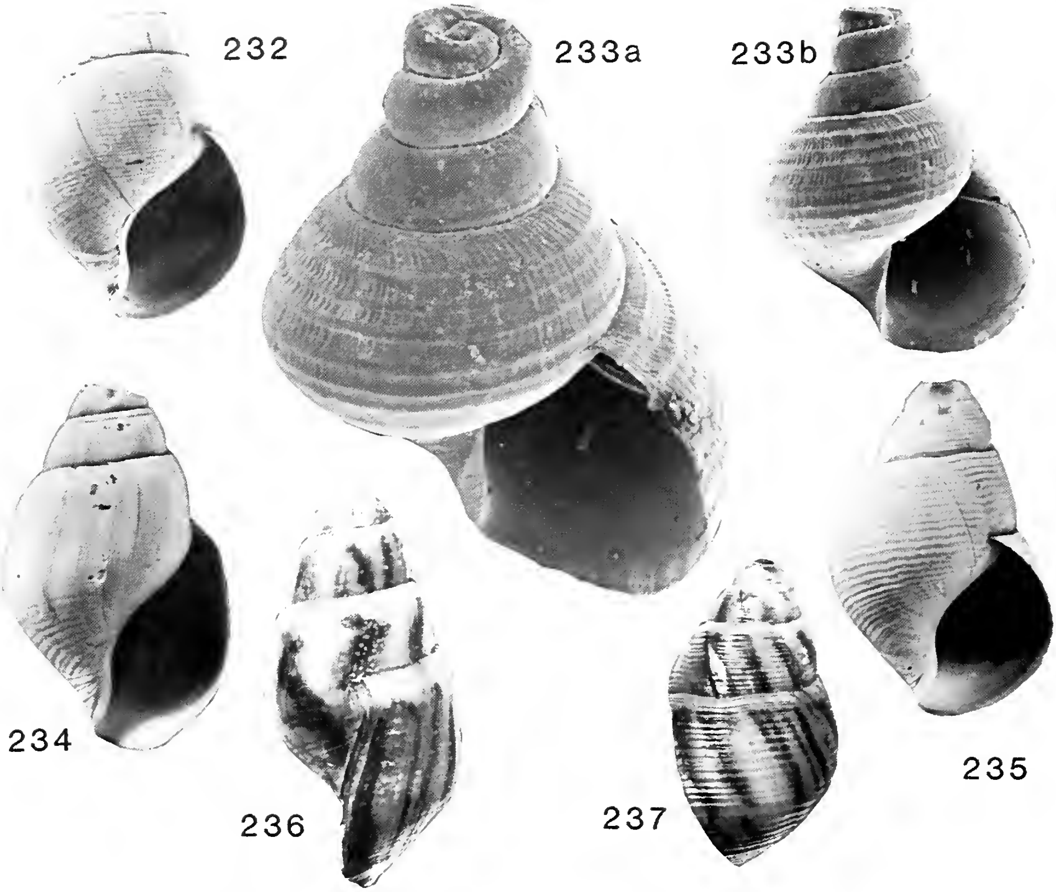
Lectotype (selected herein) of *Hemisinus zebra* Reeve. Shell figured Reeve (1860: pl. 4, figs 15c, d) and two unfigured paralectotypes. Recent, Pernambuco; Cuming Colln, BMZD 1984212.

Holotype of *Hemisinus globosus* Reeve. Recent, Pernambuco; Cuming Colln, BMZD 1984213.

FURTHER MATERIAL STUDIED. Recent: BMZD two shells figured as *Hemisinus kochi* Bernardi by Reeve (1860: pl. 5, fig. 21a, b and fig. 21c, d); Brazil, Cuming Colln, and one accompanying shell; BMZD 49.1.5.28–35, including (28–31) four shells and one embryonic shell labelled *H. globosus* Reeve; Para.

Fossil: All late Caenozoic, Iquitos, Peru, PIMUZ. Described and figured by de Greve (1938: pl. 4) as *Semisinus sulcatus* (Conrad): no. 312, figs 22, 23; no. 315, fig. 19; no. 317, figs 21, 24; no. 319, fig. 17; no. 321, fig. 18.

FURTHER RECORDS AND DISTRIBUTION. Recent, Brazil (Bernardi 1856). No author has given a more precise locality for specimens they identified as *H. kochi*. Reeve's (1860) nominal species were recorded from either Brazil or Pernambuco (= Recife) or Para: this locality data appears to be merely repeated by Brot (1878) and by von Ihering (1902). Fossil: Late Caenozoic, Iquitos (de Greve 1938), including an immature sinistral shell (1938: text-fig. 23).



Figs 232–237 *Hemisinus kochi* (Bernardi). Recent; 'Pernambuco' = Recife, Brazil; Cuming Colln. **232**, BMZD 1984213/1; holotype of *Hemisinus globosus* Reeve, figured by Reeve (1860: pl. 6, fig. 26a, b); front, × 2. **233**, embryonic shell obtained from inside holotype of *H. globosus*, BMZD 1984213/2. a, frontal oblique, × 36; b, front, × 20. **234**, BMZD 1984212/1; **lectotype** (selected herein) of *Hemisinus zebra* Reeve, figured by Reeve (1860: pl. 4, figs 15c, d); front, × 2. **235**, BMZD 1984212/2; one of the two previously unfigured paralectotypes of *H. zebra* Reeve; same details as lectotype; side, × 2. **236**, BMZD 1984211/1; **lectotype** (selected herein) of *Hemisinus pulcher* Reeve, figured b Reeve (1860: pl. 4, figs 15a, b); front, × 2. **237**, BMZD 1984211/2; one of two hitherto unfigured paralectotypes of *H. pulcher* Reeve; same details as lectotype; side, × 2.

DIAGNOSIS. Moderately stout, very variable *Hemisinus*; spire angle between 28° and 42°; subsutural grooving present; spiral sculpture of grooving varying from almost obsolete up to about seventeen grooves on spire whorls and double that number on body whorl; collabral sculpture lacking except for sigmoid growth lines of variable strength; whorl profile from slightly to moderately biconvex; shell colour white with brown axially arranged wavy lines of varying thickness, sometimes broken up into spots or dashes on interspaces between grooves; periostracum, brown. Soft parts, unknown; operculum typical of genus.

DESCRIPTION. The earliest part of the shell is almost always decollated and is unknown in any of the adult specimens. Embryonic shells, washed out of adults, have rather broad biconvex early whorls followed by up to two whorls in which the spiral grooving similar to that of the adult develops. Most of the features described in the above diagnosis vary considerably between different shells but remain fairly constant on any particular individual. The main exception to this is that the convexity of the last whorl is sometimes greater than that of preceding spire whorls.

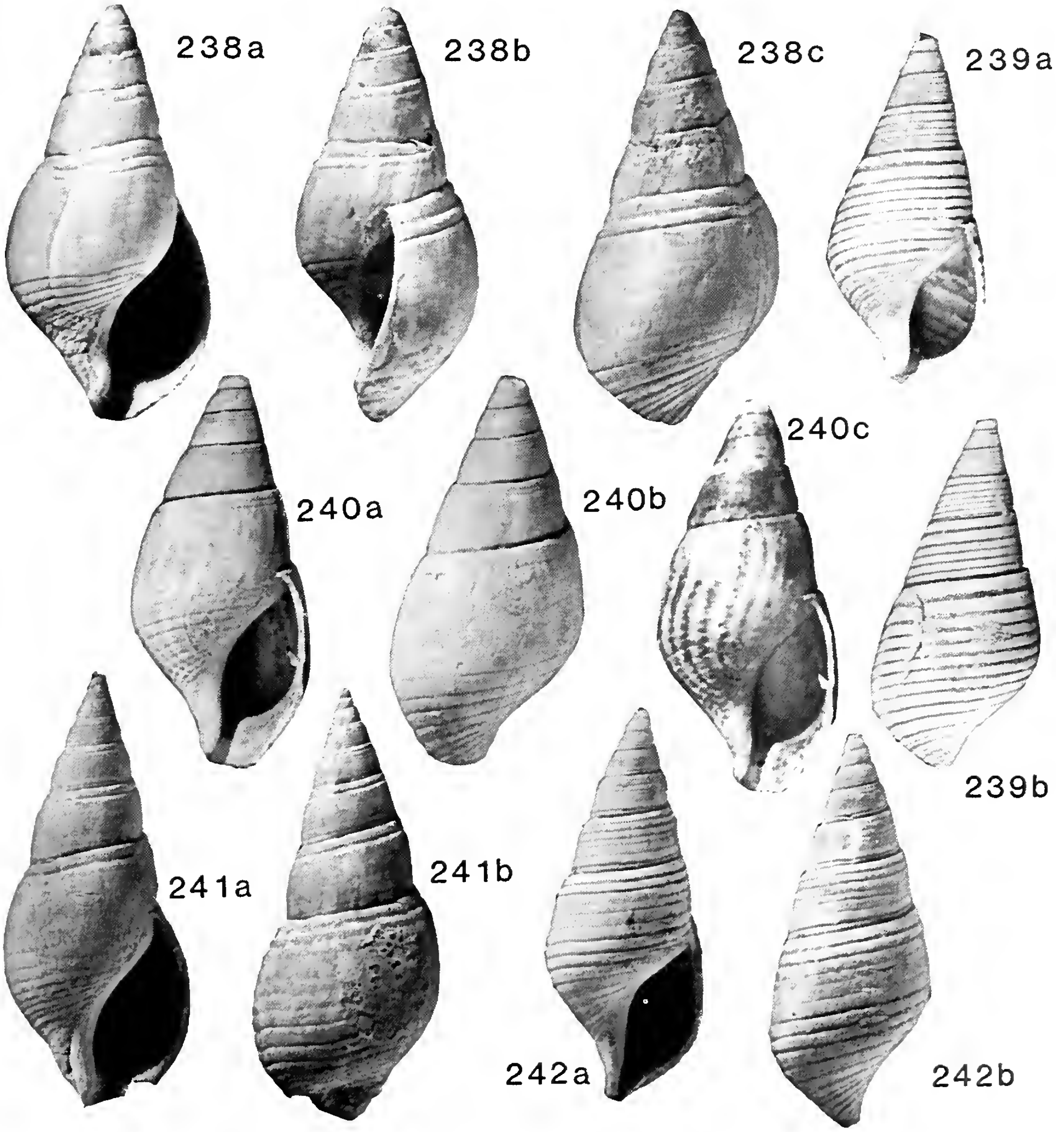
The colour pattern varies from one extreme of more or less collabral broad wavy bands, as exemplified by *H. zebra*, *H. pulcher* and *H. obesus*, to the other of collabrally arrange rows of dashes situated on the interspaces between the spira grooves, with between seven and fifteen rows per whorl: suc patterning is most developed on one of the paralectotypes o *H. punctatus*. Reeve's illustration of this species is composite being made up of the strong colour patterning of this specimen superimposed on the outline of the lectotype.

DIMENSIONS. In mm.	h	br	hap	h/br	sa
Recent:					
Type illustration, *Melania kochi* Bernardi, 1856	30.6	15.4	14.6	1.99	38°
H. kochi (Bernardi), figd Reeve 1860: pl. 5, fig. 21	32.5	16.5	16.8	2.00	42°
Lectotype, *H. punctatus* Reeve	30.5	14.5	13.0	2.10	36°
Paralectotype, *H. punctatus* Reeve	25.7	12.7	12.8	2.15	36°
Paralectotype, *H. punctatus* Reeve	*22.9	9.6	11.9	–	28°
Lectotype, *H. obesus* Reeve	*30.3	18.2	15.5	–	40°
Lectotype, *H. pulcher* Reeve	*23.2	15.6	–	e1.5	52°
Lectotype, *H. zebra* Reeve	*25.0	15.3	–	e1.82	53°
Holotype, *H. globosus* Reeve	*20.8	14.7	–	e1.60	58°

* = decollated, or otherwise extensively damaged.

DIMENSIONS. In mm.	h	br	hap	h/br	sa
Fossil:					
PIMUZ 312, Iquitos	13.5	6.6	6.4	2.15	40°
PIMUZ 315, Iquitos	29.8	14.9	14.0	2.00	37°
PIMUZ 317, Iquitos	24.6	12.5	12.9	2.09	41°
PIMUZ 319, Iquitos	13.7	5.9	–	2.32	33°
PIMUZ 321, Iquitos	12.0	5.8	11.3	2.07	37°

REMARKS. Both Brot (1878) and von Ihering (1902) largely repeated Reeve, thus contributing relatively little new information. For instance, Brot's figure of *H. obesus* Reeve is a copy of the original illustration. The bulk of Reeve's material was said to be from Pernambuco (Recife) and shows strong links between the various nominal species that he described. Bernardi's type material of *H. kochi* has not been studied but the specimens figured in Reeve (1860) and Brot (1878) agree well with his original illustration (1856). Reeve's shells of *H. kochi* are also very close to the type series of his *H. punctatus*. Individual specimens in this series, in which the apical angle varies between 28° and 36°, may be linked with individual fossils from Iquitos (PIMUZ) originally identified by de Greve (1938) as *Semisinus sulcatus* Conrad, and subsequently quoted in the synonymy of this species given by Parodiz (1969). These Iquitos fossils clearly belong here rather than



gs **238–242** *Hemisinus kochi* (Bernardi). Pebasian; Iquitos, Peru; specimens previously identified by de Greve (1938) as *Semisinus sulcatus* (Conrad). **238**, PIMUZ 317; shell figured by de Greve (1938: pl. 4, figs 21, 24). a, b, c, front, side, rear, all × 2.5. **239**, PIMUZ 321; shell figured by de Greve (1938: pl. 4, fig. 18). a, b, front, rear, × 4. **240**, PIMUZ 312; shell figured by de Greve (1938: pl. 4, figs 22, 23). a, b, c, front, rear, and front to show colour patterning, all × 4. **241**, PIMUZ 315; shell figured by de Greve (1938: pl. 4, fig. 19). a, b, front, rear, × 2. **242**, PIMUZ 319; shell figured by de Greve (1938: pl. 4, fig. 17). a, b, front, rear, × 4.

allied to *H. brasiliensis* (Moricand), (below), the senior synonym of *H. sulcatus* Conrad. *H. brasiliensis* exhibits far less variation than *H. kochi*. It is more acicular and its spiral grooving is much more regular in both numbers and intensity.

No specimens of the small (h = 20 mm) but superficially rather similar *Hemisinus schneideri* Brot (1878: 386; pl. 40, figs 2, 2a), described from the Rio Marañon, have been seen. Von Ihering (1902: 670) compared it with *Hemisinus [Melania] osculati* (Villa, 1857), which also occurs in the Upper Amazon and unspecified areas of Peru, Ecuador and Colombia (Brot 1878: 379, von Ihering 1902: 669). BMZD specimens identified as *Hemisinus aspersus* Reeve (1860), a species regarded by both these authors as one of the junior synonyms of *H. osculati* (Villa), lacks the apertural features of *Hemisinus*. The type series of *H. aspersus* cannot be found in BMZD.

Hemisinus brasiliensis (Moricand, 1838) Figs 243–247

* 1838 *Melanopsis brasiliensis* S. Moricand: 144; pl. 3, figs 12, 13.
. 1847 *Melania brasiliensis* (S. Moricand) Philippi: 169; pl. 4, fig. 1.
*v 1859 *Melania venezuelensis* (Dunker MS) Reeve: pl. 13, fig. 81.
v. 1860 *Hemisinus brasiliensis* (S. Moricand) Reeve: pl. 1, fig. 5.
*v 1860 *Hemisinus tenellus* Reeve: pl. 2, fig. 6.
. 1860 *Melanopsis brasiliensis* S. Moricand; J. Moricand: 301; pl. 12, fig. 7.
*v 1871*b* *Hemisinus sulcatus* Conrad: 194; pl. 10, fig. 2.
. 1878 *Hemisinus venezuelensis* (Dunker) Brot: 391; pl. 40, fig. 10; pl. 41, figs 9, 9a.
. 1878 *Hemisinus brasiliensis* (S. Moricand); Brot: 392 (*pars*); pl. 40, figs 12, 12a–c.
. 1914 *Hemisinus brasiliensis* (S. Moricand); Pilsbry *in* Baker: 657.
. 1969 *Aylacostoma sulcatus* (Conrad) Parodiz: 141 (*pars*; not pl. 14, figs 6, 7).

MATERIAL STUDIED. NYSM 9226, the holotype of *H. sulcatus* Conrad, Pichana. The lectotype, selected herein, of *Melania venezuelensis*, the original of Reeve's (1859) pl. 13, fig. 81, and an unfigured paralectotype; Porto Cabello, Venezuela (BMZD 1984215, Cuming Colln). The lectotype, selected herein, of *Hemisinus tenellus*, the original of Reeve's (1860) pl. 2, fig. 6, and two unfigured paralectotypes; Pernambuco (BMZD 1984216, Cuming Colln). The shell figured by Reeve (1860: pl. 1, fig. 5) as *H. brasiliensis* (S. Moricand); Pernambuco (BMZD 1984214, Cuming Colln).

DISTRIBUTION. Recent: Villa de Barra, Bahia Province, Brazil (S. Moricand). Recife (Pernambuco), Brazil (Reeve). Venezuela (Reeve). Alcobaca, left bank, lower Tocantins River, Para Province, Brazil (Pilsbry *in* Baker).

Fossil: Late Caenozoic; Pichana (Conrad), Iquitos (de Greve).

DIAGNOSIS. Comparatively acicular *Hemisinus* with spire angle of *c.* 30°; whorls weakly biconvex in outline; spiral sculpture of six to eight narrow grooves on spire whorls with double the number on the body whorl and with strongest groove immediately below suture; collabral sculpture absent except for growth lines.

DESCRIPTION. There are 8 – 10 barely convex whorls. The aperture is about two-fifths shell height, the apical angle is between 28° and 33° and the height to breadth ratio about 2.5:1. The apices of all the available specimens are damaged. Only one shell (Fig. 245), the hitherto unfigured specimen found with that figured by Reeve (1859) as *M. venezuelensis*, shows details of the early stages. Its first whorl is badly damaged and the second, which is strongly convex and twice as broad as high, is worn. On it, two spiral bands appear: these are added to later at the lower suture so that by the fifth whorl there are six or seven and the appearance becomes typical of the adult. The earlier whorls, however, differ from later ones in several respects. They are much more inflated, with a ramp above, and a semi-incised suture below, separated by a comparatively straight-sided median portion. The three 'facets' of the whorl side are separated by well-rounded spiral cords. These convex cords are separated by relatively strong grooves. In later whorls, the cords broaden and become flat whereas the intervening grooves barely increase in strength. The spiral bands are of variable width and any variation appears to be random. In all specimens a subsutural band or collar is formed. Growth lines are the only collabral sculptural element. They are not strong but are clearly visible on all specimens. The aperture is smooth within. Light parietal callus is present only in the holotype of *H. sulcatus* Conrad: in all other specimens light callus is confined to the columella itself.

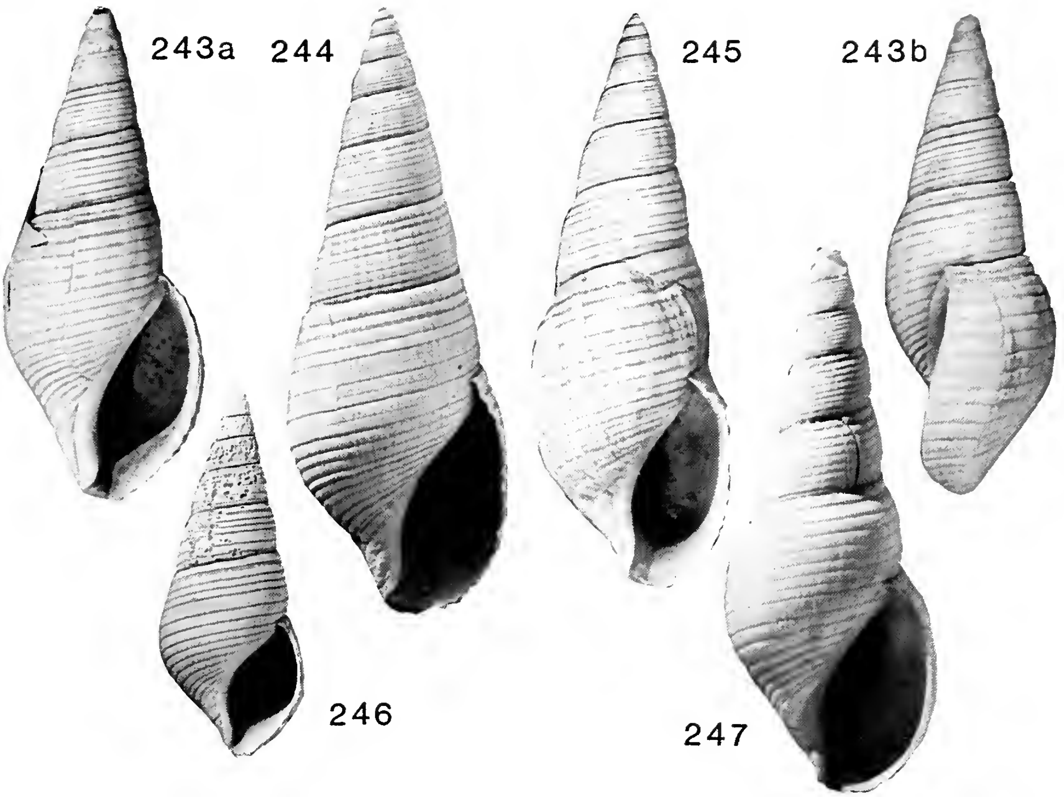
Colour patterning consists of about four elongate strong brown dashes arranged as more or less collabral rows on each spire whorl, with about eight to ten rows per whorl. There is a noticeable narrow light band just below the suture. There is a background coloration of a few alternate pale brown and light bands, which are visible through the thin periostracum and also on the inside of the outer lip.

DIMENSIONS. In mm.	h	br	hap	h/br	sa
H. brasiliensis (Moricand), figd Reeve (1860: pl. 1, fig. 5).	33.8	12.4	14.2	2.64	28°
The accompanying shell	31.8	11.8	12.2	2.70	28°
H. tenellus Reeve. Lectotype (Reeve 1860: pl. 2, fig. 6).	25.2	10.1	11.8	2.5⁺	29°
M. venezuelensis Reeve (*ex* Dunker MS). Lectotype (Reeve 1859: pl. 13, fig. 81).	19.9	8.0	7.8	2.49	30°
H. sulcatus Conrad. Holotype (excluding varix).	27.2	11.2	12.6	2.43	33°–30°

REMARKS. There seem to be no conchological reasons for keeping separate any of the species here included in the synonymy of *H. brasiliensis* (Moricand). The lectotype of *H. tenellus* Reeve has a more convex last whorl than other living shells – a feature shared with the holotype of *H. sulcatus* Conrad, and slightly reminiscent of the latter's varix. The paralectotypes of *H. tenellus* are fairly small and could easily be confused with the type series of *H. venezuelensis* (Reeve).

H. brasiliensis (Moricand) is very similar to the type species, *H. lineolatus* (Woods). The latter may be distinguished by its lack of spiral grooving. Illustrations showing its spiral colour patterning, can, however, give the false impression that it is grooved.

The holotype of *H. sulcatus* Conrad is here referred to *H. brasiliensis*, but all other specimens identified as *H. sulcatus* by subsequent authors are placed elsewhere. Those shells from Iquitos studied by de Greve (1938) are now identified as *H. punctatus* Reeve. Specimens from Três Unidos figured by Parodiz (1969) as *Aylacostoma sulcatus* are referred to *Veren*



Figs 243–247 *Hemisinus brasiliensis* (S. Moricand). **243**, NYSM 9226; holotype of *Hemisinus sulcatus* Conrad, figured by Conrad (1871: pl. 10, fig. 2); Pebasian; Pichana, Peru. a, b, front, side, × 2.5. **244**, BMZD 1984214/1; shell figured by Reeve (1860: pl. 1, fig. 5) as *H. brasiliensis*; Recent; 'Pernambuco' = Recife, Brazil; Cuming Colln; front, × 2.5. **245**, BMZD 1984214/2; previously unfigured shell from same sample as Fig. 244; front, × 2.5. **246**, BMZD 1984215; **lectotype** (selected herein) of *Melania venezuelensis* Reeve, figured by Reeve (1859: pl. 13, fig. 81); Recent; Porto Cabello, Venezuela; Cuming Colln; front, ×2.5. **247**, BMZD 1984216; **lectotype** (selected herein) of *Hemisinus tenellus* Reeve, figured by Reeve (1860: pl. 2, fig. 6); 'Pernambuco' = Recife, Brazil; Cuming Colln; front, × 2.5.

browni Etheridge. The material from Loc. 42, Mangán Formation in the Cuenca Basin described but not figured in Bristow & Parodiz (1982: 47) as *Aylacostoma sulcatus* is here reidentified as *Hemisinus* sp. (GG21225/1–6, p. 246). *Aylacostoma* sp. (GG19866/1–3, p. 261) also occurs at this locality.

Hemisinus (s.l.) ***corrosensis*** Pilsbry & Olsson, 1935

Fig. 248

v* 1935 *Hemisinus (Basistoma) corrosensis* Pilsbry & Olsson: 12; pl. 2, figs 8, 9.

v 1969 *Doryssa corrosensis* (Pilsbry & Olsson) Parodiz: 136.

HOLOTYPE. ANSP 13092, originally figured by Pilsbry & Olsson (1935: pl. 2, fig. 8). Los Corros Formation, Tertiary; Rio Succio, a branch of Rio Llano, Magdalena Valley, Colombia (Olsson & La Tour Collection). An unknown number of paratypes (not seen) are stated to be in Olsson's collection (Pilsbry & Olsson: 12), and include the specimen igured originally as pl. 2, fig. 9. Other details as above. No urther material.

DIAGNOSIS. *Hemisinus* with spire angle of 30°; early whorls mooth; spiral sculpture of 5 – 6 grooves on later spire whorls and 10 – 12 on final whorl; collabral sculpture lacking, growth lines weakly reverse sigmoid; whorls very weakly convex; sutures simple.

DESCRIPTION. The holotype is now broken into two parts. The spire is acute. The whorls are weakly convex, with the periphery just above the suture. Sculpture other than growth lines cannot be seen on the early whorls but there are five spiral grooves of unequal width on the penultimate whorl and about double this number of the final whorl as the grooving continues onto the neck. Collabral sculpture is absent except for the growth lines. Those on the smaller spire fragment do not reveal whether the basal apertural notch typical of Hemisininae was present. The aperture is pointed above, not rounded.

DIMENSIONS (from Pilsbry & Olsson). ANSP 13092 (holotype): h, 29 mm; br, 11 mm.

REMARKS. Pilsbry & Olsson referred to 'The Type' and to 'Paratypes'. The 'Type' is therefore taken to be the holotype, whose published dimensions fit those of the now broken ANSP 13092 (br = 10.7 mm). Pilsbry & Olsson's illustration (1935: pl. 2, fig. 8) is extensively retouched, and greatly enhances the very weak spiral grooving. They defined (1935: 11) *Basistoma* as being spirally grooved or corded and presumably assigned *H. corrosensis* to it for that reason. The aperture is, as far as can be judged from the damaged holotype, low in relation to the height of the spire, as in *Basistoma*. As growth lines can be seen on the early whorls of the holotype, it is clear that spiral grooving is truly absent, rather than missing on account of poor preservation. This lack of early spiral sculpture is more suggestive of *Hemisinus* and *Sheppardiconcha* than of *Basistoma*. The aperture in *Sheppardiconcha* tends to be more rounded above. This species is therefore provisionally assigned to *Hemisinus*. It does not appear to belong to *Doryssa* similar to *D. atra*, as suggested by Parodiz (1969), who was basing his decision on the original description and illustrations of *H. corrosensis*, not on new material.

The allegedly Eocene specimens identified by Boss & Parodiz (1977: 118, figs 10, 11) as *Doryssa corrosensis* (Pilsbry & Olsson) from Isla Navarra, Rio Huallaga, San Martin, Peru, appear to be misidentified. The illustrations are of internal moulds on which traces of spiral sculpture can be clearly seen.

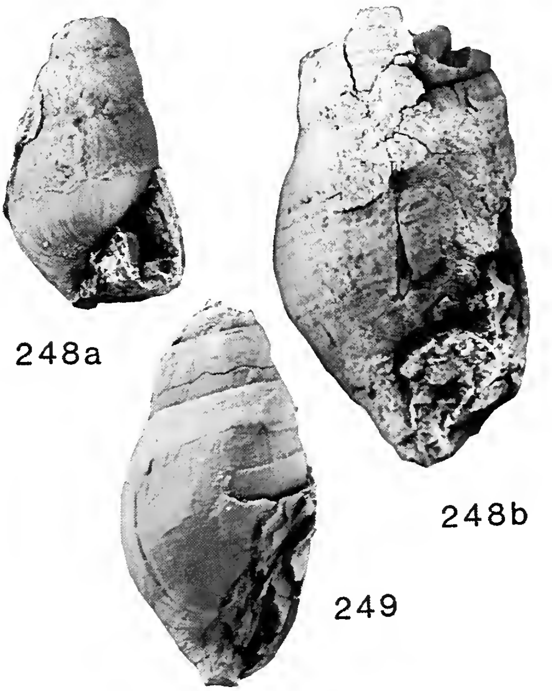


Fig. 248 *Hemisinus corrosensis* Pilsbry & Olsson. ANSP 13092; damaged holotype, figured by Pilsbry & Olsson (1935: pl. 2, fig. 8). Palaeogene, Los Corros Formation; Rio Succio, Middle Magdalena Valley, Colombia; E. La Tour Colln. a, b, top and bottom portions, × 3.

Fig. 249 *Hemisinus* sp. GG21225/1; Miocene, Mangán Formation; Loc. CRB 42, Cuenca Basin, Ecuador; Bristow Colln. × 2.

***Hemisinus* sp.** Fig. 249

v 1982 *Aylacostoma sulcatus* (Conrad); Parodiz *in* Bristow & Parodiz: 47 (*pars*).

MATERIAL STUDIED. GG22125/1–6; Loc. CRB 42, Mangán Formation, ? late Miocene, Cuenca Basin, Ecuador. No further records.

DIMENSIONS. GG22125/1: h, 20.7 mm; eh, 26.5 mm; br, 10.6 mm.

DESCRIPTION. The specimens studied are all damaged. The shell is relatively acicular with an apical angle of between 35°–40°. No spiral ribbing is present. Collabral sculpture is absent except for the growth lines which are only moderately sinuate. The whorl profile is only weakly biconvex with the periphery at the lower suture. The apertural features cannot be made out properly. Columellar callus is present but the parietal region is never clearly enough exposed to show whether callus is developed. Growth lines near the columella show that the typical *Hemisinus* basal notch is present.

REMARKS. Parodiz quoted no registration numbers so it is not clear whether his work was based on specimens in Carnegie Museum as well as those in BMPD. He commented on the variability of the material. Here, the sample from CRB 42 is divided into the present species and *Aylacostoma* sp. (GG19866/1–3), p. 261. Although many characters may be clearly seen, the species is not named on the present material because it is comparatively poorly preserved. It can be distinguished from *H. braziliensis* (Moricand) by its lack of spiral ribbing. *H. kochi* (Bernardi) sometimes almost lacks spiral ribbing but its growth lines are much more sinuate. *H. lineolatus* (Wood) is almost smooth but always has some subsutural grooving. Western South American species only provisionally accepted herein as possible *Hemisinus*, such as *H. aspersus* Reeve (1860), *H. osculati* (Villa, 1857) and *H. schneideri* Brot (1878) all apparently have a much less developed basal notch.

Genus ***LONGIVERENA*** Pilsbry & Olsson, 1935

TYPE SPECIES. *Aylacostoma tuberculata* Spix (*in* Spix & Wagner 1827: pl. 8, fig. 4), by subsequent designation of Wenz (1939: 719); Recent, Brazil.

DIAGNOSIS. Like *Aylacostoma* but sculptured with strong spiral tuberculate ribs and collabral folds; operculum as in *Aylacostoma*; ovoviviparous ? parthenogenetic; embryonic shell with spiral ribbing.

OTHER SPECIES ASSIGNED. Fossil: *Hemisinus (Longiverena) eucosmius* Pilsbry & Olsson, 1935, Tertiary (? Neogene) of Colombia, Miocene of Ecuador, Late Caenozoic, Pebasian of Peru; *Hemisinus (Longiverena) mugrosanus* Pilsbry & Olsson, 1935, Tertiary (? Neogene) of Colombia; *Longiverena colombiana* sp. nov. (p. 249), Late Caenozoic, La Tagua. Recent: None.

DISTRIBUTION. ? Neogene only: Colombia, Ecuador, Peru. Recent: eastern Brazil.

REMARKS. Pilsbry & Olsson (1935) erected *Longiverena* as a 'section' of *Hemisinus* for elongate shells with rounded whorls sculptured with spiral cords or grooves and axial folds or ribs. This was to accommodate several mid-Tertiary species they were describing from the Magdalena Valley. They listed the various 'sections' of *Hemisinus* that they recognized along with one species of each which happened to be living and, in the case of the established taxa, was also the type species; these were *Hemisinus lineolatus* Gray, *Basistoma edwardsi* (Lea) and *Verena crenocarina* Spix (*sic*). The species they mentioned for *Longiverena* was *tuberculata* Spix. However, they gave no type designation, though it seems clear that *tuberculata* would have been their choice, and Wenz (1939) designated this as type species. Morrison (1952, not seen;

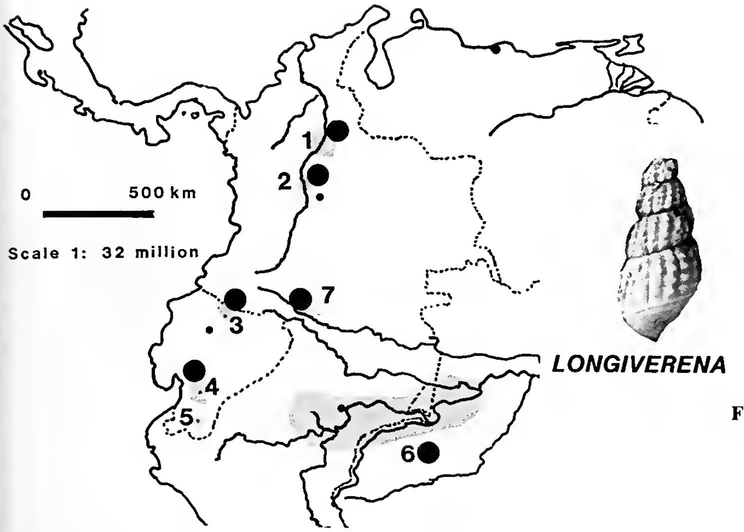


Fig. 250 Neogene distribution of *Longiverena*. Key as for Fig. 6 (p. 177). Inset: *L. eucosmia* (Pilsbry & Olsson), × 2; Mugrosa formation; Magdalena Valley, Colombia.

1954: 377) independently made the same choice; his 1952 paper was an abstract of a meeting report and is possibly not valid.

Wenz (1939: 719) gave the distribution of the genus as being Oligocene, ?Europe; Oligocene, Colombia; Recent, South America and West Indies. I am unaware of any species from outside South America.

Aylacostoma glabrum Spix and *Longiverena tuberculata* (Spix) appear to be very similar in many important respects except that *L. tuberculata* is strongly sculptured whilst *A. glabrum* is almost smooth. In the future, increased understanding of the South American fauna may lead to this distinction being regarded as not of generic significance. This would, however, raise the problem of the generic assignment of the fossil species, with the exception of *L. colombiana* sp. nov., here placed in *Longiverena*, as they would be most unlikely to fit comfortably in *Aylacostoma* in any future reclassification.

Longiverena tuberculata (Spix, *in* Spix & Wagner 1827)

Figs 251–255

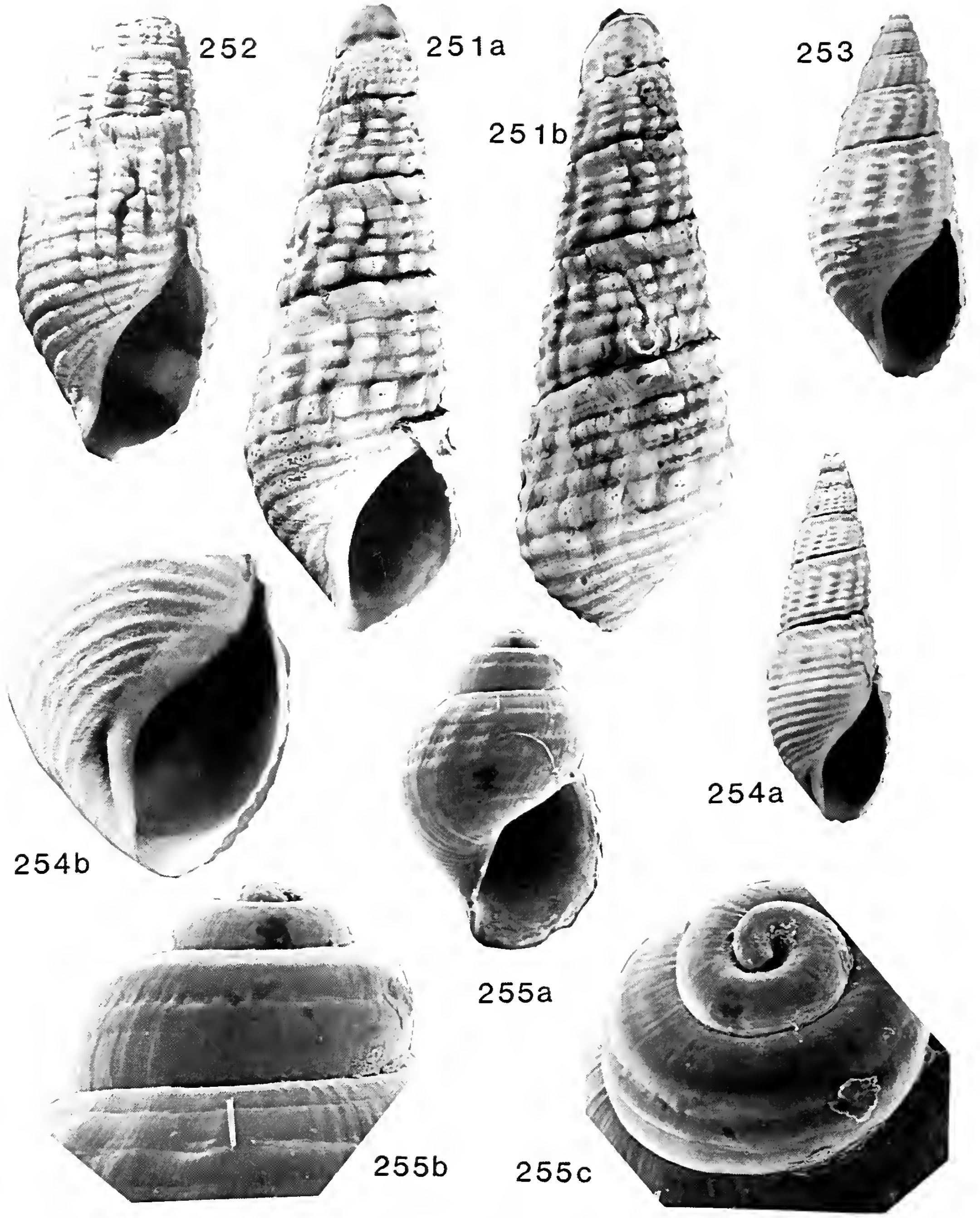
*v 1827 *Aylacostoma tuberculata* Spix, *in* Spix & Wagner: pl. 8, fig. 4.
v. 1827 *Melania tuberculata* Wagner, *in* Spix & Wagner: 15.
*v. 1860 *Hemisinus olivaceus* Reeve (*ex* Behn MS): pl. 3, fig. 12a, b.
. 1878 *Hemisinus tuberculatus* (Wagner) Brot: 397; pl. 41, figs 10, 10a–d.
. 1902 *Hemisinus tuberculatus* (Wagner); von Ihering: 667
. 1935 *Hemisinus (Longiverena) tuberculatus* (Spix); Pilsbry & Olsson: 11.
. 1939 *Hemisinus (Longiverena) tuberculatus* (Wagner); Wenz: 719, fig. 2078.
. 1954 *Aylacostoma (Longiverena) tuberculata* Spix; Morrison: 377.
. 1983*a* *Aylacostoma tuberculata* Spix = *Melania tuberculata* Wagner; Fechter: 222.

LECTOTYPE (selected herein) of *A. tuberculata* Spix, the specimen almost certainly figured by Spix 1827; the nine accompanying shells are paralectotypes. Recent, Mandiocca, Prov. St Sebastian, southern Brazil (Wagner, 1827). Staats. Zool. Mus. München (Spix Colln). The lectotype (selected herein) of *Hemisinus olivaceus* Reeve is the specimen figured by Reeve (1860); the two accompanying shells are paralectotypes. Recent, Pernambuco; Cuming Colln, BMZD 1984217.

OTHER MATERIAL. Fifteen adult and two embryonic shells; Recent, Brazil, BMZD 69.6.2.21, examined. Also recorded from the Recent of Rio de Janeiro by Ihering (1902). Distribution Recent only, Brazil.

DIAGNOSIS. *Longiverena* with spire angle of about 20°; early whorls convex-sided, expanding moderately rapidly; shoulder of varying strength developed on later whorls.

DESCRIPTION. Most specimens are decollated. If complete, they would be up to 50 mm in height, with the aperture about one third shell height, and comprise ten whorls. The incremental angle is moderately obtuse for the early whorls but soon reduces to about 20° for the later whorls. Two embryonic shells extracted from adults in sample BMZD 69.6.2.21 have reached the stage where the adult type of sculpture is developed. Examination of these embryonic shells and those of young snails with a separate existence from the same sample has failed to detect any differences, such as change in sculpture, which might mark the transition from life in the oviduct to life outside it. The embryonic shell has about four whorls. The first two are wide, convex-sided, and rather sunken; the third has two spiral ribs increasing in number to six. The third and fourth whorls are strongly convex. On succeeding whorls a subsutural constriction is present, which sometimes develops into a ramp of varying strength. The whorl side below the shoulder is virtually straight-sided except for some constriction at the lower suture, with the periphery lying just above. Spiral sculpture consists of 5–6 ribs on the spire whorls and 10–14 on the final whorl. Traces of secondary ribbing occur on some specimens including the lectotypes of both *L. tuberculata* and *L. olivacea*. The ribs are



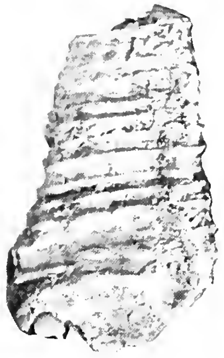
Figs 251–255 *Longiverena tuberculata* (Spix). Recent, Brazil. **251**, **lectotype** (selected herein) of *Aylacostoma tuberculata* Spix, figured by Spix (1827: pl. 8, fig. 4). Mandiocca, St Sebastian Province, southern Brazil; Spix Colln, Staats. Zool. Mus. München. a, b, front, rear, × 2.5. **252**, BMZD 1984217; **lectotype** (selected herein) of *Hemisinus olivaceus* Reeve, figured by Reeve (1860: pl. 3, figs 12a, b). Brazil. Front, × 3. **253–255**, all from same sample BMZD 69.6.2.21 of *L. tuberculata*, Brazil; Mrs Burton Colln. **253**, front, × 3. **254**, a, front, × 1.5; b, oblique view of neck of body whorl and aperture, × 3. **255**, embyronic shell extracted from adult in same sample; a, front, × 20; b, apex, × 50; c, oblique view of apex, × 50.

of varying width, most are well rounded but the two most adapical rows tend to develop pointed tubercles where they cross the underlying collabral folds. In the troughs between these folds the spiral ribbing tends to be weak. The number of collabral folds decreases from as many as twenty on early whorls to 10–15 on later whorls. The growth lines are weakly opisthocyrt on spire whorls and, at the aperture, form a reverse sigmoid labrum. The aperture is constricted above into a weak canal, and is notched below. The inner lip is callused, but the parietal region is only weakly so in smaller shells.

256

257

258



259

Figs 256–259 *Longiverena colombiana* sp. nov. Late Caenozoic; La Tagua, Colombia; Eden Colln. **256**, GG19943; **holotype**, Loc. 33/480–560; front, ×2.5. **257–259**, paratypes. **257**, GG19944; Loc. 33/480–560, × 2.5. **258**, GG19945; Loc. 33/480–560, × 2.5. **259**, GG19941; Loc. 54, × 5.

260

261

262

igs 260–262 *Longiverena colombiana* sp. nov. Paratypes, latex casts of external moulds. Late Caenozoic; Loc. 44, La Tagua, Colombia; Eden Colln. **260**, GG21573; × 2. **261**, GG21572; × 4. **262**, GG 21574; × 4.

IMENSIONS. In mm.	h	br	hap	hbw	h/br	sa
ectotype of *Aylacostoma* *berculata*, Staats. Zool. Ius. Munchen	*38.0	13.2	12.4	22.0	e3.1	20°
ectotype of *Hemisinus* *livaceus*, BMZD	*23.6	10.3	12.0	18.0	–	20°
MZD 69.6.2.21	36.7	13.4	13.1	20.6	2.74	21°
MZD 69.6.2.21	18.5	8.1	7.5	12.2	2.28	32°

= decollated

EMARKS. Spix' collection contained ten shells of this species. he shell here selected as lectotype is the only one which ould be his figured specimen. Comparisons between this species and the fossil species assigned to *Longiverena* are given under the latter.

Longiverena colombiana sp. nov. Figs 256–262

HOLOTYPE. BMPD GG19943; Late Caenozoic; Loc. 33/480–560 cm, La Tagua (Eden Colln). The following are paratypes: GG19944–7, GG19991/1–5, information as above; GG19992–3, Loc. 33/570–670 cm; GG19941–2, Loc. 54; GG21572–4, Loc. 44; all La Tagua (Eden Colln).

NAME. 'Colombian'.

DIAGNOSIS. Medium-sized *Longiverena* with sculpture of about six evenly-spaced angular spiral ribs separated by wide interspaces and on later whorls crossing up to 20 strongly curved collabral folds per whorl; whorls comparatively broad; sutures incised; early whorls straight-sided, later whorls convex with periphery low down.

Description. All the apices and apertures are broken. In addition, most of the shells are partly crushed and the shell surface is seldom particularly well preserved. It is estimated that the height of the largest specimens would have been between 30 and 35 mm and the spire angle about 25°. The rate and sequence of development of the sculpture appears to be inconstant: some early whorls are smooth except for a prominent spiral rib above the incised lower suture, sometimes accompanied by a rather less prominent rib forming a subsutural collar. The rest of the spiral sculpture develops from grooves which rapidly broaden to form wide interspaces between narrow sharp ribs. The collabral folds are strongly opisthocyrt and vary in strength from specimen to specimen but are of reasonably constant strength in any one individual. Their spacing is also fairly constant so their number increases with whorl diameter, up to a maximum of 20 by the last whorl. The folds die away towards the lower suture and seldom affect the lowest spiral rib. GG19942, a crushed juvenile specimen, shows fine reticulate sculpture between the spiral ribs of early whorls. In adult specimens a callus pad is developed on the parietal region of the inner lip; other apertural features are not shown on the available material.

Dimensions. Holotype, GG19943: h, 24.7 mm, c34 mm; br 12.9 mm; sa 25°.

Remarks. This species may be distinguished from *L. tuberculata* (Spix) by its relatively broader whorls which never bear a shoulder, but the sculpture of the two species is closely similar. In *L. colombiana* there is no wide gap between the two most adapical ribs as there is in *L. tuberculata*. In addition, its opisthocyrt growth lines and collabral ribs are more evenly curved than those of *L. tuberculata* in which the most backward point tends to be rather high in the whorl, more or less at shoulder level. The collabral folds of *L. colombiana* tend to be more numerous and rather weaker than those of *L. tuberculata*.

L. colombiana is very similar to *L. eucosmia* (Pilsbry & Olsson), below. The two are provisionally treated as being distinct as the sculptural elements in *L. colombiana* appear to be considerably less regular, in both size and spacing, than in *L. eucosmia*, which, in addition. seems to be consistently smaller. In view of the synonymy given herein for *L. eucosmia*, it is felt that had these two nominal species occurred together, evidence of their close association might well lead one to conclude that they should be treated as no more than separate subspecies.

Longiverena eucosmia (Pilsbry & Olsson, 1935)

Figs 263–267

*v 1935 *Hemisinus (Longiverena) eucosmius* Pilsbry & Olsson: 13; pl. 3, fig. 2.

*v 1935 *Hemisinus (Longiverena) lapazanus* Pilsbry & Olsson: 13; pl. 3, figs 3, 4.

*v 1935 *Hemisinus (Longiverena) hopkinsi* Pilsbry & Olsson: 14; pl. 3, fig. 8.

*. 1935 *Hemisinus (Longiverena) laciranus* Pilsbry & Olsson: 14; pl. 3, fig. 5.

*. 1935 *Hemisinus (Longiverena) waringi* Pilsbry & Olsson: 14; pl. 3, fig. 9.

*v 1938 *Semisinus peyeri* de Greve: 104; pl. 4, figs 7–11.

*. 1941 *Hemisinus peyeri dickersoni* Palmer *in* Liddle & Palmer: 42; pl. 6, figs 15–18.

v. 1969 *Aylacostoma (Longiverena) eucosmius* (Pilsbry & Olsson) Parodiz: 146; pl. 16, figs 10, 11, 13.

v. 1969 *Aylacostoma (Longiverena) peyeri* (de Greve) Parodiz: 148.

. 1969 *Aylacostoma (Longiverena) waringi* (Pilsbry & Olsson) Parodiz: 148; pl. 16, fig. 1.

. 1969 *Aylacostoma (Longiverena) peyeri dickersoni* (Palmer) Parodiz: 149.

v 1982 *Aylacostoma dickersoni* (Palmer); Parodiz *in* Bristow & Parodiz: 48.

Lectotype of *H. eucosmius* Pilsbry & Olsson, 1935, selected herein: ANSP 13088, shell figured Pilsbry & Olsson, pl. 3, fig. 2. Mugrosa Formation, Tertiary, Well 660, depth 1803–1815 feet. The two accompanying shells on the same core sample are paralectotypes.

Lectotype of *H. lapazanus* Pilsbry & Olsson, 1935, selected herein: ANSP 13090, original of their pl. 3, fig. 3. The original of their pl. 3, fig. 4 and two other shells are paralectotypes. All Mugrosa Formation, near El Centro, Square Mile 16S, 8E (O.C. Wheeler Colln).

Lectotype of *H. hopkinsi* Pilsbry & Olsson, 1935, selected herein: ANSP 13089, original of their pl. 3, fig. 8, same details as *H. lapazanus*. The accompanying specimen is a paralectotype.

Holotype of *S. peyeri* de Greve, PIMUZ 356, selected as 'typus' by him (1938: 105; pl. 4, figs 9, 11). PIMUZ 358, 359 and 360 are paratypes; all Late Caenozoic, Pebasian; Iquitos, Peru (Peyer Colln).

Other material. BMPD GG19865, Loc. CRB1, Basal Azogues Formation, Miocene; Cuenca Basin, Ecuador (identified as *A. dickersoni* by Parodiz *in* Bristow & Parodiz, 1982: 48), has been studied.

Further records. As *Hemisinus peyeri dickersoni* Palmer from its type locality (Liddle & Palmer, 1941: 36, map) = Loyola Formation (Miocene), southwest side of Cojitambo, Cuenca Basin, Ecuador (Bristow & Parodiz, 1982: 12, 48). As *Hemisinus (Longiverena) laciranus* Pilsbry & Olsson (1935), from La Cira Formation, Tertiary (Miocene), near La Cira, Colombia, ANSP 13078 (O.C. Wheeler Colln). As *Hemisinus (Longiverena) waringi* Pilsbry & Olsson (1935), from La Cira Formation, near Zopffs, ANSP 13072 (W.W. Waring Colln).

Distribution. Miocene, Cuenca Basin, Ecuador; Mugrosa and La Cira Formations, Tertiary (? both Miocene), Magdalena Valley, Colombia; Late Caenozoic, Pebasian, Iquitos, Peru.

Diagnosis. Small *Longiverena* with spire angle of about 30°; whorls biconvex; sculpture of three to five spiral ribs per whorl, expanded into strong, rather square tubercles where they cross the 9 – 18 opisthocyrt collabral folds per whorl; body whorl below periphery with up to about five spiral ribs, lacking collabral folding.

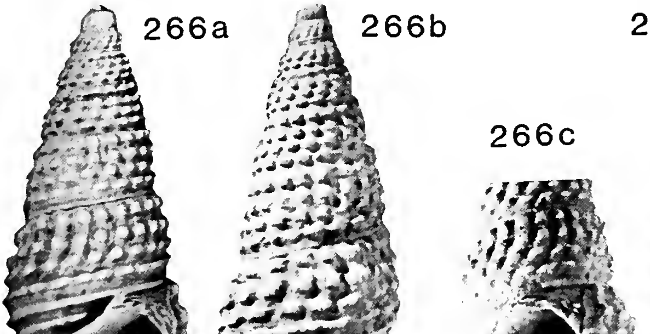
Description. The apex has never been seen. The best specimens are those described as *S. peyeri* de Greve from Iquitos; seven whorls are present in the holotype PIMUZ 356. The sculpture is first seen on its third whorl and is, by then, of adult character. The spiral sculpture consists of 3 – 5 ribs on each body whorl separated by interspaces of approximately

264

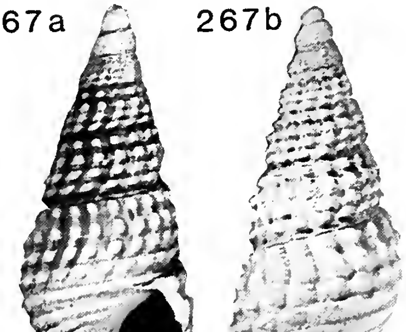
263

265

Figs 263–265 *Longiverena eucosmia* (Pilsbry & Olsson) and *L. eucosmia mugrosana* (Pilsbry & Olsson). **263**, ANSP 13088; bedding plane in borehole core with **lectotype** (selected herein) of *Hemisinus (Longiverena) eucosmius* Pilsbry & Olsson, figured by Pilsbry & Olsson (1935: pl. 3, fig. 2). Well 660, depth 1803–1815 feet, Middle Magdalena Valley, Colombia (the two accompanying and damaged paralectotypes were neither figured nor discussed by Pilsbry & Olsson); × 4. **264**, *Longiverena eucosmia mugrosana* (Pilsbry & Olsson), ASNP 13087; holotype of *Hemisinus (Longiverena) mugrosanus* Pilsbry & Olsson, figured by Pilsbry & Olsson (1935: pl. 3, fig. 1), Olsson & La Tour Colln; × 4. **265**, GG19865; latex cast of external mould, *L. eucosmia*; specimen recorded as *Aylacostoma dickersoni* (Palmer) by Bristow & Parodiz (1982: 48); Miocene, Basal Azogues Formation; Loc. CRB 1, Cuenca Basin, Ecuador; Bristow Colln; × 4.



266a 266b 266c



267a 267b

Figs 266–267 *Longiverena eucosmia* (Pilsbry & Olsson). Specimens described as *Semisinus peyeri* de Greve; Pebasian; Iquitos, Peru; Peyer olln. **266**, PIMUZ 356 ; holotype, figured by de Greve (1938: pl. 4, figs 9, 11). **267**, PIMUZ 358; paratype, figured by de Greve (1938: pl. 4, figs 8, 10). a, b, front, rear. All × 5.

e same width. The spacing of the ribs varies. In some ecimens a definite subsutural ring is formed and sometimes ere is a particularly wide gap between the topmost spiral nd the one immediately below. The ribs are thickened into osses where they cross the rather strong, sigmoid collabral lds, of which there are about eight on early whorls, increasg to 14 – 18 on later whorls. They decrease in strength below the periphery and normally die away by the lower suture so that the four or five spiral ribs on the lower half of the body whorl are devoid of collabral tuberculations. The aperture is not complete in any specimen either seen or figured elsewhere. The two best-preserved appear to be one of the syntypes (in ANSP) of *Hemisinus peyeri dickersoni* Palmer (*in* Liddle & Palmer 1941: pl. 6, fig. 16) and the

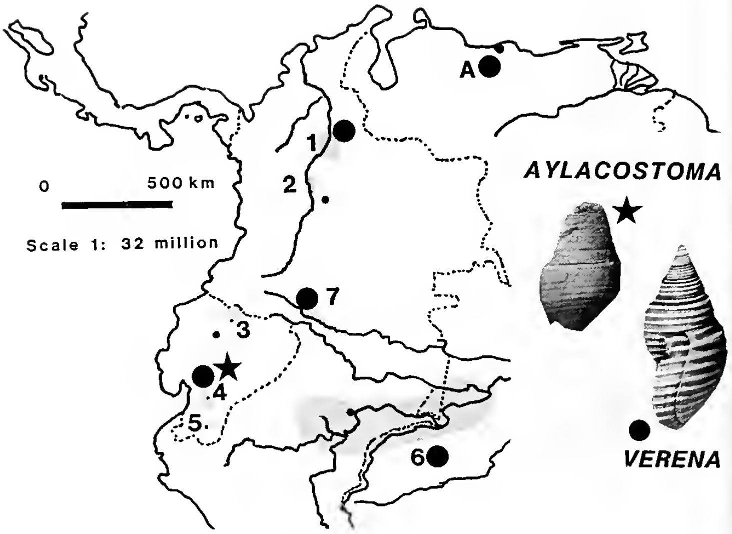


Fig. 268 Neogene distribution of *Verena* and *Aylacostoma*. Key as for Fig. 6 (p. 177). ●, *Verena*; ★, *Aylacostoma*. Inset: top left, *Aylacostoma* sp.; Miocene, Cuenca Basin, Ecuador; bottom right, *Verena browni* (Etheridge); Puerto Nariño, Colombia. Both × 2.

holotype of *Semisinus peyeri* de Greve (PIMUZ 356). The inner and outer lip meet adapically to form a moderately obtuse arch. The columellar and parietal callus pad has a definite rim on its left margin because it stands proud of the main shell surface. The base of the aperture is produced anteriorly in a way reminiscent of the pouring lip of a jug to form a basal notch.

Dimensions. In mm.	h	br	hap	h/br	sa
ANSP 13088, lectotype of *L. eucosmia*	*12.6	5.9	–	–	–
ANSP 13089, lectotype of *L. hopkinsi*	*15 (P&O)	–	–	–	28°
ANSP 13090, lectotype of *L. lapazana*	*14 (P&O)	–	–	–	30°
ANSP 13072, *L. waringi*, type illustration.	14 (P&O)	–	–	–	–
ANSP 13078, *L. lacirana*, type illustration	*11.5 (P&O)	–	–	–	–
PIMUZ 356, holotype of *L. peyeri*	13.2	5.2	5.4	2.54	28°
PIMUZ 358, paratype of *L. peyeri*	11.9	5.0	4.5	2.38	32°

(P&O) = Measurements from Pilsbry & Olsson (1935); * = decollated or other damage.

Note. Most of the specimens are too incomplete for meaningful measurements to be made. Measurements of spire angles are prone to error in the case of specimens partly embedded in matrix and are best omitted.

Remarks. One of the important but less obvious features uniting the nominal species placed in synonymy here is that the spiral ribbing is not markedly dominant over the collabral folding as in *S. tuberculifera* (Conrad) and *S. coronata* (Etheridge), both of which occur at Iquitos with the present species. The apertural features given in the above description and the character of the ribbing are those of *Longiverena*. Parodiz (1969) synonymized the Colombian species *H. lapazanus*, *H. hopkinsi* and *H. laciranus* under the name *H. eucosmius*. His illustrations of the species are copies of Pilsbry & Olsson's originals: thus Parodiz pl. 16, fig. 10 = *hopkinsi*; fig. 11 = *lapazanus* (Pilsbry & Olsson's fig. 4); fig. 13 = *eucosmius*. He did not refigure *H. laciranus*. This synonymy is accepted here, and to avoid confusion the species remains described under the specific name *eucosmia* even though the best specimen is probably the lectotype of *H. hopkinsi* and, moreover, the type locality of *H. eucosmius*, being in a borehole, is not ideal. *H. laciranus* and *H. waringi*, from the La Cira Formation, are the only two of these five synonyms which are not confined to the underlying Mugrosa Formation. On *H. lacirana* the sculptural elements are weaker and more widely spaced than usual. However, they are essentially of the same type as seen in other specimens assigned to *L. eucosmia*. *H. waringi* from the La Cira Formation was based on an external mould (ANSP 13072) which is clearly not sagittal, and thus appears more acutely spired that it really is. It, too, is here accepted as a synonym of *L. eucosmia* on the character of its sculpture.

Hemisinus (Longiverena) mugrosanus Pilsbry & Olsson (1935: 13; pl. 3, fig. 1 – ANSP 13087) was also described from the Mugrosa Formation. It would seem to be closely related to these above-mentioned species but is here considered to be a distinct subspecies of *L. eucosmia* because its sculpture is not of spiral ribs but of spiral grooves cutting the collabral sigmoid folds.

Both the well-preserved *Semisinus peyeri* de Greve from Iquitos and the rather fragmentary *Hemisinus peyeri dickersoni* Palmer from the Cuenca Basin are assigned to *L. eucosmia* because of their virtually identical sculpture, whorl shape and profile. Pilsbry (1944: 146) and Parodiz (*in* Bristow & Parodiz 1982: 48) regarded both as being specifically distinct, but I cannot detect any appreciable differences between them. BMPD GG19865 from CRB 1 in the Cuenca Basin was identified as *A. dickersoni* by Parodiz. It is a single damaged external mould which shows sculpture typical of *L. eucosmia*.

The differences between *L. eucosmia* and the very similar *L. colombiana* are discussed under the latter, p. 250.

Genus *VERENA* H. & A. Adams, 1854

Type species. *Melanopsis crenocarina* S. Moricand, 1841. Recent, eastern Brazil (Bahia, Para). By monotypy (H. & A. Adams 1854: 308).

DIAGNOSIS. Comparatively stout Thiaridae with broad sloping ramp and angular shoulder; spire angle 35°–80°; aperture about half shell height; columella truncated above anterior notch as in *Hemisinus*; spiral ribbing strong; collabral sculpture weak or absent except for growth lines; aperture with weak sinus developed on ramp, outer lip prosocyrt; operculum not seen; presumed ovoviviparous (see under *V. crenocarina* (below), embryonic shells extracted from inside adult).

SPECIES ASSIGNED. Recent: The type species only. Fossil: *Hemisinus (Verena) crenocarina ava* Pilsbry & Olsson, 1935, = *Hemisinus (Verena) laevicarina* Pilsbry & Olsson, 1935, both ?Miocene, La Cira Formation, Colombia; *Ampullaria guaduasensis* Anderson, 1928, see p. 256; *Melanopsis? browni* Etheridge, 1879, Late Caenozoic, Pebasian, Canamá, Três Unidos, Puerto Nariño; *Verena* sp. (aff. *browni*, p. 258), Miocene, Mangán Formation, Cuenca Basin, Ecuador; *Verena lataguensis* sp. nov. (p. 258), Late Caenozoic, La Tagua, Colombia; *Hemisinus barloventoensis* Macsotay, 1968, Miocene, Cumaca and Siquire Formations, northern Venezuela.

DISTRIBUTION. Neogene and Recent, northern South America (Colombia, Ecuador, Peru, Brazil, Venezuela).

REMARKS. *Pyrgulifera* (Meek, 1877), a widespread Cretaceous to Eocene genus, is of similar shape but its columella reaches the abapical edge of the shell and is not truncated as in *Verena*. There is no reason, therefore, for thinking that the two genera are closely related. Parodiz (1969: 144–145) placed *Gonioconcha striata* Bonarelli (1927) and *Hypsipleura (?) bracklebushi* Bonarelli (1927), both from the Palaeocene of Argentina, in *Verena*. Their type illustrations suggest that some relationship with contemporaneous *Pyrgulifera* would be more likely than with later *Verena*. Parodiz (1969: 140) also tentatively placed *Hemisinus (Verena) avus* Pilsbry & Olsson in *Pyrgulifera*. Here, it is reassigned to *Verena* and is regarded as no more than a subspecies of *V. crenocarina*. The poorly preserved *Ampullaria guaduasensis* Anderson is also thought to be close to *V. crenocarina*. The other fossil species dealt with herein have more acute spires but are assigned to *Verena* because they possess the ramp, spiral sculpture, apertural features and growth lines typical of the genus.

Verena crenocarina (S. Moricand, 1841) Figs 269–272

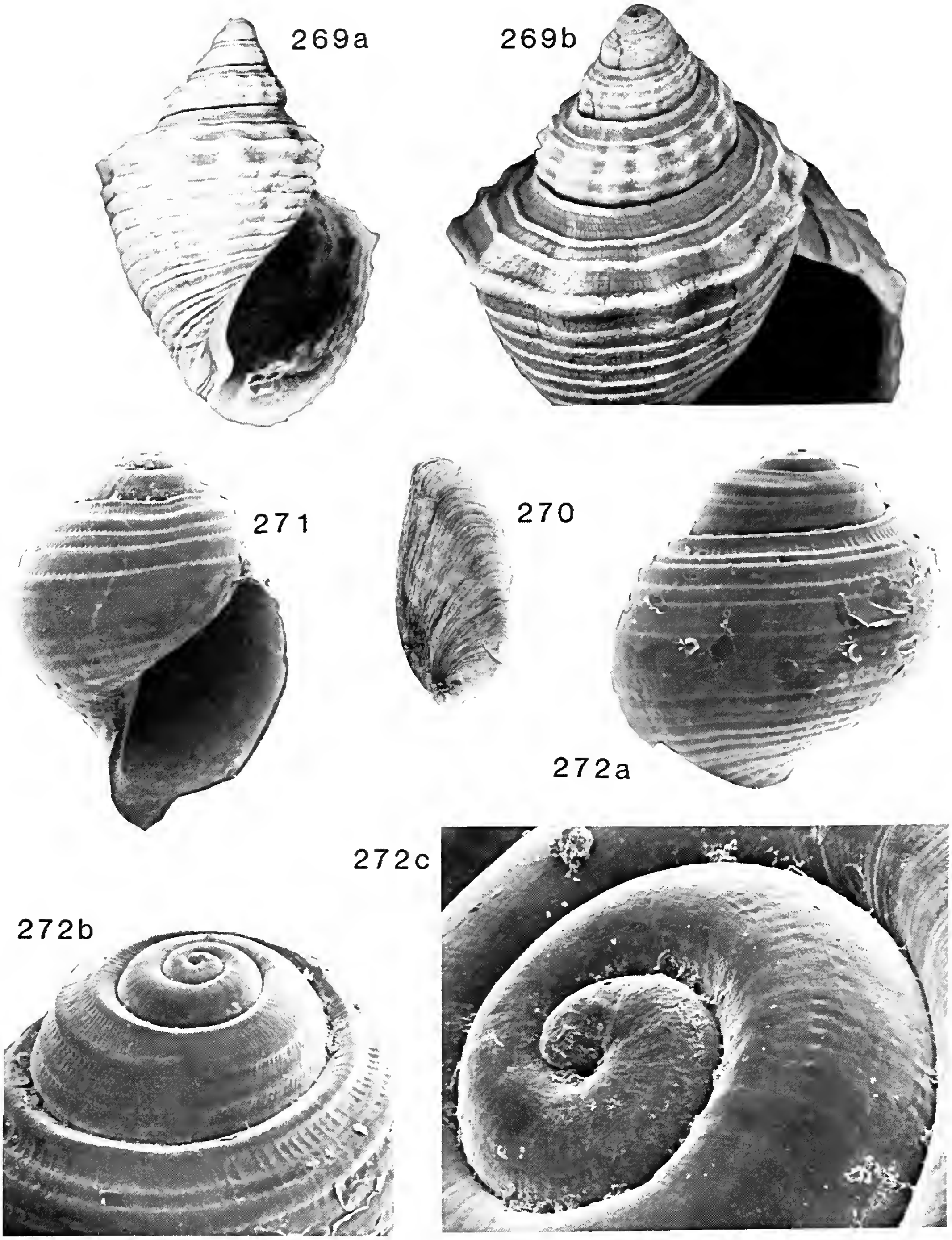
* 1841 *Melanopsis crenocarina* S. Moricand: 61; pl. 4, figs 10, 11.
*? 1844 *Melania cingulata* Jonas: 51.
. 1847 *Melania crenocarina* (Moricand) Philippi: 174; pl. 4, fig. 14.
. 1854 *Verena crenocarina* (Moricand) H. & A. Adams: 308.
. 1859 *Verena crenocarina* (Moricand); Chenu: 296, fig. 2055.
. 1860 *Hemisinus crenocarina* (Moricand) Reeve: pl. 4, fig. 19.
. 1878 *Hemisinus crenocarina* (Moricand); Brot: 378; pl. 41, figs 4, 4a.
. 1902 *Hemisinus crenocarina* (Moricand); von Ihering: 667.
? 1924 *Purpura woodwardi* Roxo: 49; pl. 1, figs C, C′, D.
. 1954 *Aylacostoma (Verena) crenocarina* (Moricand) Morrison: 377.
. 1967 *Aylacostoma (Verena) woodwardi* (Roxo) Santos & Castro: 414, figs 1–3.

MATERIAL STUDIED. All Recent, Brazil; 5 shells, Para (BMZD1984218); 3 shells, Brazil (BMZD 1984219); 3 shells (+ 2 embryonic shells extracted from adults, 1982), Brazil, Cuming Colln (BMZD1984220/1–5).

FURTHER RECORDS. Recent: type locality, Rio de Pedra Branca, Bahia Province, Brazil (Moricand, 1841). Fossil: Late Caenozoic, Pebasian; Três Unidos, Peruvian bank of Rio Javari (?Roxo, 1924; ? Santos & Castro, 1967).

DIAGNOSIS. Large stout *Verena* with spire angle of up to 80°; shoulder distinctly coronate; spiral sculpture of up to two ribs on ramp, two more below carina on spire whorls and 14 ribs on last whorl; collabral sculpture of about twelve folds per whorl; operculum filling two-thirds aperture.

DESCRIPTION. The shell is stout. The spire angle increases from about 60° to 80° with growth as the rather crenulate carina at the shoulder increases in strength. The apex is known only from two embryonic shells obtained by washing out an adult specimen (BMZD Cuming Colln). The apices of all adults are missing. The embryonic shells are ficiform and reminiscent of the genus *Tonna* both in shape and ribbing. The two earliest whorls are smooth and much broader than high. Up to four spiral ribs are developed by the third whorl. The adapical rib is strong and separated from the previous whorl by a canaliculate suture. The other ribs are weaker and more rounded. On the last whorl present in these embryonic shells, up to eight spiral ribs may occur: these die out below the periphery. The early whorls of adult shells are strongly convex with the periphery at their lower suture, and their ribbing pattern is basically similar to that on the preceding embryonic whorls. The canaliculate suture develops into a subsutural shelf which does not increase in strength with growth. The rib below it forms an incipient shoulder. This is the strongest and most angular of the spiral ribs and is separated from the suture by a concave interspace. Below this rib, three or four spiral bands are separated by narrow grooves. On later whorls, the second rib below the suture strengthens to form the carinate shoulder. Eventually, one or rarely two less prominent additional ribs are developed on the ramp. The (usually two) ribs below the shoulder become stronger and further apart. On the body whorl up to about 14 spiral ribs are present. Some are of secondary strength, but their arrangement appears haphazard, the common pattern of alternating primary and secondary ribs being absent. The collabral sculpture, consisting of 10 – 12 folds per whorl, is comparatively weak. It is strongest near the shoulder, thus making the spiral ribs crenulate, with the carina at the shoulder being the most strongly affected. A shallow sinus is present on the ramp: below the shoulder the growth lines are prosocyrt. The aperture is broad and notched below. The columellar callus is weak and the parietal callus above it is increasingly so. The aperture is smooth within except for impressions of the external spiral ribbing close to the mouth itself. The shell is covered with dark brown periostracum. The inside of the aperture may be brown, white, or in one case, is white with two brown bands. The operculum is present in only one BMZD shell, and fills two-thirds of the aperture.



Figs 269–272 *Verena crenocarina* (S. Moricand). Recent, Brazil. **269**, BMZD 1984218; Para, history unknown. a, front, × 2; b, oblique view showing sculpture, × 4. **270**, BMZD 1903.2.4.1784; operculum; × 3. **271**, BMZD 1984220/2; embryonic shell extracted from an unfigured specimen (BMZD 1984220/1) in the Cuming Colln sample which contains the shell figured by Reeve (1860: pl. 4, fig. 16); front, × 20. **272**, BMZD 1984220/3; second embryonic shell extracted from same Cuming Colln sample. a, rear, × 20; b, oblique view of apex and early spire whorls, × 30; c, oblique view of apex, × 100.

273

274

275

276

igs **273–276** *Verena crenocarina ava* (Pilsbry & Olsson). La Cira Formation, probably Miocene; Middle Magdalena Valley, Colombia. **273**, ANSP 13079a, **lectotype** (herein selected) of *Hemisinus (Verena) laevicarina* Pilsbry & Olsson; oblique view of spire with shell axis rotated through about 90° anticlockwise compared with Pilsbry & Olsson (1935: pl. 3, fig. 10); Rio Oponcito, near Guanabanus; × 3. **274–276**, ANSP, unregistered; casts of external moulds in decalcified mudstone of *Hemisinus (Verena) ava* Pilsbry & Olsson, from type locality, near Zopffs; × 3.

IMENSIONS. In mm.	h	br	hap	h/br	sa
MZD, Para	*34.6	26.7	23.5	–	–
MZD, Para	*35.2	25.4	23.0	–	–
MZD, Para	31.2	22.9	22.9	1.36	78°
MZD, Cuming Colln.	22.1	15.7	15.7	1.41	–

= decollated or otherwise extensively damaged.

EMARKS. *Verena crenocarina* (S. Moricand) is not only the ype but also the only living species known of the genus. The lustrations (Roxo 1924, Santos & Castro 1967) of *Purpura oodwardi* suggest that it is conspecific with *V. crenocarina*, nd there can be no doubt it was correctly assigned to *Verena* y Santos & Castro. The relationship between *V. crenocarina*, *str.* and *V. crenocarina ava* (Pilsbry & Olsson) is discussed nder the latter, below. *V. guaduasensis* (Anderson) (p. 256) also very similar to both these subspecies. Other fossil ecies of *Verena* are all more acicular.

erena crenocarina ava (Pilsbry & Olsson, 1935)

Figs 273–276

v. 1935 *Hemisinus (Verena) avus* Pilsbry & Olsson: 15; pl. 3, figs 6, 7.
v 1935 *Hemisinus (Verena) laevicarina* Pilsbry & Olsson: 15; pl. 3, figs 10–12.
1969 ? *Pyrgulifera avus* (Pilsbry) [*sic*] Parodiz: 140; pl. 15, figs 8, 9.
1969 *Aylacostoma (Verena) laevicarina* (Pilsbry & Olsson) Parodiz: 145; pl. 15, figs 13, 14.

ECTOTYPE of *H. (V.) avus*, selected herein: ANSP 13071a, iginal of Pilsbry & Olsson (1935: pl. 3, fig. 7), a broken ould in decalcified mudstone, ? Miocene, La Cira Formation, ar Zopffs, La Cira District, Colombia (W. Waring Colln). umerous broken moulds ANSP 13071, with *Doryssa* and *chydon* in decalcified mudstone, are paralectotypes: they include the specimen described by Pilsbry & Olsson (1935: 15) as an aberrant form and figured by them (pl. 3, fig. 6). Details as for lectotype. The lectotype of *H. (V.) laevicarina*, selected herein, is ANSP 13079a, the original of Pilsbry & Olsson (1935: pl. 3, fig. 10), ? Miocene, La Cira Formation, Rio Oponcito near Guanabanus, Colombia (A. A. Olsson & E. La Tour Colln). The two shells ANSP 13079, figured by Pilsbry & Olsson (1935: pl. 3, figs 11, 12), are paralectotypes. No other material.

DISTRIBUTION. ?Miocene, La Cira Formation, Colombia only.

DIAGNOSIS. Like *V. crenocarina crenocarina*, but smaller, and lacking strong crenulations on the carinate shoulder, with less concave ramp, and slightly more acute spire with spire angle of 65°–70°.

DESCRIPTION. The early whorls are convex; the carinate shoulder and concave ramp above it develop later, as in *V. crenocarina*, *s.str.* (S. Moricand). The spiral sculpture is variable. The illustration of the lectotype of *V. crenocarina ava* (Pilsbry & Olsson 1935: pl. 3, fig. 7) shows three strong spiral ribs on the spire whorls and ten on the body whorl, separated by wide interspaces. On other moulds it appears to consist of rather broad convex bands separated by fairly narrow interspaces. The collabral sculpture is comprised of up to twenty folds per whorl. These appear to be formed by the bunching of the growth lines.

DIMENSIONS. In mm.	h	br	sa
Lectotype of *V. crenocarina ava*, ANSP 13071a	12.0	7	70°
Lectotype of *V. laevicarina*, ANSP 13079a	17.5	11	65°

Note. Dimensions of these incomplete specimens are from Pilsbry & Olsson (1935), and were apparently quoted to the nearest 0.5 mm. The spire angles are from their illustrations.

REMARKS. Neither Pilsbry & Olsson's (1935) text nor their extensively retouched and cut-out illustrations suggest that the type material of *Hemisinus (Verena) avus* consists of numerous broken moulds associated with *Longiverena* and *Pachydon* in blocks of decalcified mudstone.

Parodiz (1969: 140) tentatively assigned this species to *Pyrgulifera* but re-examination of this material establishes that the original placement of it in *Verena* was correct. *V. laevicarina* from the same formation appears to be synonymous. Its type material consists of worn, semi-decorticated, shells in a coarse sandstone. The very strongly carinate shoulder appears to be a preservational feature and traces of spiral ribbing typical of *Verena* may be seen on these specimens. None of the available specimens of *V. crenocarina ava* attains the size of the very similar living *V. crenocarina, s.str.* Several apparent differences such as spire angle and whorl profile are features which appear to change with growth. At present the two are treated as being distinct, with *V. crenocarina, s. str.* being distinguished by its less crenulate carina at the shoulder.

Verena guaduasensis (Anderson, 1928) Fig. 277

*v 1928 *Ampullaria guaduasensis* Anderson: 23; pl. 1, figs 19, 20.
. 1977 *Pomacea quaduasensis* (Anderson) [*sic*] Boss & Parodiz: 109.

HOLOTYPE. CAS 2721, 'Eocene . . . Guaduas Beds, near San Juan de Rio Seco, upper valley of Rio Magdalena' (Anderson 1928). This is probably Santa Teresa Formation of late Oligocene to early Miocene age, possibly at km 106, Cambao to Bogotá highway (Butler 1939, 1942; Porta 1966). No other material.

Fig. 277 *Verena guaduasensis* (Anderson). CAS 2721, internal mould; holotype of *Ampullaria guaduasensis* Anderson, figured by Anderson (1928: pl. 1, figs 19, 20), originally described as being from the supposedly Eocene Guaduas Beds from near San Juan de Rio Seco, but probably from the late Oligocene or early Miocene Santa Teresa Formation at km 106 on the Cambao to Bogotá Highway. Front, × 2.5.

DIMENSIONS. h, 20.6 mm; br, 15.1 mm; sa, *c.* 80°.

REMARKS. The unique holotype is an internal mould to which some shell material still adheres. Its shape and apertural features justify its assignment to *Verena*, and it may indeed belong to either *V. crenocarina, s.str.* (S. Moricand) or its subspecies *V. crenocarina ava* (Pilsbry & Olsson), although no decision can be reached in the absence of any details of shell sculpture. The age was given as Eocene by Anderson, but is here redated as probably Miocene, or at the earliest, late Oligocene. Boss & Parodiz (1977: 109) placed this species in *Pomacea*, a member of the Ampullariidae, and suggested that the age might be Pleistocene. Both this reidentification and their age determination appear to be completely without justification.

Verena browni (Etheridge, 1879) Figs 278–282

* 1879 *Melanopsis? browni* Etheridge: 87; pl. 7, fig. 4.
. 1924 *Melanopsis? browni* Etheridge; Roxo: 46.
. 1969 *Aylacostoma sulcatus* (Conrad) Parodiz: 141 (*pars*); pl. 14, figs 6, 7.
. 1981 *Aylacostoma (Aylacostoma) browni* (Etheridge) Costa: 644; pl. 1, figs 11, 12.

TYPE MATERIAL. Described by Etheridge from the Late Caenozoic, Pebasian, Canamá. Whereabouts of specimens unknown.

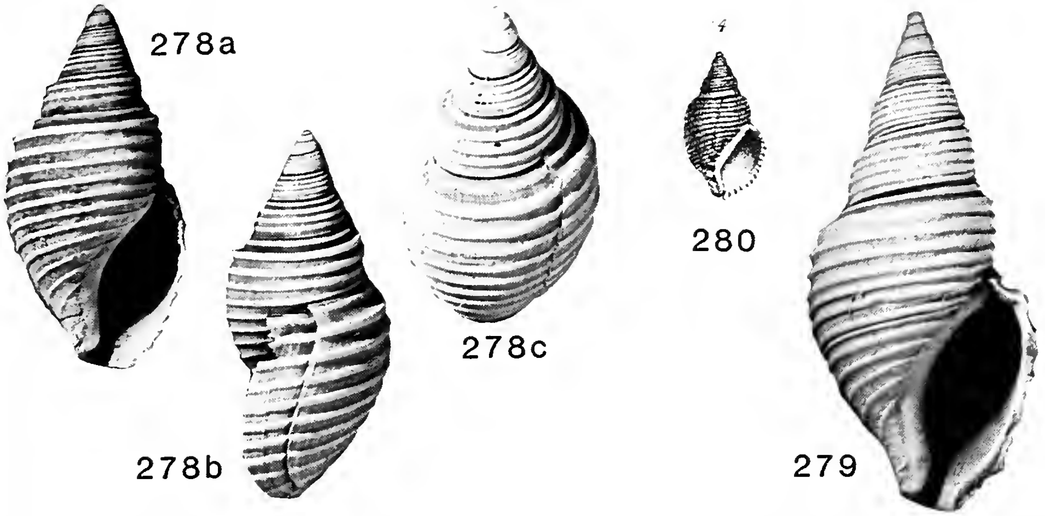
MATERIAL. BMPD GG19895–9, GG19916–7 (about fifty shells), Late Caenozoic, Pebasian; Puerto Nariño (Weeda Colln); studied. Otherwise recorded from Pebasian of Canamá (Etheridge 1879) and of Três Unidos (Roxo 1924, Parodiz 1969, Costa 1981). Late Caenozoic, Pebasian only; Upper Amazon Basin, Peru, Colombia.

DIAGNOSIS. Narrow *Verena* up to 25 mm high; spire angle 45°–55°; ramp, not very prominent, bordered by strong subsutural cord and another on shoulder; about three further strong cords visible on spire whorls and up to ten on final whorl; collabral sculpture lacking except for growth lines.

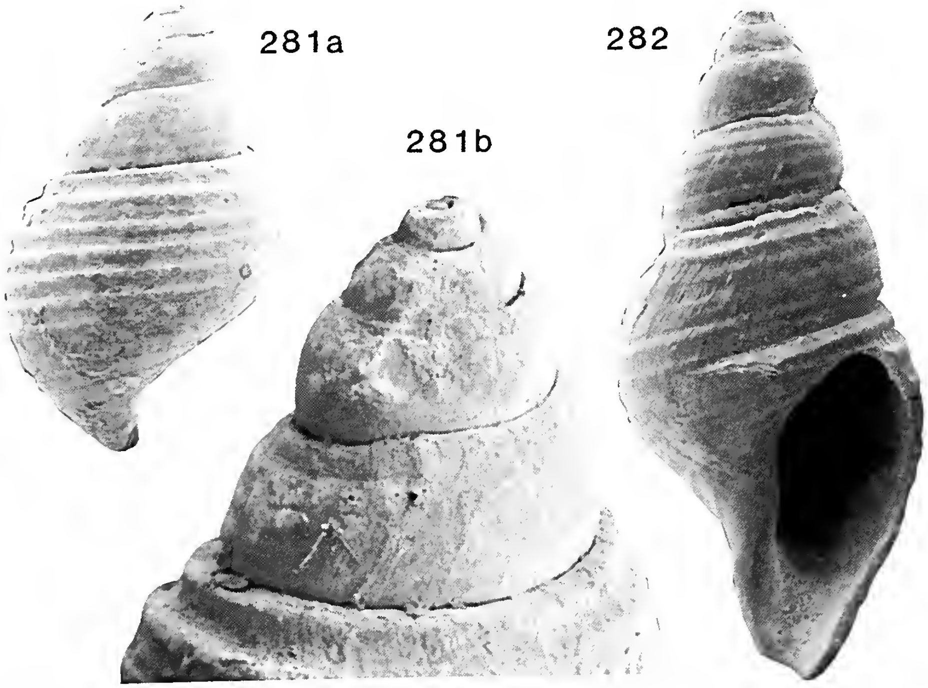
DESCRIPTION. There are up to ten convex whorls whose peripheries lie at, or just above, the suture. The concave ramp first appears on the fourth or fifth whorl and is not prominent until at least two whorls later. Its slope varies from almost horizontal to about 20° from the vertical. The first three or four whorls form a smooth apex ornamented only by strongly opisthocyrt–opisthocline growth lines. For the first whorl or so, the apex is almost planorbiform as in the living species of Hemisininae examined herein.

Spiral sculpture first appears on the third or fourth whorl as grooving. Within a whorl or so, the grooves become broader than the intervening cords and the adult sculptural pattern comes into being. The cords are rounded in section. The subsutural cord is of variable strength and juts out from the suture to give the ramp a stepped appearance. The strongest cord is that at the shoulder. Rare secondary spirals occur in some specimens. Very weak spiral striae may be seen, forming a reticulate pattern with the stronger growth lines. The growth lines are strongly prosocyrt except for a sinus developed below the suture. This leads those on early whorls, in particular, to be weakly sinusigeral in appearance. The aperture is typical of the genus and is virtually smooth within, with columellar callus obscuring nearly all traces of spiral sculpture. A definite posterior channelling or notch is developed.

DIMENSIONS. In mm.	h	br	hap	h/br	sa
Etheridge 1879: pl. 7, fig. 4.	19.5	12.5	11.4	1.56	50°
Parodiz 1969: pl. 14, fig. 6.	22.8	12.4	14.0	1.84	60°
Costa 1981: pl 1, fig. 11.	–	–	–	2.15	47°
GG19917	23.0	10.2	10.2	2.24	43°
GG19895	12.9	6.3	6.3	2.04	47°



igs 278–280 *Verena browni* (Etheridge). Pebasian. **278**, GG19895; Puerto Nariño, Colombia; Weeda Colln. a, b, c, front, side, and oblique iews, all × 4. **279**, GG19917; same details as Fig. 278; front, × 4. **280**, copy at original size of Etheridge's type illustration (1879: pl. 7, fig. 4); Canamá, Peru. Magnification not exactly known.



gs 281–282 *Verena browni* (Etheridge). Pebasian; Puerto Nariño, Colombia; Weeda Colln. **281**, GG19916; a, rear, × 20; b, slightly oblique view of early spire whorls and apex, × 40. **282**, GG19986; front, × 20.

EMARKS. Etheridge's type material from Canamá was never nong those specimens presented to the BM by him and gistered in 1879. As the original illustration is poor and the esent material does not come from the type locality, it ems inadvisable to select a neotype. Some doubt as to the rrectness of the present identification must remain as rather nilar species occur at La Tagua (*V. lataguensis* sp. nov., p. 8) and in the Cuenca Basin (herein determined as *V.* sp. . *browni*). Furthermore, Etheridge's rather poor illustra- n is of a comparatively stout shell (see dimensions). The fact that Canamá lies in the same general area as Três Unidos and Puerto Nariño may be taken as evidence in favour of the determination being correct.

The newly collected material from Puerto Nariño is clearly conspecific with the shell figured by Parodiz (1969) as *Aylocostoma sulcatus* Conrad from Três Unidos. Parodiz later (Bristow & Parodiz 1982: 49) recognized that the Três Unidos material, referred to by Roxo (1924) and independently redescribed by Costa (1981), belonged to *browni* rather than *sulcatus*.

Parodiz also (Brown & Parodiz 1982: 48) reidentified as *Aylacostoma browni* specimens figured by de Greve (1938: pl. 4, fig. 18 and text-fig. 19) as *Semisinus sulcatus* (Conrad). De Greve's text-fig. 19 is of *Liris tuberculata* de Greve whilst his pl. 4, fig. 18 is herein reassigned to the living *Hemisinus kochi* (Bernardi 1856): see p. 240.

Material from the Cuenca Basin identified by Parodiz (*in* Bristow & Parodiz 1982: 48) as *Aylacostoma browni* is herein identified as *Verena* sp. aff. *browni*. The distinctions between *V. browni* and *V. lataguensis* sp. nov. are dealt with under the latter.

Fig. 283 *Verena* aff. *browni* (Etheridge). Miocene, Mangán Formation; Loc. CRB 42c, Cuenca Basin, Ecuador; Bristow Colln; rear, × 3.

Verena sp. aff. *browni* Fig. 283

v 1982 *Aylacostoma browni* (Etheridge); Parodiz *in* Bristow & Parodiz: 48, fig. 22.

MATERIAL. All Mangán Formation, Miocene, Cuenca Basin, Ecuador: BMPD GG19867/1–4, Loc CRB 42c; GG19868/1–2, Loc. CRB 36a; studied. Other material in Carnegie Museum, CM 46804 (20 specimens), CRB 42 (as above) (Bristow & Parodiz 1982: 49).

REMARKS. Parodiz identified the material both in Carnegie Museum and BMPD as *A. browni* and this is presumably the source of the identifications in faunal lists given in Bristow & Parodiz (1982: 10, 14). Several of these records, however, are not given in their systematic account (1982: 48–49). Neither the material in BMPD studied herein nor Parodiz' fig. 22 are of true *V. browni*. They are of a species with variable but generally lighter spiral sculpture and with a broader ramp. It also lacks the strong spiral rib which forms a subsutural collar in *V. browni*. One BMPD specimen, GG19869, may be the source of their record (1982: 10) of the species from the Loyola Formation (CRB 18b); it is very poorly preserved but does not appear to be a *Verena*.

Verena lataguensis sp. nov. Figs 284–285

HOLOTYPE. GG19920, Late Caenozoic; CAE 33/480–560 cm, La Tagua (Eden Colln). G19921–2, same data, and GG19923, CAE 33/560 cm, are paratypes.

NAME. From locality of La Tagua.

DIAGNOSIS. Small aciculate *Verena* with spire angle of about 35°; narrow concave ramp present; delicate spiral sculpture of six to eight sharp ribs below angular shoulder on spire whorls and between twelve and twenty ribs present on final whorl. Collabral sculpture lacking.

DESCRIPTION. All the specimens are incomplete and partly crushed. Examination of GG19922, the only shell with early whorls present, suggests that a complete adult would be of nine to ten whorls. A subsutural collar is of variable strength but never prominent. The ramp is otherwise smooth, narrow and strongly concave. The carina at the shoulder is no stronger than other spiral ribs. Below the shoulder there are 6 – 8 spiral ribs on spire whorls, and 12 – 20 on the final whorl. The ribs are always fine but are separated by interspaces which vary from about as thick as one rib (in the holotype) to over twice as wide (in paratype GG19921). Collabral sculpture is absent except for growth lines. These are typical of *Verena*, with a sinus developed on the ramp and of prosocyrt form below the shoulder. The apertures of all specimens are damaged. In the holotype weak callus is developed along the entire length of the aperture.

DIMENSIONS. In mm.	h	br	hap	hbw	sa
Holotype, GG19920	9.0	5.3	4.6	7.4	*c*. 35°
Paratype, GG19921	9.1	6.0	5.8	8.8	–

Note. The above dimensions (h, hbw) indicate that little of the shell above the body whorl is present in these specimens. Spire angle measurement is only meaningful in the case of the holotype.

REMARKS. This species differs from *V. browni* Etheridge in being smaller and in having much finer and more numerous spiral ribs. It also appears to have a more acute apical angle. It is also similar to *Verena* sp. aff. *browni* from the Cuenca Basin. This is also rather acicular but has fewer and stronger ribs. The other known species of *Verena* all have much stouter shells.

Hemisinus barloventoensis Macsotay (1968: 301; pl. 1, figs 6, 7, 9, 10) from the Miocene of Venezuela is very similar. It may be distinguished, however, by its much more noticeable ramp, which accounts for nearly half the height of the spire whorls. This gives its shell a distinctly turreted, or stepped, appearance.

Genus *AYLACOSTOMA* Spix, 1827

[= *Aulacostoma* Agassiz, 1846: 10, unjustified emendation; no species mentioned].

TYPE SPECIES. *Aylacostoma glabrum* Spix, 1827, by subsequent designation of Morrison (1954: 376). Recent, Brazil.

DIAGNOSIS. Acicular, with pronounced ramp and shoulder developed on last whorl or so; spiral sculpture weak, mainly of grooving tending to be concentrated on ramp; collabral sculpture virtually absent; aperture notched below; operculum auriculate, approximately half whorl of rapidly expanding spiral.

OTHER SPECIES ASSIGNED. Fossil: *Aylacostoma* sp., Mangán Formation, Miocene; Ecuador; see p. 261. Distribution Neogene and Recent, northern and central South America.

Figs 284–285 *Verena lataguensis* sp. nov. Late Caenozoic; Loc. 33/480–560, La Tagua, Colombia; Eden Colln. **284**, GG19920, **holotype**; a, b, front, rear, × 5. **285**, GG19921, paratype; a, b, front, rear, × 5.

REMARKS. Morrison's designation of the type species (1954: 376) was: 'Genotype: (*Aylacostoma glabrum* Spix)= *Aylacostoma (Aylacostoma) scalare* (Wagner) 1827'. Parodiz (1969: 141) follows this almost exactly but attributes the designation to Morrison (1952): this is an abstract of a meeting report which I have not seen and may be invalid. A previous type designation by Cossmann (1909: 126) was: Genotype *Aulacostoma scalaris* Spix'. This is not accepted here as valid because *scalaris* – a Wagner name – was not one of the species names originally used in conjunction with *Aylacostoma*. In any case *Melania scalaris* Wagner is here egarded as a junior objective synonym of *Aylacostoma glabrum* Spix. Similar treatment is accorded herein to all other new names proposed by Wagner (1827) for species amed by Spix in the illustrations of their joint work.

Aylacostoma and *Aulacostoma* were placed in the synoymy of *Hemisinus* Swainson, 1840, by both Thiele (1929: 01) and Wenz (1939: 718). As *Aylacostoma* is valid and has riority over *Hemisinus*, such an arrangement is unacceptble. One other species, *Aylacostoma tuberculata* Spix, was riginally assigned to the genus, and is the type species of *Longiverena* Pilsbry & Olsson 1935 (see p. 246). Adams & Adams (1854: 291) listed nine living species, including *A. scalare* but not *A. tuberculata*, as belonging to *Aylacostoma*. In spite of this, the type species is probably the only living representative of the genus.

ylacostoma glabrum Spix, 1827 Figs 286–291

v 1827 *Aylacostoma glabrum* Spix: pl. 8, fig. 5.
v 1827 *Melania scalaris* Wagner: 15.
1854 *Aylacostoma scalaris* (Wagner) H.&A. Adams: 299.
1859 *Aylacostoma scalaris* (Wagner); Chenu: 289, fig. 1966.
v 1860 *Hemisinus behni* Reeve: pl. 2, figs 8a–f.
v 1860 *Hemisinus tenuilabris* (*ex* Behn MS) Reeve: pl. 5, figs 22a, b.
1878 *Hemisinus brasiliensis* (Moricand); Brot: 392 (*pars*: 'var.' = *Melania scalaris* Wagner).
1878 *Hemisinus behni* Reeve; Brot: 383; pl. 39, figs 12, 12a–c.
1878 *Hemisinus tenuilabris* Behn (= Reeve); Brot: 384; pl. 40, figs 1, 1a.
1902 *Hemisinus behni* Reeve; von Ihering: 674.
1902 *Hemisinus tenuilabris* Reeve; von Ihering: 688, fig. 4.
. 1902 *Hemisinus tenuilabris* Reeve 'var. nov.' *araguayana* von Ihering: 669, fig. 5.
. 1954 *Aylacostoma (s.str.) glabrum* Spix = *scalare* (Wagner); Morrison: 376.
. 1983*a* *Aylacostoma glabrum* Spix = *Melania scalaris* Wagner; Fechter: 222.

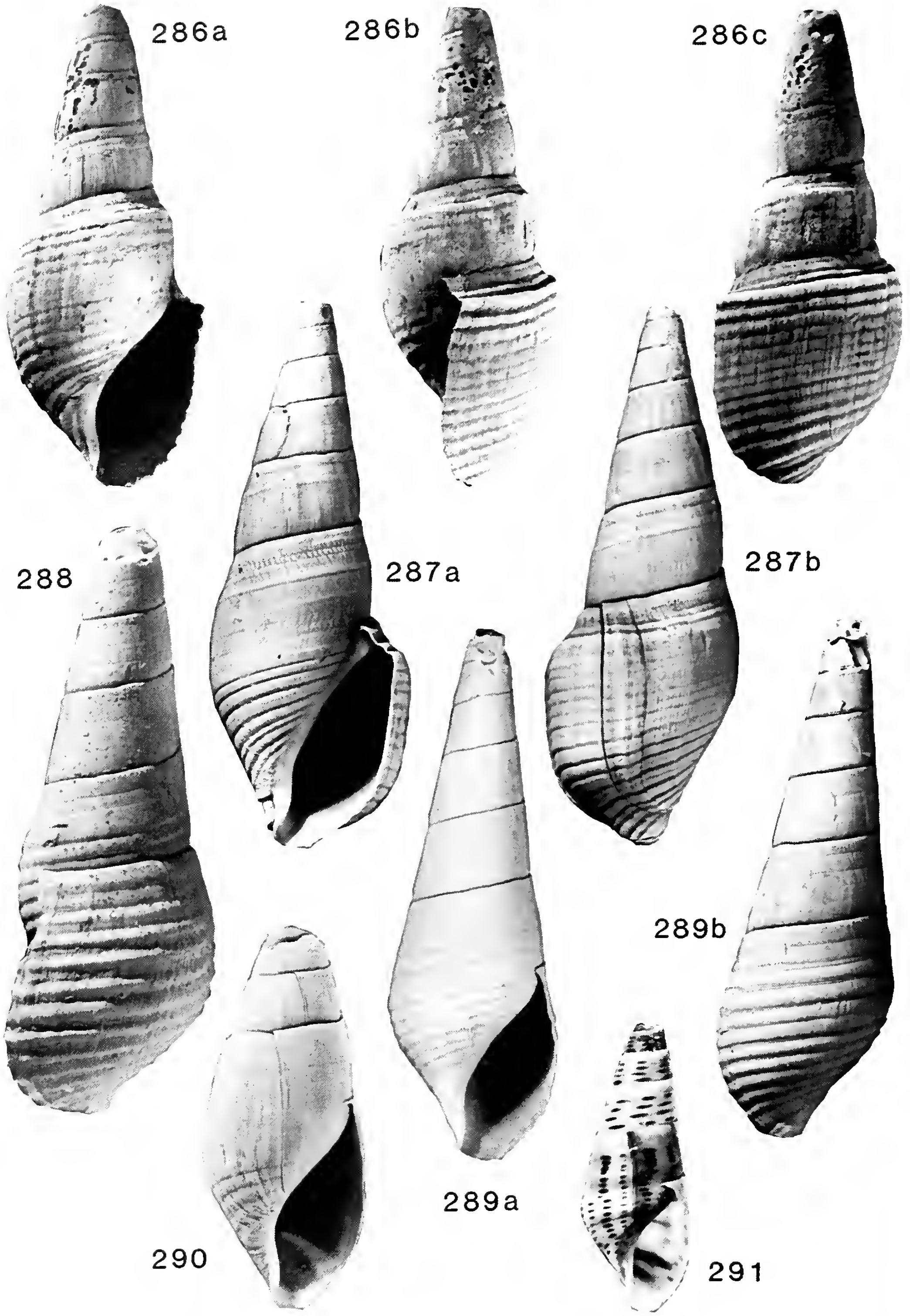
HOLOTYPE of *Aylacostoma glabrum* Spix, = holotype of *A. scalaris* (Wagner), Zool. Staatsmus. München, figured Spix (1827). Recent, Mandiocca, St Sebastian Province, Brazil. Also studied: the lectotype of *Hemisinus behni* Reeve, selected herein, figured Reeve 1860: pl. 2, figs 8a, b. The two accompanying shells (pl. 2, figs 8c, d, e, f) are paralectotypes. All Recent, Pernambuco, Brazil (Cuming Colln, BMZD 1984221). Also the lectotype of *H. tenuilabris* Reeve, selected herein, figured Reeve 1860: pl. 5, figs 22a, b; the two accompanying shells are paralectotypes. All Recent, Brazil (BMZD 1984222). Also 15 shells from Recent of Rio Grande Franca, São Paulo Province, Brazil, identified by von Ihering (1902) as belonging to three 'varieties' of *H. tenuilabris* 'Behn' (BMZD 1903.12.5.1–15).

DISTRIBUTION. Recent, eastern Brazil only.

DIAGNOSIS. *Aylacostoma* with tall straight-sided spire. Ramp and shoulder variable, developed only on whorls more than 25 mm below apex. Apical angle of spire whorls 25°, increasing to about 30° by final whorl. Spiral sculpture developed on later whorls only, otherwise almost smooth except for subsutural grooving and slight bunching of growth lines; growth lines only slightly sinuate.

DESCRIPTION. All the specimens are decollated. Up to five spire whorls are almost straight-sided, having very weakly incised sutures. The final whorl and sometimes part of the penultimate whorl is variable. It may be strongly shouldered with a marked ramp, as in the holotype of *A. glabrum*, the lectotype of *A. behni* and some of the BMZD specimens identified as *H. tenuilabris* 'var.' by von Ihering. In other specimens, including the type series of *Hemisinus tenuilabris* Reeve, it remains almost straight-sided above the periphery. Intermediates exist between these two extremes. The early whorls are virtually smooth except for weakly opisthocyrt growth lines which tend to become bunched, as on the body whorl of the holotype of *A. glabrum* itself.

Spiral sculpture varies considerably. Grooves separate rather broad, convex bands on the body whorl of large specimens, with the strongest sculpture occurring below the periphery. Comparatively small specimens, including the type



Figs 286–291 *Aylacostoma glabrum* Spix. Recent, Brazil. **286**, holotype in Zool. Staatsmus. München; figured by Spix (1827: pl. 8, fig. 5); Mandiocca, St Sebastian Province. a, b, c, front, side, rear, all × 2.5. **287–289**, *Hemisinus behni* Reeve. Pernambuco (= Recife); Cuming Colln. **287**, BMZD 1984221; **lectotype** (selected herein), figured by Reeve (1860: pl. 2, figs 8a, b). a, b, front, rear, × 2. **288**, BMZD 1984221 paralectotype, figured by Reeve (1860: pl. 2, figs 8c, d); side, × 2. **289**, BMZD 1984221; paralectotype, figured by Reeve (1860: pl. 2, figs 8e f). a, b, front, rear, × 2. **290**, BMZD 1984222; **lectotype** (selected herein) of *Hemisinus tenuilabris* Reeve, figured by Reeve (1860: pl. 5, fig 22a, b); Brazil; Cuming Colln; front, × 2. **291**, BMZD 1903.12.5.7; small shell of '*H. tenuilabris* Reeve' with periostracum removed with bleach to show colour patterning; Saõ Paulo, from H. von Ihering; front, × 2.

series of *Hemisinus tenuilabris* Reeve, are virtually smooth except for this last feature. The growth lines remain weakly sinuate even on the body whorl and no proper sinus is developed in the region of the ramp. Callus on the inner lip is comparatively weak, even in the largest specimens. The basal apertural notch is easily seen.

Two opercula were found loose with the three shells in the type series of *H. behni* Reeve. They are both about 11 mm high and 5 mm broad, and presumably belonged to shells whose apertures measured about 18 × 9 mm.

Dimensions. In mm.	h	br	hap	hbw	h/br	eh/br	sa
Holotype of *A. glabrum* Spix	*30.6	12.8	12.4	18.6	2.4	3.0	24°–30°
Lectotype of *A. behni* Reeve	*45.8	16.9	18.7	28.5	2.7	2.8	25°–28°
Lectotype of *A. tenuilabris* Reeve	*29.8	13.8	17.4	23.0	2.2	2.9	22°

* = decollated or otherwise badly damaged.

Remarks. Sample BMZD 1903.12.5.1–15, identified by von Ihering, contains shells resembling the types of all three nominal species included in this synonymy. Brot's (1878: 392) placement of *Melania scalaris* Wagner and *A. glabrum* Spix in the synonymy of *Hemisinus brasiliensis* Moricand is without foundation. His illustrations (1878: pl. 40, fig. 12, 12a–c) of *H. brasiliensis* are correctly identified, but none of his illustrations are of shells resembling *A. glabrum*.

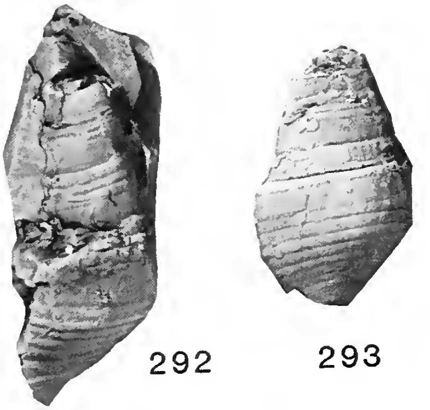
Aylacostoma sp. Figs 292–293

v 1982 *Aylacostoma* sp. Bristow & Parodiz: 49.

Material studied. BMPD GG19866/1–3, CRB 42, Miocene, Mangán Formation; Cuenca Basin, Ecuador. No other record.

Description. Because of crushing and other damage the apical angle cannot be measured properly, but it probably lies between 30° and 35° in this rather acicular species. Both GG19866/2 and the reverse side of GG19866/1 show the ramp and semi-angular shoulder typical of *Aylacostoma*. The spiral sculpture is variable and consists of grooves with rather wide interspaces. On GG19866/1 the grooving is concentrated on the ramp and on the neck region of the body whorl, and is absent from the peripheral region. On GG19866/2, grooving is absent only from the ramp. GG19866/3 differs from GG19866/1 in that spiral grooving is developed on the periphery of the last whorl although absent from the peripheral region of spire whorls. Collabral sculpture is absent except for growth lines which are moderately sinuous with only a very weak sinus developed on the ramp. The only apertural features which can be made out are the columellar callus and indications, from the growth lines, of the presence of a basal notch.

Dimensions. In mm.	h	eh	br	sa
GG19866/1	22.6	30.0	9.5	–
GG19866/2 (laterally crushed)	18.3	23.5	11.2	–



Figs 292–293 *Aylacostoma* sp. Miocene, Mangán Formation; Loc. CRB 42, Cuenca Basin, Ecuador; Bristow Colln. **292**, GG19866/1. **293**, GG19866/2. Both × 2.

Remarks. This material is part of the sample from CRB 42 from which Bristow & Parodiz (1982) also identified *A. sulcatus* (Conrad). These other specimens are discussed under *Hemisinus* sp. The present specimens are here assigned to *Aylacostoma*, because of the definite ramp and shoulder which are first developed at a much smaller shell size than in the living *A. glabrum* Spix. In the latter the spiral sculpture also tends to be rather variably developed. No comparable fossil species are known.

Subclass **PULMONATA** Cuvier, 1834
Order **BASOMMATOPHORA** Keferstein, 1864
Superfamily **LYMNAEACEA** Blainville, 1825
Family **FERRISSIIDAE** Walker, 1917

[Subfamily Ferrissiinae Walker, 1917: 2, *nom. transl.* ?Zilch, 1959: 126]

Genus ? ***HEBETANCYLUS*** Pilsbry, *in* Baker 1914

Type species. *Ancylus moricandi* d'Orbigny, 1837: 355. Recent, Brazil.

Remarks. The supraspecific arrangement of this group has not been fully investigated because of its unimportance in the faunas studied herein. Thiele (1931: 482–3) did not recognize Ferrissiinae Walker and regarded *Hebetancylus* as a section of *Protancylus (Burnupia)* within the Ancylidae. Zilch (1959: 105) placed *Protancylus* (Recent, Celebes) in the Planorbidae, whilst *Burnupia* (Ferrissiidae) has a living South African type species. Zilch's work is possibly the first in which Ferrissiinae are raised to family level. These simple, patelliform, shells exhibit few easily recognized distinguishing features, and Walker placed much reliance on radulae to distinguish between genera. Zilch arranged a number of subgenera, including South American *Hebetancylus*, in the living Tasmanian genus *Ancylastrum* Bourguignat. The present specimen is provisionally assigned to *Hebetancylus* on its similarity in shell shape to illustrations (Zilch, 1959: 127, fig. 418) of the much larger (length 10–12 mm) type species, *H. moricandi* (d'Orbigny). Type material of this species was catalogued (Gray, 1854: 26, species no. 242) as being absent from the

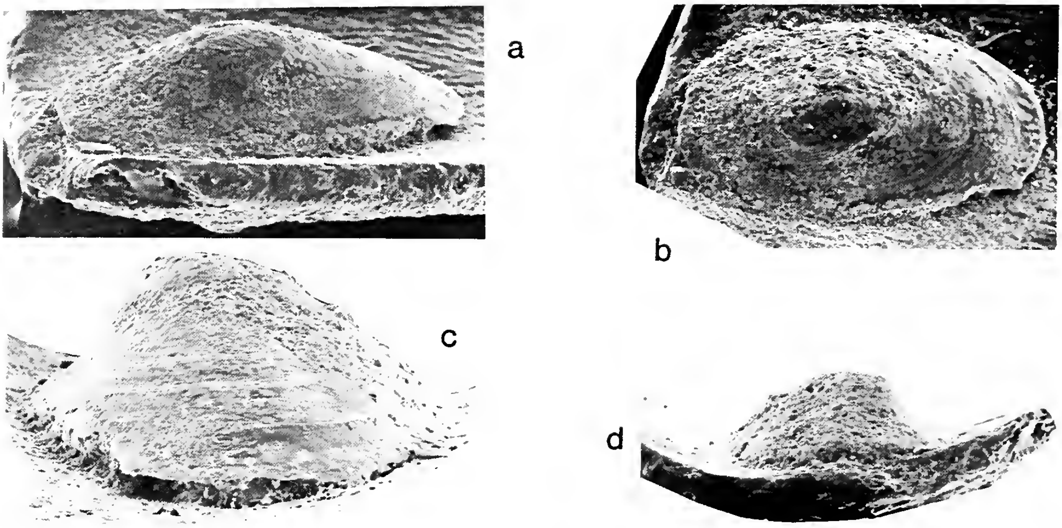


Fig. 294 *Hebetancylus* sp. Pebasian; Pichana, Peru; Hauxwell Colln. GG21570; specimen attached to fragment of bivalve shell. a, right hand side, × 50; b, apical view, × 50; c, front, × 100; d, rear, × 50.

d'Orbigny Collection in BMZD, and no authenticated specimens from other sources are available for comparison in BMZD.

Uncancylus (Pilsbry, 1914) (Recent, Brazil) is radially ribbed and has a pointed apex, whilst the Recent Peruvian *Anisancylus* (Pilsbry, 1924) is more tumid than *Hebetancylus* and its apex is situated near the left margin of the shell.

The present occurrence is thought to be the first definite fossil record of Ferrissiidae from South America. Parodiz (1969: 168) provisionally referred *Ancylus humboldti* Mayer Eymar (1900) from the ?Palaeocene of Chile to *?Palaeoancylus* of the Ancylidae. Willard's (1966: 66) record of the brachiopod *Lingula* in a Pebasian fauna from Negro Urca may possibly be based on a member of the Ferrissiidae, many of which can resemble *Lingula* in shape.

The Ferrissiidae live in fresh water. Pilsbry (1914) recorded *Gundlachia* living on dead leaves and other debris on the bottom of pools.

?Hebetancylus sp. Fig. 294

Material studied. BMPD GG21570, Late Caenozoic, Pebasian; Pichana, Peru. Obtained from washings, 1982, from residues of Hauxwell Colln, 1870. No other records.

Dimensions. l, 1.1 mm; br, 0.6 mm; h, 0.25 mm.

Description. The shell is elongate oval and over twice as long as broad. It is comparatively low, with both the anterior and posterior slopes lying at about 30° from the horizontal. The apex is possibly rather worn and is smoothly rounded. It is situated not far behind mid-shell length and is bent, not very strongly, to the left. Traces of growth lines are visible only on part of the anterior slope.

Remarks. The shell is not sufficiently well preserved to reveal any changes that may have occurred representing any postneanic metamorphosis. This, and its small size, make firm generic determination unwise. The shell adheres, presumably as in life, to a broken fragment of a bivalve, probably *Mytilopsis*.

Order **STYLOMMATOPHORA** Schmidt, 1855
Superfamily **ORTHALICACEA** Albers & von Martens, 1860

[Orthalicea (rank unknown) Albers & von Martens, 1860: 209, *nom. transl.* Burch, 1976: 132 as Orthalicoidea. = Superfamily Bulimulacea Fischer, 1883: 474, as Bulimulidae, *nom. transl.* Thiele, 1931: 651]

Although both Thiele (1931) and Zilch (1960) use the name Bulimulacea for the superfamily, Orthalicacea clearly has priority, as has been recognized in recent years by a few authors (Baker 1956: 133; 1963: 226; Burch 1976: 132) whilst Parodiz (1969: 179) used both names. The early works of Albers & von Martens (1860) and Tryon (1866*a*) were ignored by subsequent authors. In Fischer's (1883) classification, the Bulimulidae and Orthalicidae both had familial rank. Pilsbry (1899: 99; 1902: viii, x, lvii) produced his own classification, apparently in ignorance of Fischer's work, in which the Orthalicinae were placed as a subfamily of the Bulimulidae. This difference in rank of at least one grade has persisted in most later works of substance (Strebel 1909; Thiele 1931; Zilch 1960).

Family **ORTHALICIDAE** Albers & von Martens, 1860

[*nom. transl.* Tryon, 1866*a*: 223; also Fischer, 1883: 473; Taylor & Sohl, 1962: 12]

Genus ***ORTHALICUS*** Beck, 1837

[*Orthalicus* Beck, 1837: 59]

Type species. *Buccinum zebra* Müller, 1774: 138. By subsequent designation of Herrmannsen, 1847: 159, as *Bulimus zebra* Müller, Recent, probably South America. See Remarks, below.

Generic distribution. Recent; tropical South America, Central America, West Indies (Zilch 1960: 514). Southern

Florida, near sea, inferred to be introduced (Pilsbry 1946: 31). Fossil, first record herein: Late Caenozoic, Upper Amazon Basin. [*Orthalicus* is a tree snail.]

DIAGNOSIS. Orthalicidae with a regular bucciniform shell shape; spire angle constant throughout growth, except for a rather obtuse apex; columella, simple, not strongly twisted; shell with microsculpture of spirally and collabrally arranged rows of pits.

REMARKS. No attempt has been made to resolve the designation or identity of the type species of *Orthalicus*. Hermannssen's (1847) designation was of *Bulimus*, not *Buccinum*, *zebra* Müller. Pilsbry (1899: 104) argued that Müller's original description was too vague to be recognizable, though Rehder (1945) suggested that *B. zebra* was probably conspecific with *Orthalicus maracaibensis* Pfeiffer (1856) and *Bulimus undatus* Bruguière (1789). This last-named species was chosen by Zilch (1960: fig. 1795) to illustrate the genus *Orthalicus*.

Parodiz (1969: 179–184) recorded six fossil 'Bulimulacea', including one member of the Orthalicinae, from the Eocene onwards in South America. None resemble the present species, which he did not mention.

Orthalicus linteus (Conrad, 1871) Fig. 295

*v 1871*b* *Bulimus linteus* Conrad: 195; pl. 10, fig. 9.
. 1878 *Bulimus linteus* Conrad; Boettger: 149.

HOLOTYPE. NYSM 9157, Late Caenozoic, Pichana (Hauxwell Colln). No other material studied.

FURTHER DISTRIBUTION. Pebas, two young shells (Boettger, 1878).

DIAGNOSIS. *Orthalicus* with very regularly arranged microsculpture of close-set shallow pits; growth lines not bunched into rugae; spire angle about 50°; columella simple, untwisted, not plicate.

DESCRIPTION. The specimen is damaged, the apex eroded and the last half whorl largely decorticated; about six whorls are present. Although the lower part of the aperture is missing, the internal mould virtually corresponds with the true height of the shell. During fossilization, the external shell of the last and penultimate whorls have been forced apart. Where undamaged, the suture is simple and abutting, and not carinate as Conrad described. The whorl is gently convex in profile and is widest at the abapical suture. With the exception of the apex, which is more obtuse, the spire angle remains constant at about 50° throughout growth. The aperture had been carefully cleaned, presumably by Conrad, but there is no sign of a columellar plication. Traces of thin callus remain on the inner lip. The microsculpture consists of minute shallow pits arranged both spirally and along the prosocline growth lines.

DIMENSIONS. h,40.5 mm; br,25.7 mm; hap,20.8 mm; sa *c.* 50°

REMARKS. Conrad (1871*b*) pointed out that this was the only land snail in Hauxwell's collection from Pichana. The infilling of matrix typical of Pichana shows that it is definitely a fossil specimen. Living species of *Orthalicus* that I have examined possess a similar type of microsculpture but, in all cases, it is both much coarser and more irregular than in *O. linteus*. In addition, their growth lines are frequently bunched into rugae. Many living species illustrated by Tryon (1899) and Strebel (1913) appear to have a shell shape very similar to that of *O. linteus*, but it is felt that these comparisons are not exhaustive enough to show conclusively that *O. linteus* is extinct. Although it is certainly very unlikely to be of any great geological age, it is definitely a fossil specimen.

Conrad (1871*b*), whose work preceded the classifications of both Fischer (1883–7) and Pilsbry (1899–1902), assigned his species to *Bulimus*. As mentioned above, his description referred to the last whorl being slightly carinated at the suture. This, however, is because of damage to the shell, and is of no taxonomic significance; the suture would have been abutting in the original state as with the earlier whorls.

Conrad suggested that his species had some affinity with *Plectostylus* Beck, but the latter is pupiform with a relatively large body whorl and small aperture. Its spire angle reduces from about 90° to under 50° by the final whorl. Moreover, in *Plectostylus* the widest point of its whorls lies well above the suture (Zilch 1960: 483, fig. 1699). The simpler and more regularly geometrical growth and resulting shape of Conrad's fossil species is strongly reminiscent of Orthalicidae, and, in

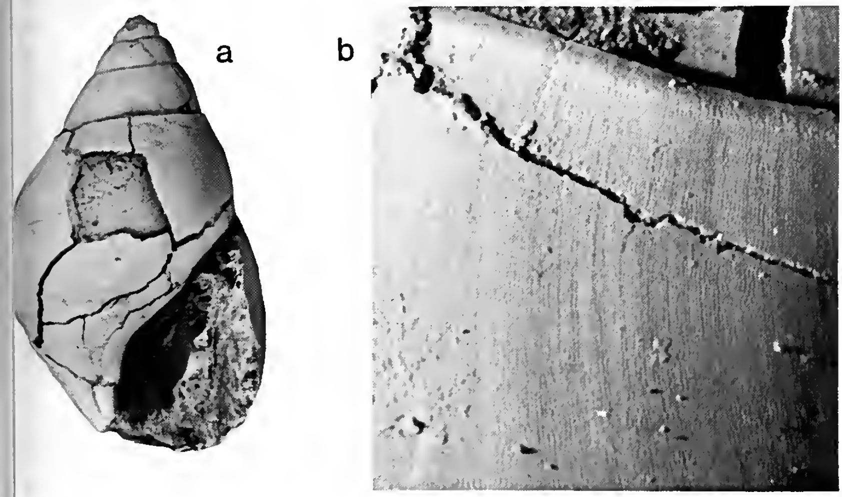


Fig. 295 *Orthalicus linteus* (Conrad). Pebasian; Pichana, Peru; Hauxwell Colln. NYSM 9157; holotype of *Bulimus linteus* Conrad, figured by Conrad (1871: pl. 10. fig. 9). a, front, × 1.5; b, microsculpture of upper sutural region of right hand side of body whorl, × 10.

particular, of *Orthalicus* itself. Features in common include a similar type of microsculpture and apertural features, as well as a rather simple, untwisted columella lacking a plication. *B. linteus* Conrad is therfore assigned to *Orthalicus* with confidence, even though distinctions between genera are so dependent on anatomical features.

Class **BIVALVIA** Linné
Subclass **PALAEOHETERODONTA** Newell
Order **UNIONOIDA** Stoliczka (= NAIADES, auctt.)

Parodiz & Bonetto (1963) separated the Mutelacea as a distinct superfamily from the Unionacea; the Mutelacea comprising the African family Mutelidae Gray, 1847 and the South American Mycetopodidae Gray, 1840, both of which have lasidium larvae as opposed to the better known glochidia of the Unionacea. In addition, the present preliminary survey, confined to South American naiades, suggests that the two superfamilies may have a significant difference in their shell structure. All Mycetopodidae examined have markedly thicker prismatic layers than do the Hyriidae (Unionacea).

The classification of Parodiz & Bonetto is followed here, in preference to that used by Haas (1969*a*; *in* Moore 1969*b*). Haas also gave contradictory views on the authorship of suprageneric taxa in these two works, whereas, after careful checking, Parodiz & Bonetto (1963) have proved to be substantially correct.

The original distinction between lasidium and glochidium larvae was noted by von Ihering (1893), whose work Simpson (1900: 502) regarded as the then most important discovery in the study of the naiades. The acceptance of the implications of Ihering's observation seems to have been delayed, largely owing to the lack of confirmation by other workers. Ortmann (1911: 129–130) distinguished between Hyriinae with glochidia and Mutelinae with lasidia, but placed both in the same family Mutelidae. He persisted in giving the same classification (1921), even though he illustrated (1921: 469, text-fig. 4) the glochidia of twelve species of Hyriinae (mainly *Diplodon*) but omitted any information on the lasidia of Mutelinae dealt with in this later work. Marshall (1931*a*: 18–19) pointed out that von Ihering was the only worker to have seen lasidia and seemed to dismiss his observations as unfounded. Cox (*in* Moore 1969: N96), however, briefly noted the existence of three types of 'Unionacean' larvae: the **glochidium**, the **haustorial** larva of the African *Mutela bourguignati* (Ancey), and thirdly the **lasidium** of some South American species, whose developmental history still had to be studied in detail. Cox was apparently unaware of the work of Parodiz & Bonetto (1963), whilst his reference to the development of *Mutela bourguignati* was presumably based on the work of Fryer (1961), though it was not referred to in any of the Bivalve *Treatise* bibliographies. Parodiz & Bonetto had, however, discussed Fryer's results at some length. They had concluded that although there were differences between haustorial and lasidium larvae, their basic structure was broadly similar and that the inclusion of both in the Mutelacea was justifiable, whilst both were clearly very different from the glochidium of Unionacea.

The correct classification of Woodward's (1871) '*Anodon*' *batesi* from Pichana, p. 275, presented a problem. It has a shell outline reminiscent of some smooth-shelled *Diplodon* (Hyriidae), *Anodontites* (Mycetopodidae) and even the Central American *Brachyanodon* Crosse & Fischer, 1893 (Unionidae, Anodontinae). Taylor, Kennedy & Hall (1969), when working on bivalve shell structure, were unaware of the superfamilial separation of the Mutelacea by Parodiz & Bonetto (1963) (J. D. Taylor, personal communication). By chance, with the exception of two members of the Etheriidae, all the other naiades whose shell structure they had examined were Unionacea (*sensu* Parodiz & Bonetto): none were Mutelacea. I have therefore examined, without sectioning, several species of both *Diplodon* and *Anodontites*. In *Diplodon* the outer prismatic layer is too thin to be seen clearly. The shell structure of *Triplodon* (Hyriidae) is similar. In contrast, in *Anodontites* the prismatic layer is noticeably thicker and the honeycomb patterning of the shell surface below the periostracum is also clearly visible under low magnifications: '*A*.' *batesi* Woodward is here placed with confidence in *Anodontites* because it shows this shell structure. Other South American Mutelacea showing this coarse, easily visible, prismatic layer are *Mycetopoda*, *Fossula* and *Monocondylaea*. It thus appears that such differences in shell structure may well be a feature separating the two superfamilies, but such a proposition needs more thorough testing. This feature has been noted before: Marshall (1931*a*: 19) wrote that in some South American Mutelidae the prismatic layer was very thick.

Marshall's main line of research was concerned with the sculpturing of the periostracum, which may also be a diagnostic character at superfamilial level. Initially, he noted (1925: 1) the absence in *Diplodon* and other 'Unionidae' of microscopic radiating threads which were present in South American 'Mutelidae' (=Mycetopodidae). Expanding this study to a world-wide basis, he concluded that these striae occured in virtually all 'Mutelidae' (=Mutelacea) with the possible exception of *Mycetopoda* (1925: 12).

Taxonomy of naiades at both generic and specific level is complicated by the vast number of nominal species which have been erected. G. B. Sowerby illustrated nearly seven hundred species in his rather uncritical monographs of *Unio* (1864–68) and *Anodon* (1867–70). Later, Simpson (1900: 505–7) still recognized as valid over one thousand species in his catalogue, in spite of efforts to eliminate unnecessary taxa in synonymy. Of the 101 species of living Unionacea (all Hyriinae) from South America, he assigned 73 to *Diplodon*, s.l., whilst some 80 species of Mutelacea were from that continent. Considerably fewer species were recognized as distinct by Haas (1969*a*), but many of his synonymies and hence details of distribution remain suspect. The lack of comparative material on which to base taxonomic decisions is highlighted by the fact that the BMZD general (i.e. other than type and figured) material of South American naiades amounts to only seven drawers containing under 500 shells. Study of fossil forms is often further hampered by, among other things, the lack of knowledge of the hinge in a group in which there is often remarkable similarities of the external shell in unrelated toothed and edentulous genera.

In view of the relatively few South American fossil species known (26 in Parodiz, 1969) and the difficulties of establishing their relationships with each other and with living taxa, the naiades are of little stratigraphical value except in purely local contexts. An example of such use is the distribution of *Diplodon longulus* (Conrad), p. 270, which provides some confirmation that Singewald's (1928) locality at Paucarpata is Pebasian.

Naiades, probably because of their exclusively fresh-water distribution, are uncommon in the Pebasian. The holotype of *Anodontites batesi* (Woodward, 1871) is the only specimen

Table 1 List of Naiades from Pebasian and related localities. For full list of Cuenca Basin fossils see both Bristow & Parodiz (1982) and herein, pp. 339–41.

A, dealt with in further detail below. B, dealt with by Parodiz (1969). C, material thought to be lost as it is neither listed in Richards (1968, ANSP), nor Clarke (1906, NYSM), nor present in BMPD.

	Bivalve allied to *Mulleria* Conrad, 1871*b*: 192; Pichana. In NYSM; see Clarke, 1906. Presence noted in introduction to paper, fossil not described.
A	*Anodon batesi* Woodward, 1871: 103; pl. 5, fig. 10; Pichana. See p. 275.
C	*Anodonta pebasana* Conrad, 1874*a*: 29; pl. 1, fig. 5; ? Pebas.
ABC	*Triquetra longula* Conrad, 1874*a*: 29; pl. 1, fig. 10; ? Pebas. See p. 270.
ABC	*Triquetra longula* ('young') Conrad, 1874*a*: 30; pl. 1, fig. 13; ? Pebas. see p. *271*.
C	*Haplothaerus capax* Conrad, 1874*b*: 83; pl. 12, figs 1, 2, 3; Iquitos.
	Unio sp.; Boettger, 1878: 498; Pebas (fragment).
C	*Anodon* sp.; Etheridge, 1879: 84; cliffs near Canamá, shell fragments only.
C	*Unio* sp.; Etheridge, 1879: 84; as above.
	Anodonta sp.; Roxo, 1924: 45; Três Unidos, Peru, fragments.
	Unio sp.; Roxo, 1924: 45; Cachoera das Tracoas, Brazil, abundant shells, not identified because of lack of comparative material and literature.
	Hyria corrugata (Lamarck); Roxo, 1924: 45; Três Unidos, Peru [= *Prisodon*].
	Castalia ambigua (Lamarck); Roxo, 1924: 45; locality not given.
AB	*Prodiplodon singewaldi* Marshall, 1928*a*: 2; pl. 1, figs 3, 6; Paucarpata, Marañon River. See *Diplodon longulus*, p. 270.
B	*Prodiplodon bassleri* Marshall, 1928*a*: 3; pl. 1., fig. 1; Pebas.
AB	*Prodiplodon paucarpatensis* Marshall, 1928*a*: 4; pl. 1, fig. 4; Paucarpata, Marañon River. See *Diplodon longulus*, p. 270.
AB	*Eodiplodon gardnerae* Marshall, 1928*a*: 4; pl. 1, figs 2, 8; Pebas. Placed in *Diplodon* by Parodiz (1969: 70; pl. 3, figs 2, 4); see p. 267.
AB	*Eodiplodon pebasensis* Marshall, 1928*a*: 5; pl. 1, figs 5, 7; Pebas. Placed in synonymy of *D. gardnerae* by Parodiz (1969: 70; pl. 3, figs 1, 3 which are copies of Marshall's type illustrations); see p. 267.
	Anodontites ?; Marshall, 1928*a*; 6; Taropoto, Peru, fragments only.
	Castalioides laddi Marshall, 1934: 78, figs 1–3; 'Pleistocene', Venezuela.
	'Nayad' shell fragment; de Greve, 1938: 19, text-fig. 1; Iquitos (See Willard, 1966, below).
A	*Hyria* sp.; de Greve, 1938: 20; pl. 7, figs 24, 25; Iquitos. See *Diplodon longulus*, p. 270.
	Hyria trinitaria Maury 1925*b*; Palmer, 1945: 12; pl. 1, figs 1–10; Late Caenozoic, Venezuela.
	Hyria weisbordi Palmer, 1945: 13; pl. 3, figs 11, 12; as above.
	Prodiplodon tipswordi Palmer, 1945: 16; pl. 3, figs 4, 9–12; as above [= *Diplodon*].
	Castalioides laddi Marshall; Palmer, 1945: 17; pl. 2, figs 17–22; 'Plio-Pleistocene', Venezuela.
A	*Trilodon* (*sic*) et *Triplodon latouri* Pilsbry (*sic*, for *Triplodon latouri* Pilsbry & Olsson, 1935); Willard, 1966: 66, 67, 90; pl. 56, fig. 1; Negro Urca on Rio Negro 200 km NW of Iquitos (figured specimen) and Barranco, above Rumi Tuni 225 km N of Iquitos on Rio Napo. Misidentified; see under *Diplodon longulus* (Conrad), p. 270.
	Anodontites lacivensis (*sic*) Pilsbry & Olsson (for *Anodontites laciranus* Pilsbry & Olsson); Willard 1966: 90; pl. 56, fig. 2; Iquitos. Misidentified; probably same as 'Nayad-shell' of de Greve, 1938, above.
A	*Diplodon (Ecuadorea)* sp. aff. *bristowi* Parodiz *in* Bristow & Parodiz, 1982; herein; La Tagua, Loc. 54. See p. 273.

known from Pichana. The Naiades are represented only by shell fragments of large specimens of Mutelacea from both Puerto Nariño and Weeda's La Tagua locality (p. 172). A single valve referred herein to *Diplodon* (*Ecuadorea*) sp. aff. *bristowi* Parodiz (p. 273) was found at La Tagua, Loc. 54. With the exception of Roxo's (1924) reference to abundant shells of *Unio*, all the records below are of few, often single shells. In contrast, naiades are a more important element in both the Cuenca Basin (Liddle & Palmer 1941, Bristow & Parodiz 1982) and Venezuelan Pliocene faunas described by Palmer (1945). Four species, all assigned to different genera, were described by Pilsbry & Olsson (1935) from the La Cira Formation fauna, which totalled fourteen molluscan species in all.

Parodiz (1969) reviewed some of the Pebasian species. His comments on both generic and specific synonymies are extremely useful. Unfortunately his records are far from complete and his re-illustrations of type specimens are accompanied by sometimes ambiguous plate explanations. A new list, Table 1, of all Pebasian and other relevant species is therefore given in date order. No Pebasian species are known to occur in other deposits though two were identified as living species (Roxo, 1924).

Superfamily **UNIONACEA** Fleming, 1828

[*nom. transl.* Thiele, 1934: 815, *ex* Unionidae Fleming, 1828: 415].

Family **HYRIIDAE** Swainson, 1840

[*nom. transl.* Parodiz & Bonetto: 1963: 204, *ex* Hyrinae Swainson, 1840: 282 *et* Hyrianae Swainson, 1840: 379].

Subfamily **HYRIINAE** Swainson, 1840

[*nom. conserv.* under Article 40 of I.C.Z.N. (1961); see Haas *in* Moore, 1969*b*: N457].

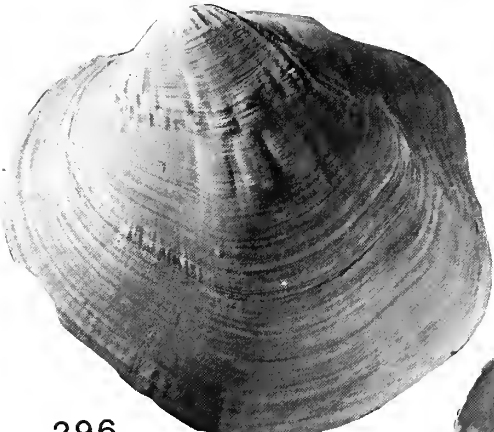
Parodiz & Bonetto (1963) appear to be the first authors to use the family name Hyriidae. Presumably their quotation of Hyriadae 'Agassiz, 1847' can refer only to his *Nomenclatoris zoologici*, the molluscan part of which appeared in 1845. In it (1845: 43), Hyrianae is listed but there is no reference to Hyriidae. Both editions of the accompanying *Index universalis* (1846, 1848) gave the same usage.

The Hyriinae are the only members of the Unionacea found in South America both during the Caenozoic and at the present day (Parodiz & Bonetto 1963: 196; map 3). Other subfamilies of the Hyriidae live in Australia.

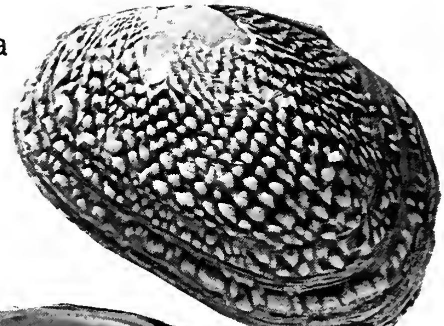
Genus ***DIPLODON*** Spix, 1827

TYPE SPECIES. *Diplodon ellypticum* Spix, *in* Spix & Wagner 1827, by subsequent designation of Simpson (1900: 872). Recent, Santo Francisco River, eastern Brazil.

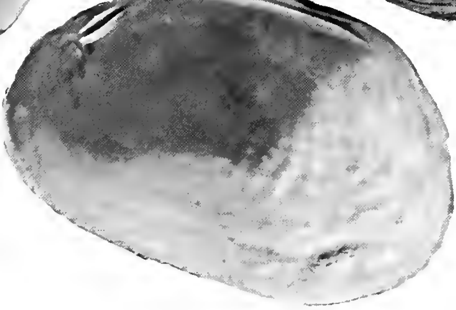
DIAGNOSIS. Moderately-sized Hyriinae, moderate- to thin-shelled; outline variable, elliptical to suborbicular, non-alate or only weakly so; hinge line slightly curved; sculpture



296



297a



297b

Fig. 296 *Rhipidodonta paranense* (Lea). Recent; Corrientes Prov., Argentina; d'Orbigny Colln. BMZD 1854.9.4.41; left valve, × 1.5.
Fig. 297 *Iridea granosa* (Bruguière). Recent; French Guiana. BMZD 1901.12.14.15; a, left valve exterior; b, right valve interior; both × 2.

basically of chevron pattern of ribs or tubercles, often confined to umbonal region, but sometimes spreading to ventral commissure; anterior and posterior regions of shell usually smooth except for moderately rugose growth lines. One or two anterior cardinals in left valve, two in right valve; dorsal cardinal tooth lamelliform; main, more ventrally situated cardinal granulose or striate, frequently bicuspid or even split into two separate teeth (see Remarks); posterior lamellar teeth elongate, two in left valve, one in right. Glochidia, parasitic or non-parasitic.

SPECIES ASSIGNED. Seventeen Tertiary fossil species (Parodiz 1969) and *Triquetra longula* Conrad (1874*a*), Pebas. For living species see Simpson (1900, 1914), who listed over 70 species, and Haas (1969*a*) who recognized 22 full species.

DISTRIBUTION. Palaeocene to Recent, South America (Simpson 1900, Parodiz 1969).

REMARKS. Parodiz (1969: 49), with further alterations in Bristow & Parodiz (1982: 22) synonymized several taxa which are given generic or subgeneric status by Haas (*in* Moore 1969*b*: N458–461). The arrangement followed here is given below and follows fairly closely that of Bristow & Parodiz (1982):

(1) *Diplodon*, s.s. [= *Diplodon*, *Iridea*, *Prodiplodon*, *Eodiplodon*, *Schleschiella*]. Shells usually longer than high; glochidia parasitic.
(2) *Diplodon (Ecuadorea)* [= *Ecuadorea*, *Castalioides*]. Shells usually longer than high; umbonal sculpture strongly developed, sometimes spreading to ventral commissure; glochidia non-parasitic.
(3) *Diplodon (Rhipidodonta)* [= *Rhipidodonta*, *Cyclomya*, *Bulloideus*]. Shells suborbicular; glochidia non-parasitic.

This scheme must be regarded as no more than a compromise. To a certain extent, shell shape and sculpture intergrade between the three subgenera, and in addition the glochidia of many species are unknown. *Bulloideus* Simpson (1900: 887), type species *Unio bulloides* Lea (1859), is here placed in *Rhipidodonta* Mörch (1853) whose type species is the rather similar (Fig. 296) *Unio paranensis* Lea (1834). Some confusion may have arisen because the illustration given by Haas (*in* Moore 1969*b*: fig. D51/2a–c) is of a completely different species, being based on a misidentified figure from Küster (1861: *Anodonta* pl. 85, fig. 3). None of the fossils dealt with below are referable to *Rhipidodonta*. All the other *Treatise* illustrations of the taxa referred to above are correctly identified with the important exception of *Diplodon* itself: See p. 269.

Parodiz (1969) has first included *Antediplodon* Marshall (1929), from the Pliocene of Texas, in the synonymy of *Diplodon* but omitted it later (Bristow & Parodiz 1982: 22), probably a sound decision. The characters of *Antediplodon* are unclear from the original illustration (copied by Haas, *in* Moore 1969*b*: fig. D50/1). Its inclusion in *Diplodon* would represent the only occurrence of the genus outside South America, for it appears to be completely absent from Central America as well as northernmost South America (Parodiz 1969: 50; map 2). Other changes by Bristow & Parodiz (1982) include the formal recognition of *Ecuadorea* as a subgenus distinct from *Rhipidodonta*. Previously, Parodiz (1969) had formally described all the species with which he had dealt as members of *Diplodon*, though (1969: 51) he had given a key distinguishing between *Rhipidodonta* and *Diplodon* and had placed both *Ecuadorea* and *Schleschiella* in the synonymy of *Rhipidodonta*.

In *Diplodon* there are terminological problems in describing the cardinal teeth. There is a lamelliform dorsal anterior tooth in the right valve, whilst a similar tooth occurs rarely in the left valve (as in the larger syntype of *D. ellypticus* but not in other specimens referable to that species). The main cardinal tooth below is irregular in form and frequently bicuspid. In some cases the cusps are separated by such a deep cavity that they may be described as two separate teeth: different authors' descriptions become difficult to reconcile in such circumstances. Examination of the main cardinal tooth of several species assigned to *Diplodon* (s.l.) suggests that differences are not necessarily specifically diagnostic and are therefore almost certainly not of generic importance.

Subgenus *DIPLODON* Spix, 1827

[= *Iridea* Swainson, 1840; type species *Unio granosus* Bruguière 1792*b*, by monotypy; Recent, French Guiana. *Prodiplodon* Marshall, 1928*a*; type species *P. singewaldi* Marshall 1928*a*; by original designation; Neogene (?Pebasian), Paucarpata, Peru. *Eodiplodon* Marshall, 1928*a*; type species *E. gardnerae* Marshall 1928*a*, Neogene, Pebas Formation, Peru. *Schleschiella* Modell, 1950; type species *Unio burroughianus* Lea 1834, by original designation. Recent, Brazil].

Type species. See p. 265, under genus.

Diagnosis. Hyriinae with oval outline; normally non-alate; posterior angulation weak, if present; sculpture usually con-ined to umbonal region; glochidia parasitic (when known).

Species assigned. Fossil. *Triquetra longula* Conrad 1874*a*, Pebas; *Prodiplodon bassleri* Marshall 1928*a*, Pebas; *Eodiplodon gardnerae* Marshall 1928*a*, Pebas. *Prodiplodon ipswordi* Palmer 1945, ?Pliocene or Pleistocene, Venezuela.

Living. Sixteen full species and eight subspecies (Haas 969*a*: 511–526.

Distribution, Palaeocene to Recent, South America only Parodiz 1969).

Remarks. The genus is discussed at length by Parodiz (1969) nd Bristow & Parodiz (1982: 22–25). In both these works nd in Haas (*in* Moore 1969*b*) *Iridea* Swainson is placed in the ynonymy of *Diplodon*. Its type species (Fig. 297) *Unio ranosus* Bruguière is sculptured with tubercles arranged in a ivaricate pattern and covering the whole shell surface. In pite of this obvious difference, the synonymy is probably ound. *D. granosus* and *D. ellypticus* are so similar in outline, onvexity and hinge characters that some authors (e.g. Haas, 969*a*: 525) have regarded the two as no more than distinct ubspecies of *D. granosus*. It appears that the first valid type esignation is that of Simpson (1900), quoted on p. 265, and epeated in his later work (1914: 1225). Haas (*in* Moore 969*b*: N460) gave '*D. ellypticum*' as type species by original esignation. This cannot be correct as four species were llustrated by Spix (1827) under *Diplodon*, with no indication s to which was the type. The name *Diplodon* was not used in he main unionid monographs (Küster 1861 (*Unio* & *Hyria*): 38; Sowerby 1868 (*Unio*): pl. 74, fig. 382). However, it was mentioned by Chenu (1862: 142), who gave none of Spix' pecies as examples, by H. & A. Adams (1857: 497), who ave '*D. ellypticum*' as one of twenty examples, and also by ischer (1886: 1000) who gave '*D. ellipticum*' as his example as opposed to type) of the genus, which (1886: 1004) he laced in the synonymy of *Hyria*.

A further problem common to several of Spix' names ncluding *Aylacostoma*, also dealt with here, p. 258) arises ecause of name changes by various of his co-authors, ncluding Wagner. Spix was responsible for the plates, but he ied in 1826, before publication of the joint work (1827). In the text (1827: 33) by Wagner, the species is described as '*Unio ellipticus*' Wagner with '*Diplodon ellipticus*' Spix placed in synonymy. As far as is known, both text and illustrations are part of a single work and were published simultaneously. On the advice of R. V. Melville, one-time Secretary of ICZN, I now propose that *Diplodon ellypticum* Spix 1827 is treated as having priority over *Unio ellipticus* Wagner 1827. There would seem to be some natural justice in this decision. Both the sequence of events and the fact that Wagner placed Spix' name in synonymy strongly suggests that Wagner changed Spix' name rather than *vice versa*. This decision also avoids the problem created by the fact that Wagner's name is a junior homonym of both *Unio ellipticum* Rafinesque 1820, and *U. ellipticum* Barnes 1823. This homonymy led Simpson (1900: 877) to propose *Diplodon wagnerianum* as a new name for *U. ellipticus* Wagner, *non* Barnes.

Thus, the generally accepted combination *Diplodon ellypticum* Spix, 1827, remains available for the type species of *Diplodon*, with Spix' original spelling corrected for the masculine gender. Both *Unio ellipticus* Wagner (1827) and *Diplodon wagnerianum* Simpson (1900) fall into its synonymy.

Diplodon (Diplodon) ellypticus Spix, 1827 Figs 298–300

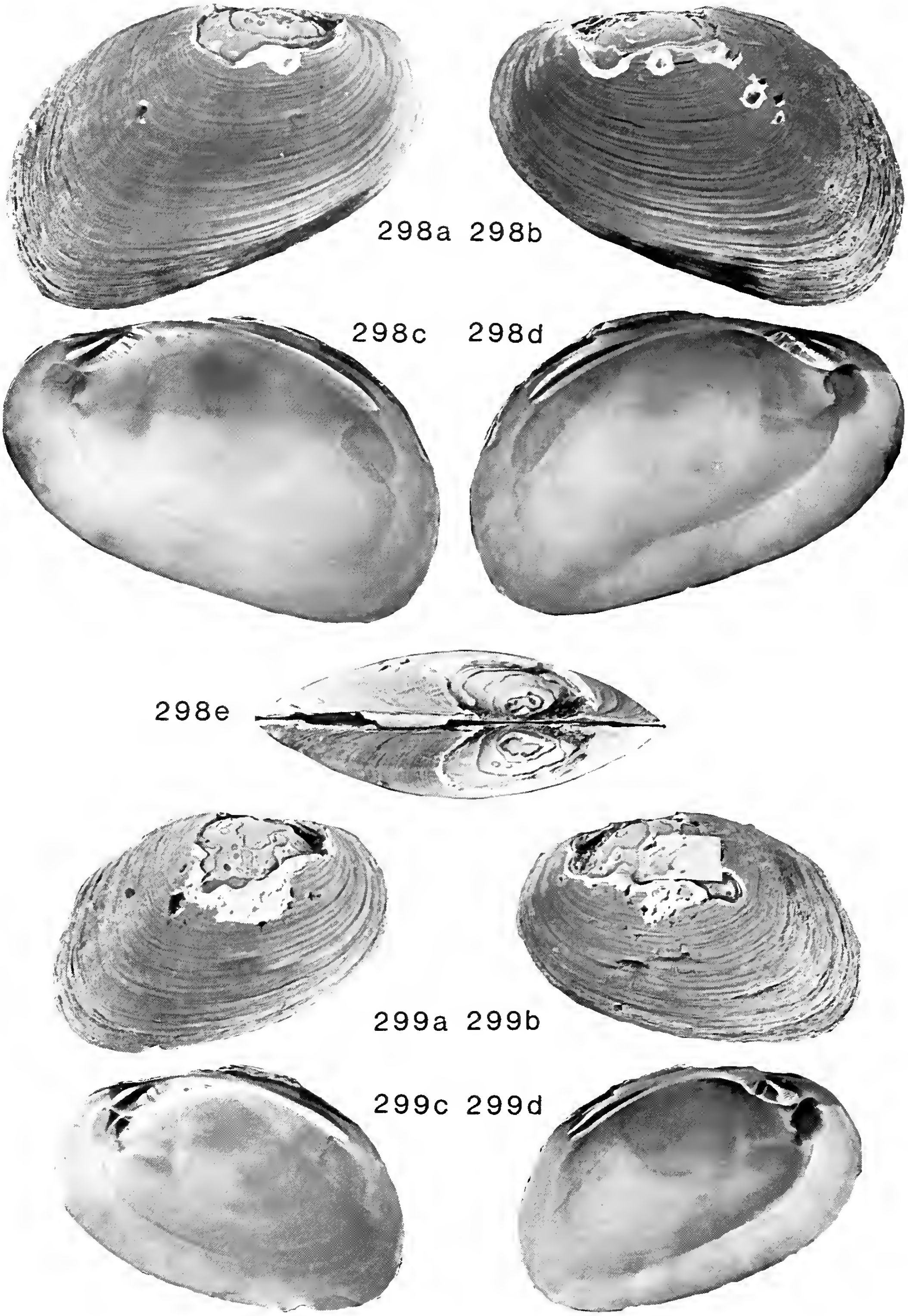
*v 1827 *Diplodon ellypticum* Spix, *in* Spix & Wagner: pl. 26, figs 1, 2.
v 1827 *Unio ellipticus* Wagner, *in* Spix & Wagner: 33.
v. 1843 *Unio multistriatus* Lea; Hanley: 176; pl. 20, fig. 35.
non 1861 *Unio ellipticus* (Spix); Küster: 238; pl. 80, fig. 2 [= *Diplodon multistriatus* (Lea)]
v. 1868 *Unio ellipticus* (Spix); Sowerby: pl. 74, fig. 382.
. 1890 *Unio ellipticus* (Spix); von Ihering: 163; pl. 9, figs 8, 9.
. 1893 *Unio ellipticus* (Spix); von Ihering: 108, 114, 115.
*. 1900 *Diplodon wagnerianum* Simpson: 877.
. 1914 *Diplodon wagnerianum* Simpson: 1251.
? 1969*a* *Diplodon (Diplodon) granosus ellypticus* Spix; Haas: 525.
v. 1971 *Unio ellipticus* (Spix); Johnson: 103.
v. 1983*b* *Diplodon ellypticum* Spix; Fechter: 243; pl. F, figs 5, 6 (shells); pl. L, figs 1, 2 (labels).

Syntypes. Two specimens, neither of which was figured by Spix but both figured by Fechter (1983*b*); Recent, Rio Santo Francisco, eastern Brazil (Spix colln), Zool. Staatssammlung, München. A lectotype is not selected: see p. 269.

Other material studied. BMZD 1907.10.28.198, shell figured both by Hanley (1843) and by Sowerby (1868) and listed by Johnson (1971); labelled Bahia, Brazil (Hanley Colln); BMZD, two shells, Rio Conejo, Brazil (colln unknown). Also occurs in Rio Piracicaba and Rio Tamanduatahy, S. Paulo, Brazil (Ihering 1893). Recent only, eastern Brazil.

Diagnosis. *Diplodon* with regularly oval outline narrowing towards anterior; greatest height at junction of ventral and posterior margins; sculpture of light irregular ribs, confined to small area around umbones.

Description. The umbones of all the few specimens available for study are eroded and the sculpture can be seen fairly clearly only on the specimen figured by Sowerby (1868). It consists of about 17 rather wrinkled ribs all lying anterior to the posterior area. They are approximately the same width as



Figs 298–299 *Diplodon ellypticus* Spix. Syntypes unfigured by Spix; Recent; Rio Saõ Francisco, Minas Gerais Province, Brazil; Spix Colln, Zool. Staatssammlung, München. **298**, specimen figured by Fechter (1983: pl. F, figs 5, 6) but not by Spix; a–e, ×1.5. **299**, a–d, × 1.5.

the major growth increments (*c.* 0.3 mm) and die out within 5–7 mm of the umbones. They are not radiating but lie subparallel to each other, more or less in a dorsoventral direction. The posterior area is smooth except for two or three randomly positioned, impersistent riblets which do not originate from the umbones. No specimens show traces of ribbing further than 10 mm from the umbones, and the remainder of the shell is smooth except for rather undulating growth increments of varying strength, and a tendency to become untidy and slightly scabrous near the valve margins. The shell is moderately thin. The beak cavities are shallow. In both dorsal and anterior view the shell is gently and simply convex, with no modification such as a posterior alation. The hinge is rather variable. In the right valve there are two cardinal teeth. The dorsal one is lamelliform, and runs forward from the umbo, diverging gently from the dorsal margin. Below it lies a much heavier cardinal tooth which is very striate, granular, and of irregular shape. It is frequently bicuspid, with the anterior cusp elongate and subparallel to the hinge whilst the posterior cusp is shorter and peg-like. There is normally one cardinal tooth in the left valve, very similar to the main cardinal of the right valve. In the largest syntype, however, there is a second, separate, cardinal tooth like the dorsal cardinal tooth present in normal right valves. There are two compressed, faintly crenulate, lamellar teeth in the left valve and one in the right. The crenulations are the surface expression of deep-seated differences in the structure of the semi-translucent nacreous shell. The ligamental nymphs appear to coincide in length with the posterior lamellar teeth, but their anterior ends are lost due to umbonal erosion. The anterior adductor scar is well marked, with the pedal protractor scar joined to its posteroventral margin. The posterior adductor scar is far less well marked, so that it is impossible to separate it from the posterior pedal retractor scar. The anterior pedal retractor scar is deep and situated below the anterior end of the cardinal teeth. The pedal elevator scarring consists of four or five irregularly positioned scars of varying shape and depth situated in the beak cavities: those of the left and right valves of the same individual do not form mirror images. The pallial line is entire and clearly visible.

DIMENSIONS. In mm.	l	h	br	l/h
Figd Spix (1827) and von Ihering (1890); specimen not seen, probably lost.	48	26	15	1.85
Unfig'd syntype (Zool. Staatssammlung, München).	49.3	31.0	16.9	1.59
Unfig'd syntype (as above).	38.8	25.0	14.1	1.55
BMZD 1907.10.28.198 (fig'd Hanley 1843; Sowerby 1868).	36.4	21.6	10.3	1.69
BMZD, Brazil	50.5	29.2	15.8	1.73
BMZD, Brazil	44.6	27.0	14.8	1.65

REMARKS. Von Ihering (1890) figured internal views of both valves of a shell from Spix' collection in Zool. Staatssammlung, München which closely resembles the type illustration (Spix 1827) in both shape and dimensions. This specimen cannot now be found, but two other shells in Spix' collection form the basis of the present description. Fechter (1983*b*: 243) wisely decided not to select either as lectotype. I also feel that lectotype selection is unjustified as there is always the possibility that the figured specimen will be found. It is a pity that von Ihering did not provide an external view. There seems little doubt, however, that he was dealing with Spix' figured specimen. In his description, he referred to the ribbing being confined to within 9–10 mm of the umbones.

Diplodon multistriatus (Lea) is quite similar to *D. ellypticus*, but may be distinguished by its coarser growth rugae, and its stronger sculpture, which persists for about 12 mm ventrally below the umbo and for up to 30 mm diagonally in a posteroventral direction. The anterior parts of both species are very similar in outline but in *D. multistriatus* the dorsal and ventral margins are more nearly parallel and the shell more elongate.

D. ellypticus and *D. multistriatus* have frequently been confused, and a synonymy of *Diplodon multistriatus* is given below to clarify the usage of various authors. Hanley (1843) figured as *Unio multistriatus* Lea the same shell that Sowerby (1868: pl. 74, fig. 382) later correctly identified as *ellypticus*. Sowerby (1868: fig. 455) also correctly identified *U. multistriatus*. He commented that it was now regarded by Lea himself as being identical with Spix' *ellypticum*, but 'if so, the shell ... merits to be figured from its very remarkable sculpture.' Lea's opinion may have been made personally to Sowerby because I have been unable to find it published elsewhere. Both von Ihering (1890) and Simpson (1900; 1914) give extensive synonymies which are only partly correct.

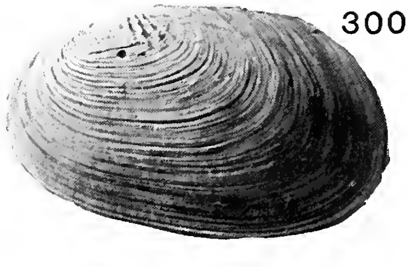
Küster (1861) figured a specimen of *U. multistriatus* as *U. ellipticus*. His misidentification persists into the Bivalve *Treatise* where his figure is copied by Haas (*in* Moore 1969*b*: N459). In *Das Tierreich*, Haas regarded 1969*a*: 525–6) *D. ellypticum* and *D. multistriatus* as two distinct subspecies of *D. granosum* (Bruguière 1792*b*). His interpretation is suspect, the work being unillustrated. Moreover, he places *D. jacksoni* Marshall in the synonymy of *D. granosum ellypticum*, but Marshall's original illustration (1928*b*: pl. 4, fig. 1) shows a species in which the umbo is raised above the hinge and the ventral margin does not slope down towards the posterior.

Diplodon gratus (Lea 1860) from southern Brazil (BMZD) and the Uruguay River (Simpson 1900: 886) was assigned by Simpson to his new subgenus *Cyclomya* (= *Rhipidodonta* herein; see p. 266). However, its resemblance to *D. ellypticus* is such that the two ought to be compared. *D. gratus* may be distinguished by its greater size, less elongate outline and an incipient alation.

Diplodon (Diplodon) multistriatus (Lea, 1831) Fig. 301

* 1831 *Unio multistriatus* Lea: 91; pl. 12, fig. 22.
v. 1847 *Unio multistriatus* Lea; d'Orbigny: 607.
*. 1848 *Unio psammactinus* Bronn, *in* Philippi: 79; pl. 5, fig. 2.
*. 1848 *Unio granuliferus* Dunker: 182.
. 1856 *Unio psammactinus* Bronn; Küster (*Unio & Hyria*): 159; pl. 45, fig. 6.
. 1858 *Unio multistriatus* Lea; Chenu: pl. 11, fig. 2, 2a, b.
. 1860 *Unio granuliferus* Dunker; Pfeiffer: 150; pl. 39, figs 1–3.
. 1861 *Unio ellipticus* Wagner *in* Spix; Küster: 238; pl. 80, fig. 2 [*non* Spix].
v. 1868 *Unio multistriatus* Lea; Sowerby: pl. 85, fig. 455.
. 1890 *Unio multistriatus* Lea; von Ihering: 165 (*pars*).
. 1900 *Unio granosus* Bruguière; Simpson: 878 (*pars*).
? 1969*a* *Diplodon (Diplodon) granosus multistriatus* (Lea) Haas: 526.
. 1969*b* *Diplodon ellypticum* Spix; Haas, *in* Moore: N460; fig. D51/5a, b [*non* Spix].

300



301

Fig. 300 *Diplodon ellypticus* Spix. Shell figured by Sowerby (1868: pl. 74, fig. 382) as *Unio ellypticus* and by Hanley (1843: pl. 20, fig. 35) as *Unio multistriatus* Lea. Recent; Bahia, Brazil, *ex* Hanley Colln. BMZD 1907.10.28.198; left valve, × 1.5.

Fig. 301 *Diplodon multistriatus* (Lea). Shell figured by Sowerby (1868: pl. 85, fig. 455) as *Unio multistriatus* Lea. Recent, Brazil; *ex* Hanley Colln. BMZD 1907.10.28.196; left valve, × 1.5.

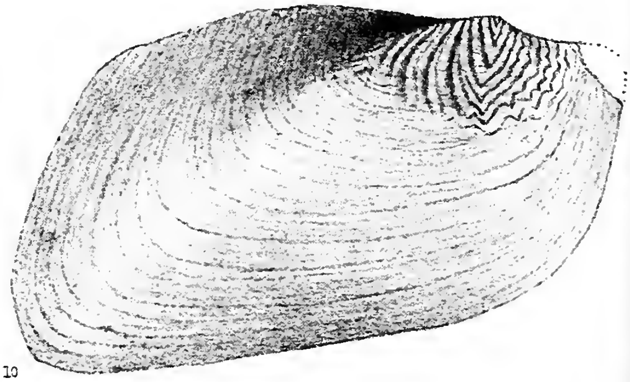


Fig. 302 *Diplodon longulus* (Conrad). Pebasian; ? Pebas, Old Pebas or Pichana, Peru; Steere Colln (presumed lost, ANSP); copy of type illustration; right valve.

HOLOTYPE. Probably lost. Lea stated that the shell he illustrated was in the collection of Mrs Mawe of London and its subsequent history is unknown. Johnson (1974*a*: 94), however, stated that USNM 84114 agrees with the illustration, but it was labelled as Moricand collection: it seems unlikely to be the holotype.

MATERIAL STUDIED. BMZD 1907.10.28.196. Shell figured by Sowerby (1868: pl. 85, fig. 455); BMZD 54.12.4.840, shell referred to by d'Orbigny (1847: 607). BMZD, 4 further specimens. Recent; occurs in coastal rivers of Brazil between Rio de Janeiro and Bahia (von Ihering 1890: 167, 1893: 115, 120); Rio Parahiva (d'Orbigny 1847).

DIMENSIONS. In mm.	l	h	br	l/h
BMZD 1907.10.28.196	43.5	23.2	12.1	1.88
BMZD 54.12.4.840	45.9	25.0	14.2	1.84

REMARKS. The above synonymy is not comprehensive. Several of the references given by both von Ihering (1890) and Simpson (1900) in their much fuller synonymies are clearly misidentifications. The shell figured by Sowerby (1868: pl. 74, fig. 382) as *U. ellipticus* (Spix) was wrongly included in *U. multistriatus* by von Ihering, who nevertheless was one of the few authors to notice that Küster's (1861) identification of *U. ellipticus* was incorrect. The type illustrations of *U. multistriatus* and *U. psammactinus* suggest that the two are conspecific, though von Ihering later changed his mind and separated the two (1893: 107). Simpson's (1900) reference of *U. multistriatus* to *U. granosus* implies an unacceptably large degree of variation within a single species.

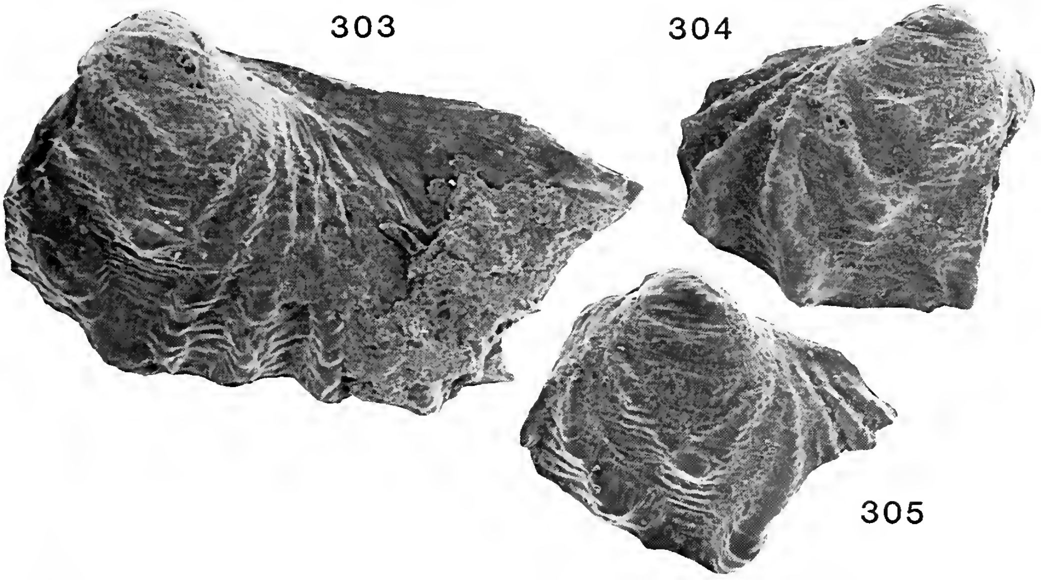
Diplodon (Diplodon) longulus (Conrad, 1874*a*) Fig. 302

* 1874*a* *Triquetra longula* Conrad: 29 (*pars*); pl. 1, fig. 10 (*non* 'young' [i.e. juvenile], p. 30; pl. 1, fig. 13).
. 1928*a* *Prodiplodon paucarpatensis* Marshall: 4; pl. 1, fig. 4.
. 1928*a* *Prodiplodon singewaldi* Marshall: 2; pl. 1, figs 3, 6.
. 1938 *Hyria* sp.; de Greve: 20; pl. 7, figs 24, 25.
. 1966 *Triplodon latouri* Pilsbry (*sic*, *pro* Pilsbry & Olsson, 1935); Willard: 90; pl. 56, fig. 1.
. 1969 *Diplodon singewaldi* (Marshall) Parodiz: 72; pl. 7, figs 1–3.
. 1969 ?*Triplodon longula* (Conrad) Parodiz: 77.

TYPE AND FIGURED SPECIMENS. Conrad's material is presumed lost, neither listed by Richards (1968) as being in ANSP, nor by Clarke (1906) as being in NYSM. Marshall's specimens are in USNM; de Greve's are in PIMUZ; Willard's, in Lehigh Univ., Bethlehem, Pennsylvania.

TYPE LOCALITY AND HORIZON (of *D. longulus*). Late Caenozoic, Pebasian; either Pebas, Old Pebas or Pichana, Peru.

FURTHER DISTRIBUTION. All presumed to be Pebasian. Paucarpata, on Marañón River, Peru (Singewald 1928, Marshall 1928*a*); Iquitos (de Greve 1938); Negro Urca, 200 km NW of Iquitos and Rumi Tuni in Napo River Valley some 225 km north of Iquitos (Willard 1966).



Figs 303–305 *Diplodon* sp. juv. Pebasian; Pichana, Peru; Hauxwell Colln. All × 50. **303**, LL28105; left valve. **304**, LL28106; right valve. **305**, LL28107; left valve.

REMARKS. As the above synonymy is constructed entirely from published illustrations, no specimens having been examined, no attempt is made here to give a formal diagnosis and description of this species. It is characterized by its relatively quadrilateral shape, with the hinge line, posterodorsal and ventral margins all being comparatively straight. The v-shaped folding in the umbonal region is also well ormed and clear. The rather similar *D. bassleri* (Marshall 1928*a*) from Pebas is considered distinct because the axis of ts v-shaped sculpture points in a more posteroventral direcion, its ventral margin is more convex, and its umbones are ituated relatively further forwards with the anterior of the hell being both smaller and lower than in *D. longulus*. *D. ongulus* resembles the living *D. charruanus* (d'Orbigny 1835*a*) (d'Orbigny colln in BMZD) from Uruguay in outline, but the culpture of the latter's umbonal region seems never to develop into the clear-cut v-shaped pattern of *D. longulus*. *D. llypticus* Spix is also similar to *D. longulus*, but is less longate. Its posterior margin is more rounded and is joined o the ventral margin by a curve of wider radius. In addition, t seems never to develop the clear-cut v-shaped sculptural pattern of the fossil species. A comparison with *Diplodon* (*Ecuadorea*) sp. aff. *bristowi* Parodiz is given on p. 273.

Parodiz (1969) tentatively placed *D. longulus* in *Triplodon* pix, 1827 (type species the living *T. rugosus* Spix, 1827, by monotypy), but not only is it too elongate to conform with hat genus but also lacks the convex ventral margin, the alate posterodorsal region and reverse v-shaped ribbing continuing into the posteroventral ridge. However, Parodiz might well e correct in his suggestion that the fragmentary specimen, which Conrad described separately (1874*a*: 30; pl. 1, fig. 13) s a juvenile of *D. longulus*, was more likely to belong to *Triplodon rugosus*. Marshall (1928*a*) erected the new genus *Prodiplodon*, designating *P. singewaldi* as type species, but I gree with Parodiz (1969) in regarding this as one of the several synonyms of *Diplodon*. Parodiz' (1969) pl. 7, figs 2, 3 re copies (the latter trimmed) of Marshall's (1928*a*) pl. 1, figs , 6, which are two different views of the holotype of *P. singewaldi*. Plate 7, fig. 1 of Parodiz is a copy of Marshall's pl. 1, fig. 4, illustrating the holotype of *P. paucarpatensis* Marshall.

Diplodon sp. juv. Figs 303–305

MATERIAL STUDIED. BMPD LL28105–7, Pebasian; Pichana, Peru (Hauxwell colln, extracted from matrix, 1982).

DIMENSIONS. LL28105, lv, l, 1.76 mm. LL28106, rv, l, 0.96 mm. LL28107 lv, l, 1.02 mm.

REMARKS. These three small specimens are all only the umbonal regions of shells, whose outlines are so badly damaged that their original shape can only be roughly deduced by examination of the growth lines. In consequence, the only measurement given above is the actual length of the specimen. All three possess well-preserved chevron sculpture characteristic of *Diplodon* but very rarely seen in adult shells in which the umbonal region is almost invariably eroded. Although these shells could conceivably belong to *D. longulus*, specific identification of such small specimens is quite impossible in the absence of a full growth series.

Subgenus ***ECUADOREA*** Marshall & Bowles, 1932

[= *Castalioides* Marshall, 1934; type species *Castalioides laddi* Marshall 1934, by original designation; Late Caenozoic, Venezuela].

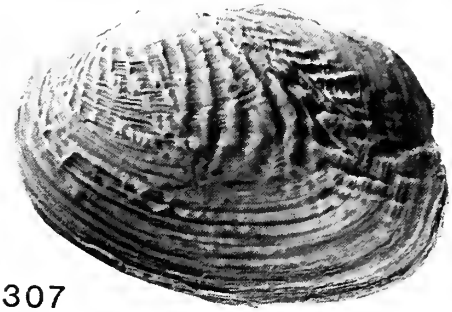
(Figs 306–310)

TYPE SPECIES. *Ecuadorea bibliana* Marshall & Bowles, 1932, by original designation; Miocene, Loyola Formation, Ecuador. = *Diplodon liddlei* Palmer, *in* Liddle & Palmer 1941, a co-occurring species.

DIAGNOSIS. Similar to *Diplodon*, s.str., in shape though generally less elongate; radial sculpture both stronger and more widespread than in *Diplodon*, s.str., often arranged in

306

307



309

308

310

Fig. 306 *Diplodon (Ecuadorea) biblianus* (Marshall & Bowles). LL27807; left valve, × 2, of specimen whose right valve was figured by Bristow & Parodiz (1982: fig. 1) as *Diplodon (Ecuadorea) guaranianus biblianus*. Miocene, Loyola Formation; Loc. CRB 28, Cuenca Basin, Ecuador; Bristow Colln.

Figs 307–308 *Diplodon (Ecuadorea) guaranianus* (d'Orbigny). **307**, BMZD 1854.12.4.841; lectotype of *Unio guaranianus* d'Orbigny, figured by d'Orbigny (1846: pl. 69, figs 10–12). Recent; Rio Parana, Prov. Corrientes, Argentina, d'Orbigny Colln. Left valve, × 3. **308**, BMZD 1965169; holotype of *Unio fluctiger* Lea, figured by Sowerby (1868, species 229). Recent; unlocalized; Cuming Colln. Left valve, × 2.

Figs 309–310 *Diplodon (Ecuadorea) hylaeus* (d'Orbigny). **309**, BMZD 1854.12.4.843; lectotype of *Unio hylaeus* d'Orbigny, figured by d'Orbigny (1847: pl. 69, figs 8, 9). Recent; Chiquitos Province, Bolivia. Left valve, × 1.5. **310**, BMZD 1854.12.4.842; paralectotype. Recent; Santa Cruz de la Sierra Prov., Bolivia; d'Orbigny Colln. Umbonal region of right valve, × 5.

chevrons and sometimes reaching to ventral commissure, sometimes covering most of shell; dentition, as for genus; glochidia non-parasitic where known.

OTHER SPECIES ASSIGNED. Fossil: *Triplodon latouri* Pilsbry & Olsson, 1935; ? Miocene, La Cira Formation, Colombia. *Diplodon (Ecuadorea) bristowi* Parodiz, *in* Bristow & Parodiz 1982; Miocene, Loyola Formation, Ecuador.

Recent: *Unio guaraniana* d'Orbigny, 1835*a*; Rio Paraña, Argentina; = *Unio fluctiger* Lea, 1859; unlocalized. *Unio hylaea* d'Orbigny, 1835*a*; Province of Santa Cruz and Chiquitos, Bolivia. *Castalia pazi* Hidalgo, 1868; Imbabura, Ecuador.

DISTRIBUTION. Miocene to Recent, South America only.

REMARKS. *Ecuadorea* is unfortunately based on an indifferently preserved fossil species. The list of living species assigned does not claim to be exhaustive: all were included in *Diplodon* (s.str.) by Haas (1969*a*) who did not deal with genera based on fossil species. Nevertheless, *Ecuadorea* appears to be comparatively less common than *Diplodon*, s.str.

D. (E.) liddlei was described by Palmer (*in* Liddle & Palmer 1941: 48) from the same locality as *D. (E.) bibliana*. The distinctions made by her and later by Parodiz (1969: 66; Bristow & Parodiz, 1982: 27) do not appear to warrant specific separation. Parodiz (Bristow & Parodiz 1982: 25) also placed *Castalioides laddi* Marshall (1934) in synonymy of *D. (E.) bibliana*: *Castalioides* and *Ecuadorea* can certainly be accepted as generic synonyms. *C. laddi* came from strata in

Venezuela thought by Marshall to be Pleistocene. Later Palmer described the species from another locality thought (1945: 11) to be either Pliocene or Pleistocene, preferably Pliocene – in any event thought to be considerably younger than the Ecuadorean *D. (E.) bibliana.*

However, it is not accepted that the two species are the same. Marshall's (1934) illustrations of the holotype of *C. laddi*, in particular his fig. 1, clearly show a sculptural pattern rather similar to that of *D. (E.) hylaeus* d'Orbigny with the posterior ridge forming the axis of chevron ribbing, in addition to the signs of chevron ribbing in the region immediately ventral to the umbo. In *D. (E.) bibliana* the chevrons are perhaps stronger below the umbones but no chevron ribbing is associated with the posterior ridge.

Parodiz (1969: 62; Bristow & Parodiz 1982: 25) placed *Triplodon latouri* Pilsbry & Olsson, 1935 in *D. (Ecuadorea)* following the doubts originally expressed by its authors about its generic assignment (1935: 16). Its hinge is unknown and it lacks both the anterior and posterior alation of *Triplodon*. Its placement in *Ecuadorea* is accepted here. Even though its sculpture consists of extremely coarse chevrons, there is a certain resemblance between it and *D. (E.) pazi* (Hidalgo) (compare Parodiz, 1969: pl. 4, figs 4, 7, 8).

Parodiz (1969: 66; Bristow & Parodiz 1982: 25) regarded *D. (E.) biblianus* as a subspecies of *D. (E.) guaranianus* (d'Orbigny). This arrangement is not accepted here. It is clear from Parodiz' arguments that he had confused *D. (E.) guaranianus* with *D. (E.) hylaeus* (d'Orbigny). Haas (1969*a*: 519–520) also appears to have been somewhat confused as he regarded *D. pazi* as a subspecies of *D. guaranianus*, in spite of its greater resemblance to *D. hylaeus*. *D. guaranianus* and *D. hylaeus* had previously (Simpson 1900: 884) been regarded as synonyms. *D. (E.) hylaeus* may be described as the stronger, more angulated species, whilst *D. (E.) guaranianus* is the more slender, more ovate species, extremely thin-shelled with the ribs visible from the interior (i.e., the reverse of the distinctions given by Parodiz). Neither species resembles *D. (E.) biblianus* closely. Bonetto (1967: 71) placed *D. bibliana* in the synonymy of the living *D. pazi*: this is not accepted here.

Johnson (1971: 85) selected 'holotypes' and 'paratypes' of the two d'Orbigny species. Correctly, these should be referred to as lectotypes and paralectotypes. Both lectotypes are now figured to remove any remaining confusion: *guaranianus* Fig. 307, *hylaeus* Fig. 309.

The unlocalized holotype of *Unio fluctiger* Lea, 1859 (BMZD 1965169) (Fig. 308) was figured by Sowerby (1866: pl. 42, fig. 229 – quoted in his text as 299). Although considerably larger (l = 33.8 mm) than typical *guaranianus*, it appears to be a synonym.

Diplodon (Ecuadorea) sp. aff. **bristowi** Parodiz, *in* Bristow & Parodiz 1982 Fig. 311

MATERIAL STUDIED. BMPD LL27889, left valve; Late Caenozoic; Loc. 54, La Tagua (Eden colln).

DESCRIPTION. Damage to the single left valve consists of partial loss of shell outline as well as crushing which has somewhat distorted both the outline and sculpture. Nevertheless, examination of the commissure suggests that the shell is virtually complete and not merely the umbonal region of a larger specimen. The hinge is unknown. The shell has a relatively small height to length ratio, a rather tumid umbo, a slight well-rounded posterior angulation and strong, irregularly bifurcating radial ribbing. No chevron patterning can be observed. About 15 ribs can be counted on the anterior and ventral parts of the shell. They reach their maximum in both strength and numbers between 10 and 15 mm from the umbo. Although weaker in later growth stages, some can still be observed reaching the ventral commissure. Growth lines are not prominent, being typical of the genus: they clearly indicate the lack of both anterior and posterior alations.

DIMENSIONS. l = 28 mm; h = 24 mm; valve breadth = 8 mm.

REMARKS. Although the rather tumid umbo is also reminiscent of *Castalia*, this feature is present to a lesser extent in *D. (E.) bibliana*. This specimen is referred to *Diplodon (Ecuadorea)* on the character of its sculpture and lack of definite posterior angulation. The sculpture is both too strong and too persistent for *Diplodon*, s.str. It is also too irregular for *Rhipidodonta*, *Triplodon*, *Castalia* and *Chevronais*. The three last-named genera have strong to very strong posterior angulations, whilst *Triplodon* is also bi-alate. The unique holotype, LL27820, of *D. (E.) bristowi* Parodiz (*in* Bristow & Parodiz 1982: 26, fig. 2; Fig. 312 herein) is an external mould showing some details of the sculpture and a rather incomplete oval outline of a crushed shell, which, like the present specimen, had a prosogyrous umbo. The two are of about the same size, but *D. (E.) bristowi* differs in having about 30 comparatively weak but rather more regular ribs. *D. (E.) bibliana* differs from both by its chevron-patterned ribbing, shown clearly by the enlarged illustration of the holotype (Marshall & Bowles 1932: pl. 1, fig. 8) and by LL27807 (Bristow & Parodiz 1982: fig. 1). Two Pebasian species, *D. longulus* (Conrad) and *D. gardnerae* (Marshall), both placed in *Diplodon*, s.str., are not dissimilar to the La Tagua fossil. Both have strong sculpture and rather prominent umbones. Their sculpture, however, is chevron-patterned and dies away relatively close to the umbo. *D. (E.) guaranianus* is the most similar living species, but it is more elongate, its umbones are less tumid and its ribbing shows definite traces of chevron patterning. The ribbing of *D. (E.) hylaeus* and *D. (E.) pazi* are also much more regular.

Superfamily **MUTELACEA** Gray, 1847

[*nom. transl.* Parodiz & Bonetto, 1963: 205, *ex* Muteladae Gray, 1847: 197]

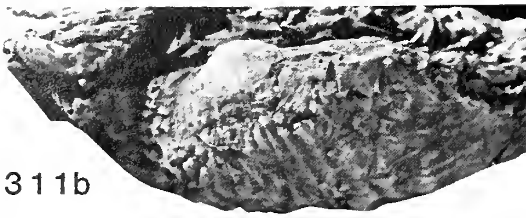
Family **MYCETOPODIDAE** Gray, 1840: 150
Subfamily **ANODONTININAE** Modell, 1942: 175

Haas (1969*a*: 548) attributed the Mutelidae to Conrad (1853: 267). Elsewhere, he also (Haas, *in* Moore 1969*b*: N446) credited Swainson (1840) with authorship of this family. Swainson, however, mentioned neither *Mutela* nor any suprageneric taxon based on it in his work.

Genus ***ANODONTITES*** (*sensu stricto*) Bruguière, 1792*c*.

[= *Ruganodontites* Marshall, 1931*a*, *b*; type species *Anodontites colombiensis* Marshall, 1921, by original designation; Recent, Colombia. *Haplothaerus* Conrad, 1874*b*; type species *H. capax* Conrad, 1874*b*, by monotypy; Late Caenozoic, Pebasian, Iquitos.]

(Figs 313–314)



311b

311a

312

Fig. 311 *Diplodon (Ecuadorea)* aff. *bristowi* Parodiz. LL27889; Late Caenozoic; Loc. 54, La Tagua, Colombia; Eden Colln. a, left valve, × 2; b, dorsal view, × 3.

Fig. 312 *Diplodon (Ecuadorea) bristowi* Parodiz. LL27820; holotype, latex cast of external mould of right valve, × 2. Miocene, Loyola Formation; Loc. CRB 18, Cuenca Basin, Ecuador; Bristow Colln.

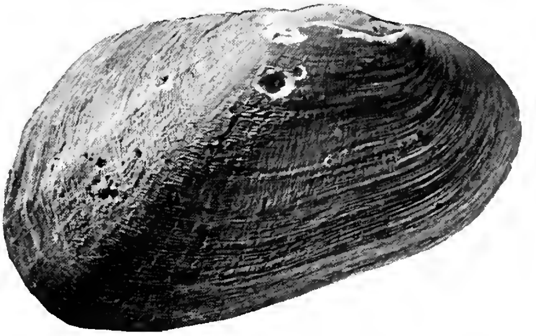


Fig. 313 *Anodontites crispata* Bruguière. Recent, type species of *Anodontites* Bruguière. BMZD 1984229; Ecuador, Geale Colln. Right valve, × 2.

Type species. *Anodontites crispata* Bruguière, 1792*c*, by monotypy. Recent, French Guiana (see Remarks).

Diagnosis. Outline variable, elongate to oval; non-alate or incipiently alate; moderately inflated; periostracum smooth to scabrous, cloth-like, with microscopic radiating rays; shell surface unsculptured except for rare radiating riblets; edentulous; pallial line entire: muscle scars comparatively shallow; outer shell layer of coarse prisms, thickening towards shell margins.

Species assigned. Fossil: (?) *Unio (?Anodon) totiumsanctorum* Hartt 1870, Palaeocene, Bahia Series; north-eastern Brazil (see Parodiz 1969: 14, 15, 84). *Anodon batesi* Woodward, 1871, Late Caenozoic, Pebasian; Pichana, Peru. *Haplothaerus capax* Conrad, 1874*b*, Late Caenozoic, Pebasian; Iquitos (Fig. 314). *Anodontites laciranus* Pilsbry & Olsson, 1935, ?Miocene, La Cira Formation; Middle Magdalena Valley, Colombia. *Anodontites olssoni* Palmer, *in* Liddle & Palmer 1941, Miocene, Biblián Sandstone; Cuenca Basin, Ecuador (see Bristow & Parodiz, 1982: 29).

Recent. Numerous species from South America (Simpson 1914: 1403–1457, Haas 1969*a*: 557–572).

Generic distribution. ?Palaeocene and Neogene to Recent, South America (see Remarks).

Remarks. The conception herein of the genus follows that of Haas (1969*a*, *in* Moore 1969*b*) except that there seems little merit in treating *Ruganodontites* as being subgenerically distinct. Haas (1969*a*: 557) gives a fuller generic synonymy and (1969*a*: 562) a more detailed, but by no means complete, synonymy of the type species, *A. crispata* Bruguière (Fig. 313), whose type material came from Cayenne (French Guiana). His synonymy includes *Anodon reticulatus* Sowerby, 1867 and *Anodonta napoensis* Lea, 1868, thus implying that the species is also present in the Upper Amazon Basin. Haas' assertion that the species also occurs both in Rio La Plata, the Pacific drainage of Ecuador, and in the Magdalena river system of Colombia is probably incorrect. Although von Ihering (1893: 121) lists the species (as *Glabaris reticulata* 'Reeve') from the Amazon Basin, it does not appear in his other faunal lists covering Rio La Plata, Rio Paraguay and southern Brazil. The Colombian record may be based on the misidentification by Ortmann (1921: pl. 41, figs 2a, 2b, 3) of *A. colombiensis* Marshall. Parodiz (1969: 83) suggests that at the present day the genus is best known from north-eastern and central South America, and that west of the Andes it is unknown south of the Equator.

Several species of *Anodontites* have a very scabrous appearance. This feature appears to be confined to the periostracum and is absent on the underlying calcareous shell surface. The features of the outer prismatic layer given in the

Fig. 314 *Haplothaerus capax* Conrad. Copy of type illustration at original size (Conrad 1874*b*: pl. 12, fig. 1). Pebasian; Iquitos; specimen presumed lost (*ex* ANSP). Magnification not known.

above diagnosis is, as explained on p. 264, probably also of superfamilial significance. At the very least, it may be used, as here, to distinguish between species of *Diplodon* and *Anodontites* which sometimes have very similar outlines.

Anodontites (Anodontites) batesi (Woodward, 1871)

Fig. 315

*v. 1871 *Anodon batesi* Woodward: 103, pl. 5, fig. 10.
*? 1874*a* *Anodonta pebasana* Conrad: 29, pl. 1, fig. 5.
1878 *Anodonta batesi* (Woodward) Boettger: 498.

HOLOTYPE. BMPD L27743, Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell colln). Holotype of *A. pebasana* Conrad presumed lost, as not located in ANSP (Johnson & Baker, 1973: 165). No further material.

DISTRIBUTION. Late Caenozoic, Pebasian only, *A. batesi* as above; *A. pebasana* either Pebas, Old Pebas or Pichana (Conrad 1874*a*).

DIAGNOSIS. Elongate *Anodontites* with minute umbones hardly projecting above long, straight, hinge line; anterior and posterior margins both meeting hinge line at definite angle; posteriorly incipiently alate; ventral margin fairly straight, sloping downwards towards posterior; shell surface smooth except for growth lines; edentulous.

DESCRIPTION. The shell of the holotype and only available specimen is partly decorticated. Its outline is considerably modified due to damage to its anterodorsal and posterior regions. Study of growth lines shows that anteriorly the ventral margin curves smoothly upwards into the anterior margin, which eventually becomes recurved and meets the hinge line at a definite angular junction. Posteriorly, the ventral margin also forms a smooth curve with the posterior margin. The latter is rather truncated in the region of mid shell-height, before being recurved into an incipient alation. The junction with the hinge line is angular. The umbones are very small, pointed and prosogyrous. In both valves, the prodissoconch appears to be depressed in the region below the umbones. The outer prismatic layer is absent from large areas surrounding the umbones in both valves. A furrow running posteroventrally from the umbo is clearly visible in the nacreous layer, but is much fainter in the outer prismatic shell layer at about 20 mm from the right umbo. The shell is otherwise smooth except for growth lines. The outer prismatic layer thickens noticeably as it approaches the commissure (i.e. in the later growth stages of the shell). The hexagonal patterning formed by this layer is visible on much of the shell surface.

DIMENSIONS. In mm.	l	(e)l	h	br	l/h
Holotype, L27743	65.4	66.5	39.5	22.2	1.68(e)
A. pebasana (from Conrad's type illustration)	42.4	–	22.5	–	1.89

REMARKS. Woodward's excellent figure shows the shape of the growth lines clearly. He was unable to find (1871: 104) any South American species of comparable form in the British Museum collections (i.e., now BMPD). *A. batesi* is immediately distinguised from virtually all known *Anodontites* by the straightness of its hinge line and by how little the umbones project above it. It bears some resemblance to three species in particular: *A. crispata* Bruguière 1792*c*, *A. trapezialis* (Lamarck, 1819) and *A. colombiensis* Marshall, 1921. Extensive synonymies of *A. trapezialis* from the Rio Solimões are given by Haas (1969*a*: 568) and Fechter (1983*b*: 227); the latter also provided good illustrations (1983*b*: pls A, B) of two junior synonyms *A. giganteus* (Spix) and *A. anserinus* (Spix). None of these three species show traces of posterior alation. The anterior margins of both *A. crispata* and *A. colombiensis* merge smoothly into their hinge lines. Although the anterior margin of *A. trapezialis* meets the hinge line at a definite angle, it is more recurved from the vertical than in *A. batesi*. Both *A. trapezialis* and *A. colombiensis* have long, straight hinge lines and low umbones, whilst the umbones of *A. crispata* are fairly prominent. *A. trapezialis* and *A. crispata* are both less elongate than *A. batesi* and their umbones are situated more posteriorly. The ventral margins of *A. batesi*

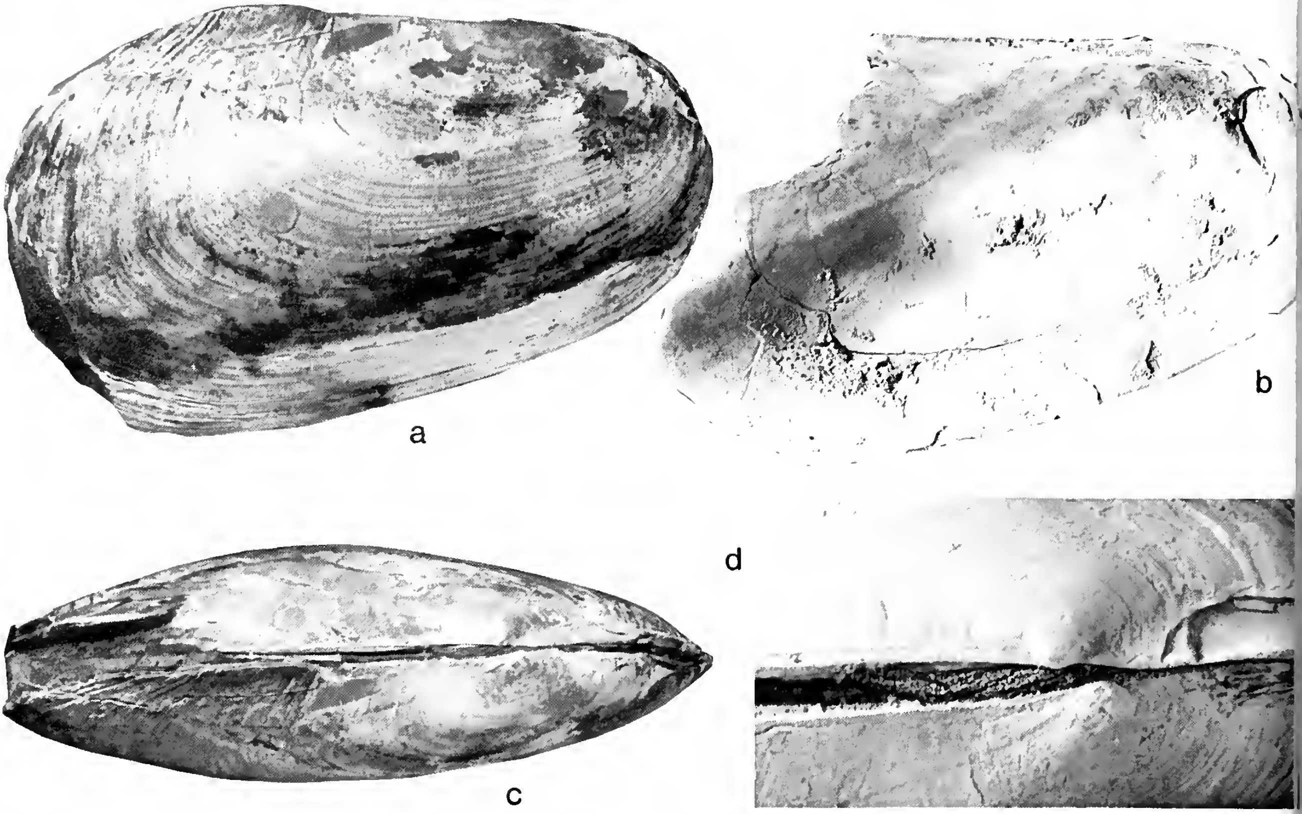


Fig. 315 *Anodontites batesi* (Woodward). L27743, holotype. Pebasian; Pichana, Peru; Hauxwell Colln. a, right valve exterior, × 1.5; b, left valve interior, dorsal view, × 1.5; c, dorsal view, × 1.5; d, umbonal region, × 4. See facing page.

and *A. crispata* are similar: both are comparatively straight and slope downward towards the posterior at about the same angle, though the ventral margin in *A. trapezialis* is more curved.

Conrad's (1874*a*) illustration of *A. pebasana* shows a shell with an outline very similar to that of *A. colombiensis*, but his description does not mention the waisting of the shell below the umbones which is such a distinctive feature of the latter species. *A. pebasana* is thus placed tentatively in the synonymy of *A. batesi*: both have remarkably small umbones and straight hinge lines. The only real differences appear to be that the ventral margin in *A. pebasana* is more parallel to the hinge than in *A. batesi* and that the latter is less elongate.

Parodiz (1969) did not deal with either species formally, but wrote (1969: 84) in his discussion of *Anodontites* that *A. pebasana* probably belonged to the genus, but was also probably likely to be based on a valve of a living species allied to *A. siliquosus* (Spix, 1827). That species lacks pointed umbones (Fechter 1983*b*: pl. E, figs 5, 6) and is best referred to *Mycetopoda* (Haas 1969*a*: 574). In the absence of Conrad's specimen, this point cannot be resolved, but the comparisons made herein strongly suggest that *A. pebasana* cannot be matched with any known living species and is therefore very likely to be fossil. The holotype of *A. batesi* is clearly a fossil, infilled with matrix typical of Pichana. Both valves of this edentulous species were in contact, as in life. This suggests that burial took place very shortly after death, which in turn implies that some truly fresh-water environment which could support naiades existed fairly close to Pichana. It is surprising that this specimen is the only naiad among over 1000 bivalves in Woodward's share of Hauxwell's collection. The only naiad in Conrad's (1871*b*) share of that collection was a 'bivalve related to *Mulleria*' which was apparently not worth illustrating.

Subclass **HETERODONTA** Neumayr, 1884
emend. von Martens, 1884
Order **VENEROIDA** H. & A. Adams, 1856

Superfamily **DREISSENACEA** Gray *in* Turton, 1840

[*nom. transl.* Gill (1871: 19) *ex* Dreissenadae (family) Gray (*in* Turton 1840: 277, 299)].

Family **DREISSENIDAE** Gray *in* Turton, 1840

[*nom. correct.* Gray (1840: 151) (see also ICZN, 1956, Direction 41)].

The suggested generic distribution of members of this superfamily, as outlined by Keen (*in* Moore 1969: N643–4) and Eames (*in* Morley Davies 1971: 244–5), and ideas on its evolution (Morton 1970), need considerable modification in the light of work by Andrussov (1897–8) which has been overlooked by some modern authors. His classification was basically similar to those of the present day in that *Dreissena* van Beneden, 1835, without a myophore, was separated from *Congeria* Partsch, 1835, which possessed one. However,

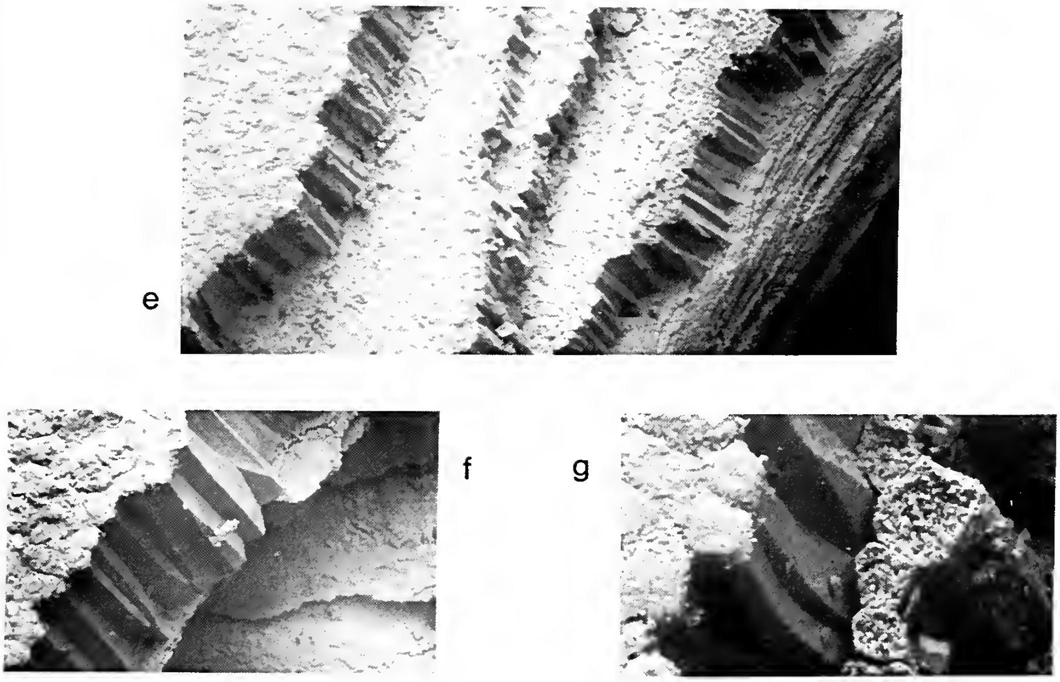
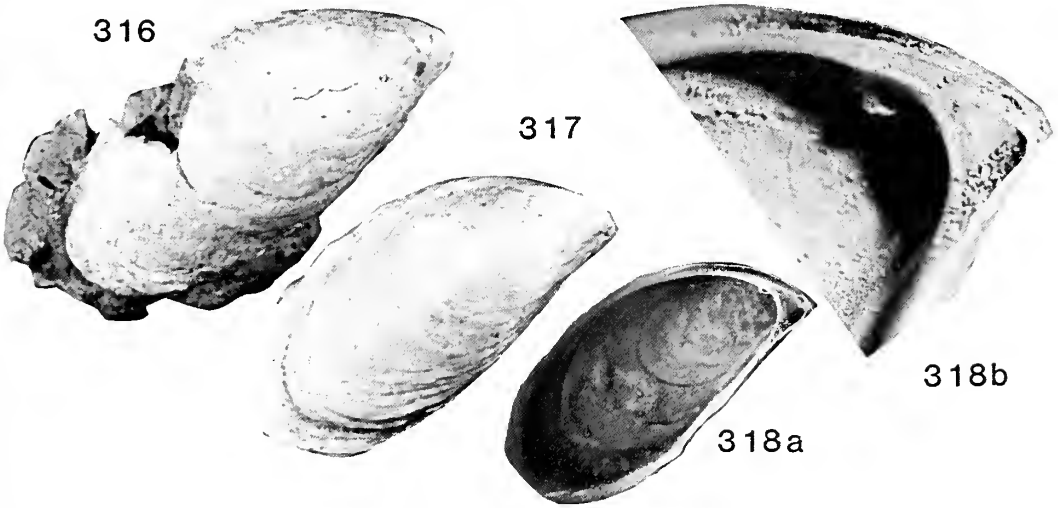


Fig. 315 *Anodontites batesi* (Woodward). L27743, holotype. Electron micrographs showing stout prisms overlying nacreous shell layer. e, × 65; f, × 130; g, × 340. See facing page.



Figs 316–318 *Mytilopsis sowerbyi* (d'Orbigny). Upper Eocene, Headon Beds, Priabonian; Hordwell, Hampshire, England. **316**, BMPD 43249; right valve external, × 4. Lectotype of *Mytilus sowerbyi* d'Orbigny, probably the specimen figured by J. de C. Sowerby (1826: *Min. Conchology* **6**: pl. 532, fig. 2) as *Mytilus brardi* 'Faujas'. **317**, LL28131, F. E. Edwards Colln; right valve external, × 4. **318**, LL28130, F. E. Edwards Colln. a, left valve internal, × 4; b, detail showing septum and apophysis, × 10.

Andrussov, who appears not to have been aware of the erection of *Mytilopsis* Conrad, 1858, which also has a myophore, divided *Congeria* into a number of 'groups' without status in nomenclature. Some have since been revised and described formally by Marinescu (1973), but none of these are of relevance to species under consideration herein. Andrussov's 'mytiliformes' (1898: 69 *et seqq.*) included the western hemisphere Recent species normally assigned to *Mytilopsis*, as well as *Dreissena fragilis* Boettger, 1878, from Pebas. Andrussov's 'modioliformes' (1898: 69, 172 *et seqq.*)

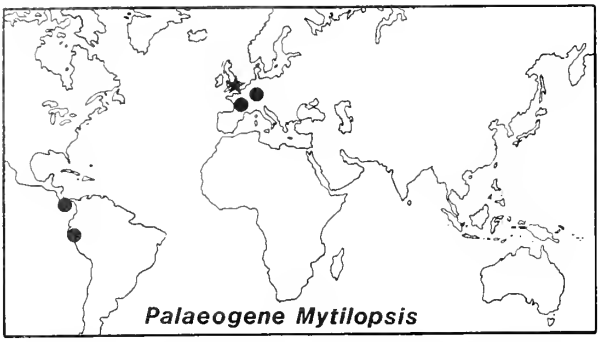


Fig. 319 Worldwide Palaeogene distribution of *Mytilopsis*. ★, Eocene record; ●, Oligocene records.

accommodated species with shapes rather similar to the 'mytiliformes' and included (1897: 175) several European Tertiary species such as *Dreissena sowerbyi* d'Orbigny, 1850 (Figs 316–318) from the Headon Beds of the English Eocene (Priabonian Stage). A re-examination of the type and other material of this species shows that it is not generically separable from *Mytilopsis*. Unnamed specimens in BMPD from Aquitanian and other mid-Tertiary horizons in France and Germany, as well as German material identified by D. Kadolsky (personal communication) as *Mytilopsis brardi* (Brongniart, 1823), confirm the basic soundness of Andrussov's observations.

It thus becomes apparent that *Mytilopsis* was far from rare in the European early to mid-Tertiary, and definitely occurs in the Upper Eocene of England. It also appears that during the late Neogene, *Mytilopsis* is replaced by *Dreissena* in Europe. This is in complete contrast to the generally accepted view that the European fossil species should all be placed in the living genus *Dreissena*, which allegedly first occured in the Eocene, whilst western hemisphere dreissenids should all be assigned to *Mytilopsis* occuring from the Upper Oligocene onwards. The earliest known western hemisphere occurrences of *Mytilopsis* appear to be the records from the Oligocene of Panama and western Peru discussed below. The fossil record, thus reinterpreted, suggests that both *Congeria* and *Dreissena* might be derived from *Mytilopsis*, rather than that *Mytilopsis* is descended in some way from *Dreissena* as has been previously held (Morton 1970).

A further consequence of this revision of the fossil history of *Mytilopsis* is that the numerous cases of its suspected introduction to new areas now need re-examination. As long as it was accepted that the genus was only found fossil in the western hemisphere, it was not reasonable to dispute that anomalous Recent records from Europe, west Africa, Fiji and India were all the result of introductions from the western hemisphere, where the genus was endemic. Morton's tentative hypothesis (1981: 26) that *M. sallei* (Recluz) may have migrated to Fiji *via* the Panama Canal since its completion in 1914 can be questioned on three grounds. First, Dall (1898: 809) had already recorded the genus (as *Congeria*) from Fiji. Secondly, the Panamanian and western Peruvian fossil records from the western part of the Panamic Pacific province during the mid-Tertiary are from areas separated from Fiji only by ocean, and, in any case, considerably predate the land bridge joining South and Central America. Thirdly, Recent species of *Mytilopsis* had already been described by the late 19th Century from the Pacific coast of Colombia and Ecuador (Keen 1971, Olsson 1961, discussed under *sallei*, p. 284): their ancestors must have reached that region before the formation of the land bridge.

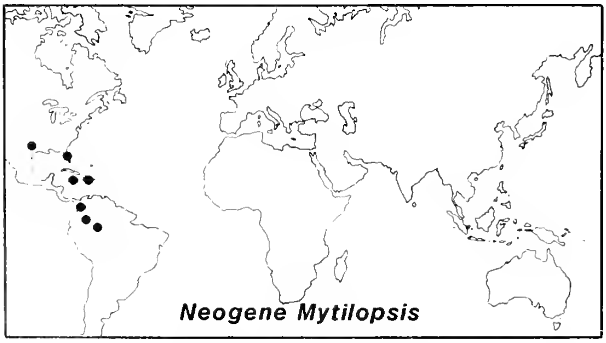


Fig. 320 Western Hemisphere Neogene distribution of *Mytilopsis*.

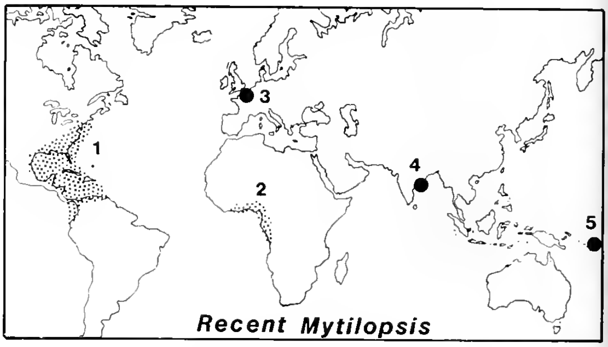


Fig. 321 Worldwide Recent distribution of *Mytilopsis*. 1, Western hemisphere; 2, West Africa (Pilsbry & Becquaert 1927, Binder 1968), probably introduced; 3, Rhine–Scheldt Delta (Adam 1960, Wolff 1969); 4, India (Morton 1981); 5, Fiji (Hertlein & Hanna 1949). 3, 4 and 5 almost certainly introduced.

Genus *MYTILOPSIS* Conrad, 1858

[= *Praxis* H. & A. Adams, 1857: 522, *non* Guenée, 1852: 28 (Lepidoptera). Although several bivalve species were originally listed under *Praxis*, no type designation has ever been made.]

TYPE SPECIES. *Mytilus leucophaetus* Conrad, 1831: 263. Recent, eastern United States, Hudson River to Gulf Coast. By subsequent designation of Dall, 1898: 808.

DIAGNOSIS. Rather small mytiliform dreissenid; apophysis present.

OTHER SPECIES ASSIGNED. Recent: other species recognized herein from the western hemisphere are *Dreissena sallei* Recluz, 1849, Caribbean, and *Septifer trautwineana* Tryon, 1866*b*, Pacific drainage, northern South America. All other nominal living species appear to fall into the synonymy either of *M. sallei* (see Marelli & Gray 1983, and p. 280 herein), *M. trautwineana* (see Olsson 1961, Keen 1971) or *M. leucophaetus* (see Marelli & Gray 1983).

Fossil: *Dreissena scripta* Conrad, 1874*a*, Late Caenozoic, upper Amazon Valley, is the only extinct western hemisphere species recognized herein as distinct. Other species include

Figs 322–323 *Mytilopsis leucophaetus* (Conrad). BMZD 1984239; Recent; Green Cove Springs, Black Creek (tributary of St John's river), Florida; attached to submerged wood, collected live 28. 6. 1983 by Messrs Dan C. Marelli & Michael J. Greenberg. **322**a, b, left valve external, internal, both × 3; c, detail showing septum and apophysis, × 10. **323**a, right valve internal, × 3; b, detail, × 10.

Dreissena sowerbyi d'Orbigny, 1850, Upper Eocene, England and *Mytilus brardi* Brongniart, 1823, Aquitanian, Europe.

GENERIC DISTRIBUTION. Fossil: Eocene–Miocene; western Europe. Late Oligocene; Panama and Pacific drainage, Peru. Neogene; Amazon, Caqueta and Magdalena Basins of northern South America, Caribbean and southern United States (Florida and Texas).

Recent (endemic): eastern seaboard, United States; Gulf of Mexico; Caribbean; Pacific coast, Panama to northern Ecuador. Recent (? introduced): Rhine–Scheldt delta (Adam 1960, Wolff 1969); west Africa (Pilsbry & Becquaert 1927: 455–7); Panama; Fiji; India (Morton 1981).

REMARKS. In this paper fossil occurrences of *M. sallei* Recluz are recognized for the first time. Those Pebasian fossils, from the Upper Amazon Valley and other South American localities, which cannot be matched with any living specimens are assigned to the extinct *M. scripta* (Conrad).

Both Keen (*in* Moore 1969: N644) and Eames (*in* Morley Davies 1971: 245) recorded the genus as living in Asia, and it is probable that they were both following Dall (1898: 809) who stated that *Congeria* occurred in China. There appears to be no evidence for this. Morlet (1884: 402) described *Dreissena crosseana* and (1892*a*: 85; 1892*b*: 329) *D. massiei* from Cambodia: examination of these (in BMZD) shows that they belong to *Sinomytilus* Thiele, 1934 (Mytilacea).

The shape of *Mytilopsis* is very simple, with few tangible diagnostic features, and because it is bysally attached and often lives crowded together, it tends to be variable. As a result, a considerable number of nominal species have been erected. Recently, however, our understanding at specific level has improved considerably following work on the Recent Pacific drainage species (Olsson 1961), the very comprehensive study of *M. leucophaetus* (Conrad) and *M. sallei* (Recluz) by Marelli & Gray (1983) and the increasing recognition that *Mytilopsis* has been introduced from the western hemisphere to other regions (Morton 1981). The resulting discontinuous geographical distribution patterns had led to a proliferation of specific names. This is analogous to the way in which new fossil species tend to be erected whenever the fauna of an isolated locality is described. De Greve (1938) was the only author dealing with South American fossil specimens who attempted to evaluate his material by comparing it with that already described from other deposits. It has been possible to take this process considerably further here, as is shown by the synonymies of *M. scripta* Conrad (p. 285) and *M. sallei* (pp. 280–2).

The recognition that *M. trigalensis* Olsson from the Oligocene of western Peru belongs to *M. scripta* and that the living Caribbean *M. sallei* occurs fossil in the Upper Amazon Basin is of interest when considering the Neogene palaeogeography of the region, but it would be dangerous to draw too firm conclusions. The Oligocene occurrences of the genus in Panama and western Peru, when the extended Tertiary Caribbean Province was in existence, mean that an invasion of the Upper Amazon region from the west cannot be ruled out. The great stratigraphical range of the species and the even greater range of the genus means that little can be deduced from it about the age of the Pebasian deposits. The fact that it is not the only living species in the fauna is, however, of some significance.

Marelli & Gray (1983) discussed the various diagnostic features by which *M. leucophaetus* and *M. sallei* might be separated. Of most potential use to palaeontologists are those which are likely to be shown by fossils. These include the more elongate shape of the former species and the differences between the septum and apophysis in the two species. In the former the apophysis is rather broad and is attached more to the rear margin of the septum than to the dorsal edge or hinge of the shell. In the latter species the apophysis is lanceolate and lies almost parallel to the dorsal margin of the shell to which it is attached. Its anterior, pointed, end tends to lie under the dorsal edge of the septum. The apophysis of *M. scripta* resembles that of *M. sallei*. Marelli & Gray's (1983) treatment of *M. leucophaetus* appears to be basically correct. However, *M. americana* (Dunker) is here transferred to *M. sallei*, whilst the holotype (BMZD, Cuming Colln) of *Mytilus tenebrosus* Reeve (1858: pl. 10, fig. 46), which was said to be from the Mississippi, is almost certainly the same specimen that Dunker (1853: 14) described as *Dreissensia cumingiana*. It is clearly a specimen of the European *Dreissena polymorpha* (Pallas). Two fossil occurrences of *M. leucophaetus* are discussed below.

Congeria lamellata Dall (1898) was described from the Plio-Pleistocene Caloosahatchee Formation of Florida. Dall stated that it was more elongate than the living *Congeria rossmassleri*

(Dunker) – here placed in *M. sallei* – and also had a different hinge. Unfortunately, he did not elaborate on this, and his illustrations of the internal features show no distinguishing features. BMPD LL28109–29, (Sowerby & Fulton Colln, 1899) from the Caloosahatchee Formation are allegedly of this species and are preserved in a white limestone. Some of the shells have been developed to show the internal features. Both these and the external shape suggest that a mixture of *M. leucophaetus* and *M. sallei* is present. Clearly, the true identity of Dall's species cannot be resolved without examining his type material. Both these species have been identified as living in Florida (Marelli & Gray 1983) and it is possible that Dall's species is unnecessary. Certainly, the majority of the thoughts that he expressed on the Dreissenacea in this particular paper cannot be accepted without rigorous checking.

Mytilopsis jamaicensis Woodring (1925: 86; pl. 10, figs 13, 14) was based on a single left valve from the Bowden Shell Bed of Jamaica; this is now dated as Pliocene, N19/20 (Blow 1969: 295–297, text-figs 27–29). The dorsal margin is comparatively short, about a third of the shell length. From the external appearance and Woodring's description and comments, it would appear that this species is very close to, if not synonymous with, *M. leucophaetus*. The record suggests that the fossil occurrence of this species extends south of its present-day range.

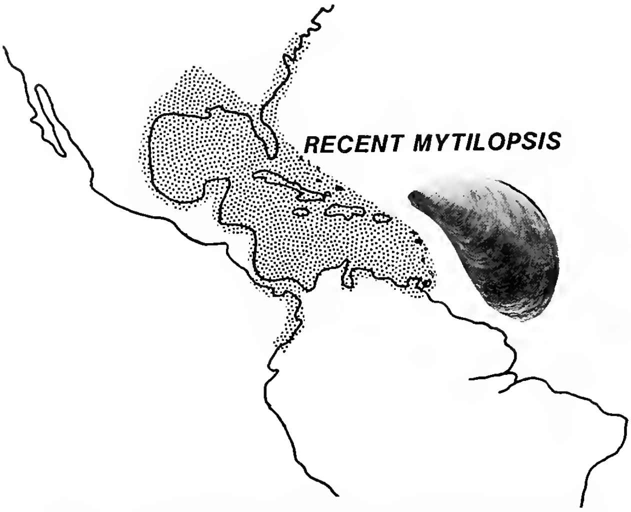


Fig. 324 Recent western hemisphere distribution of *Mytilopsis*. Inset: *M. sallei* (Recluz), eastern Mexico. × 1.5.

Ecological data. *Mytilopsis* is usually found in brackish to fresh water. It occurs in lagoons in west Africa (Binder 1968), and in the western hemisphere. Keen (1971: 114) summarized the occurrence of *M. adamsi* Morrison in fresh water lagoons of San José Island, Panama. Marelli & Gray (1983: 192) report a rather similar distribution for *M. sallei* in coastal lakes and streams, but point out that little is known about its life cycle and factors affecting its distribution. It is often highly gregarious, living byssally attached to the substrate and other shells and nestling in small holes. Salinity tolerance is very high, ranging from fresh-water to supersaline (0–50 ‰). Tolerance to changes in temperature are also high (Escarbassière & Almeida 1976, Sidall 1980, Marelli & Gray 1983). Morton (1981: 37–39) also draws attention to characteristics, such as extensible siphons, ability to close the valves and efficient cleansing internal currents, which enable *M. sallei* to cope with a high sediment load.

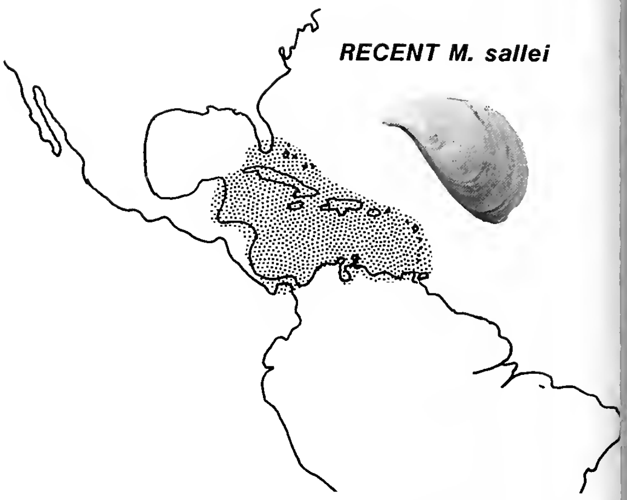


Fig. 325 Recent western hemisphere distribution of *M. sallei* (Recluz). Inset: *M. sallei* (Recluz), eastern Guatemala. × 1.5.

These characters are in keeping with a genus which is normally associated with wide seasonal variations in both salinity and temperature, and explain its ability to invade many Caribbean islands and the Pearl Islands off the Pacific coast of Panama, and to be introduced to other continents, with, or even without, the help of shipping. It is well suited to stretches of water near tropical coasts where salinities and water levels – and hence water temperatures – are likely to vary considerably between the rainy and dry seasons.

Apart from the rare records of *Mytilopsis* in marine faunas (Miocene of Dominican Republic, Maury 1917, and *M. jamaicensis* Woodring, 1925, known only from a single valve), the western hemisphere fossil occurrences of the genus are in faunas indicating reduced salinity, with the genus forming a substantial proportion of the biota.

Mytilopsis sallei (Recluz, 1849) Figs 327–344

* 1849*a* *Dreissena sallei* Recluz: 69.
. 1852 *Dreissena sallei* Recluz: Recluz: 255; pl. 10, fig. 10.
* 1852 *Dreissena domingensis* Recluz: 255; pl. 10. fig. 8.
* 1853 *Tichogonia rossmassleri* Dunker: 89.
1853 *Tichogonia sallei* (Recluz) Dunker: 91.
* 1853 *Tichogonia riisei* Dunker: 91.
1855 *Dreissenia rossmassleri* (Dunker) Dunker: 17.
1855 *Dreissenia sallei* Recluz; Dunker: 18.
* 1855 *Dreissenia morchiana* Dunker: 18.
1855 *Dreissenia riisei* (Dunker) Dunker: 19.
*. 1855 *Dreissenia americana* Recluz MS *in* Dunker: 19.
1855 *Dreissenia domingensis* Recluz; Dunker: 20.
1857 *Dreissena (Praxis) domingensis* Recluz; H. & A. Adams: 522.
1857 *Dreissena (Praxis) morchiana* Dunker; H. & A. Adams: 522.
1857 *Dreissena (Praxis) rossmaessleri* Dunker; H. & A. Adams: 522.
1857 *Dreissena (Praxis) riisei* (Dunker); H. & A. Adams: 522.

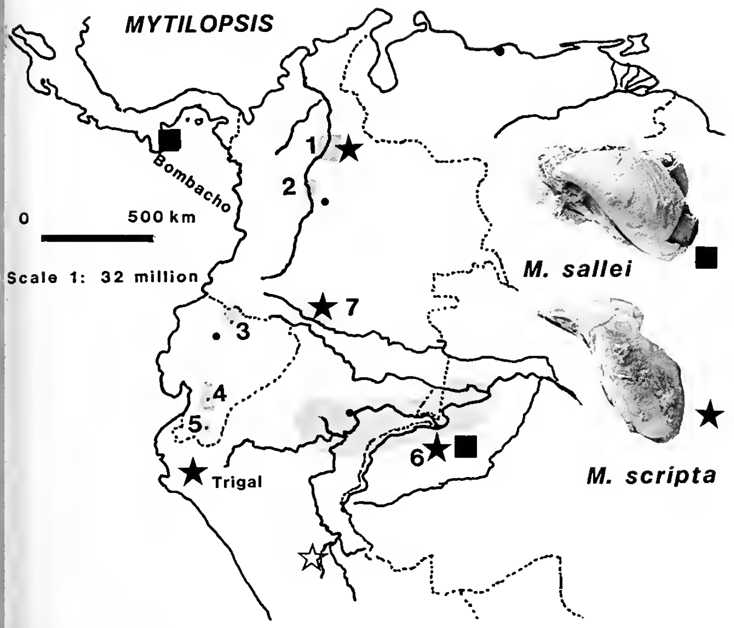


Fig. 326 Tertiary South and Central American distribution of *Mytilopsis*. Key as for Fig. 6 (p. 177). ■, *M. sallei* (Recluz); ★, *M. scripta* (Conrad); ☆ unconfirmed record. Inset: top, *M. sallei*, Canamá; bottom, *M. scripta*, Pichana. Both × 1.5.

1857 *Dreissena (Praxis) sallei* Recluz; H. & A. Adams: 522.

*v 1858 *Mytilus americanus* (Recluz MS) Reeve: pl. 10, fig. 43.

v. 1858 *Mytilus sallei* (Recluz) Reeve: pl. 10, fig. 44.

v. 1858 *Mytilus rossmassleri* (Dunker MS in Mus. Cuming (*sic*)) Reeve: pl. 10, fig. 45.

v. 1858 *Mytilus domingensis* (Recluz) Reeve: pl. 10, fig. 48.

v. 1858 *Mytilus morchianus* (Dunker) Reeve: pl. 10, fig. 51.

. 1858 *Dreissena americana* (Reeve) Fischer: 131.

1858 *Dreissena rossmassleri* (Dunker); Fischer: 132.

1858 *Dreissena morchiana* Dunker; Fischer: 132.

1858 *Dreissena sallei* Recluz; Fischer: 133.

. 1862 *Dreissena (Praxis) sallei* Recluz; Chenu: 157, fig. 782.

* 1878 *Dreissena fragilis* Boettger: 497 (*pars*); pl. 13, fig. 17, (? figs 16, 18).

. 1886 *Tichogonia sallei* (Recluz); Küster & Clessin: 17; pl. 12, figs 13, 14.

. 1886 *Tichogonia americana* (Dunker) (*sic*) Küster & Clessin: 28.

. 1886 *Tichogonia (Praxis) morchiana* (Dunker) Küster & Clessin: 18; pl. 12, figs 11, 12.

. 1886–7 *Tichogonia (Praxis) riisei* Dunker; Küster & Clessin: 25 (1886); pl. 15, figs 12, 13 (1887).

. 1886–7 *Tichogonia rossmaesleri* Dunker; Küster & Clessin: 27 (1886); pl. 15, fig. 77 (1887).

. 1886–7 *Tichogonia domingensis* (Recluz) Küster & Clessin: 26 (1886); pl. 15, fig. 14 (1887).

. 1894 *Dreissensia sallei* Recluz; Fischer & Crosse: 504, pl. 42, figs 4, 4a, 5, 6.

. 1897 *Congeria domingensis* (Recluz) Andrussov: 136; text-fig. 13B (p. 659).

. 1897 *Congeria riisei* (Dunker) Andrussov: 137; text-fig. 13F (p. 659).

. 1897 *Congeria rossmassleri* (Dunker) Andrussov: 138; pl. 20, figs 3–5; text-fig. 13C (p. 659).

. 1897 *Congeria sallei* (Recluz) Andrussov: 139; pl. 20, figs 3–5; text-fig 13E (p. 659).

. 1897 *Congeria morchiana* (Dunker) Andrussov: text-fig. 13A (p. 659).

*. 1898 *Congeria lamellata* Dall: 809 (*pars*); pl. 35, figs 13, 15 (?).

. 1900 *Dreissena sallei* Recluz; von Martens: 477; pl. 32, figs 4, 5.

*v 1906 *Dreissensia dalli* Clerc *in* Joukowsky & Clerc: 171; pl. 6, figs 1–5.

. 1917 *Mytilopsis domingensis* (Recluz) Maury: 195; pl. 39, fig. 5.

. 1924 *Dreissena acuta* Etheridge; Roxo: 44 (*pars*), figs A1, A2, A'1, A'2 (*non* figs A3, A4, A'3, A'4).

. 1938 *Congeria fragilis* (Boettger) de Greve: 49 (*pars*); pl. 9, fig. 15 (*non* figs 8, 14, 15).

. 1938 *Congeria* n. sp. aff. *fragilis* (Boettger) var. II de Greve: 54; pl. 9, figs 23–25, 27.

. 1938 *Congeria* n. sp. aff. *fragilis* (Boettger) var. III de Greve: 54; pl. 9. fig. 26.

* 1946 *Mytilopsis adamsi* Morrison: 46; pl. 1, fig. 4.

* 1949 *Mytilopsis allyneana* Hertlein & Hanna: 14; pl. 4, figs 5–8.

. 1964 *Mytilopsis leucophaetus* (Conrad); Weisbord: 206; pl. 27, figs 11, 12.

1975 *Mytilopsis sallei* (Recluz) Jones & Rutzler: 57 *et seqq*.

. 1976 *Mytilopsis sallei* (Recluz); Escarbassiere & Almeida: 165 *et seqq*.; figs 2, 4–8, 14.

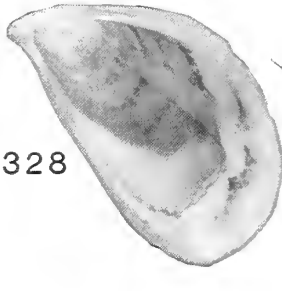
v. 1978 *Mytilopsis sallei* (Recluz); Marelli & Berrend: 144.

v. 1981 *Mytilopsis sallei* (Recluz); Morton: 25 *et seqq*.; figs 1–12.

. 1981 *Mytilopsis allyneana* Hertlein & Hanna; Morton:

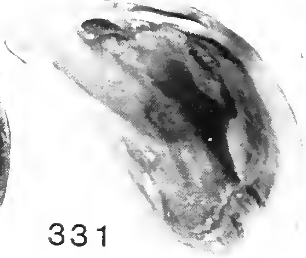

327

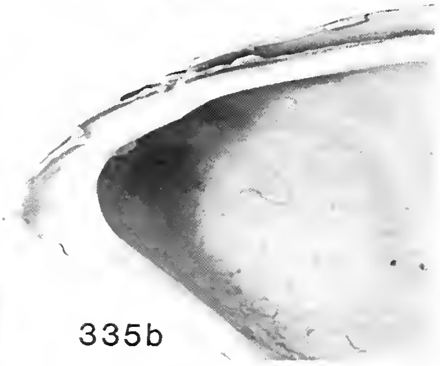

329


328


332

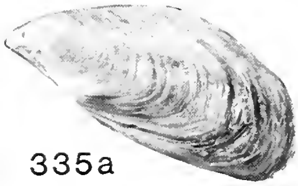

330


331


335b


334


333


335a

Figs 327–334 *Mytilopsis sallei* (Recluz). Recent; western hemisphere. **327**, BMZD 1984230; left valve external, × 2.5. Shell figured as *Mytilus sallei* (Recluz) by Reeve (1858: pl. 10, fig. 44); Central America; Cuming Colln. **328**, BMZD 1984230; right valve internal, × 2.5; shell from same sample as Fig. 327. **329**, BMZD 1984230; left valve internal showing septum and apophysis, × 10; shell from same sample as Fig. 327. **330**, BMZD 1984231; left valve, × 2.5; Laguna Bacalar, eastern Mexico; D. C. Marelli Colln. **331**, BMZD 1984231; right valve interior, × 2.5; same sample as Fig. 330. **332**, BMZD 1984233; left valve, × 2.5; shell figured as *Mytilus rossmassleri* (Dunker *MS* in *Mus. Cuming*) by Reeve (1858: pl. 10, fig. 45), labelled (erroneously) 'United States'; Cuming Colln. **333**, BMZD 1984235; right valve, × 4; shell labelled as *Mytilus riisei* Dunker; Vieque Island; Cuming Colln. **334**, BMZD 1984236; left valve, × 2.5; shell figured as *Mytilus domingensis* (Recluz) by Reeve (1858: pl. 10, fig. 48); Dominican Republic; Cuming Colln.

Fig. 335 *Mytilopsis africanus* (van Beneden). BMZD 1984238: a, left valve external, × 1.5; b, right valve internal showing septum and apophysis below, × 4. Shell figured by Reeve (1858: pl. 10, fig. 47); Recent; Senegal; Cuming Colln.

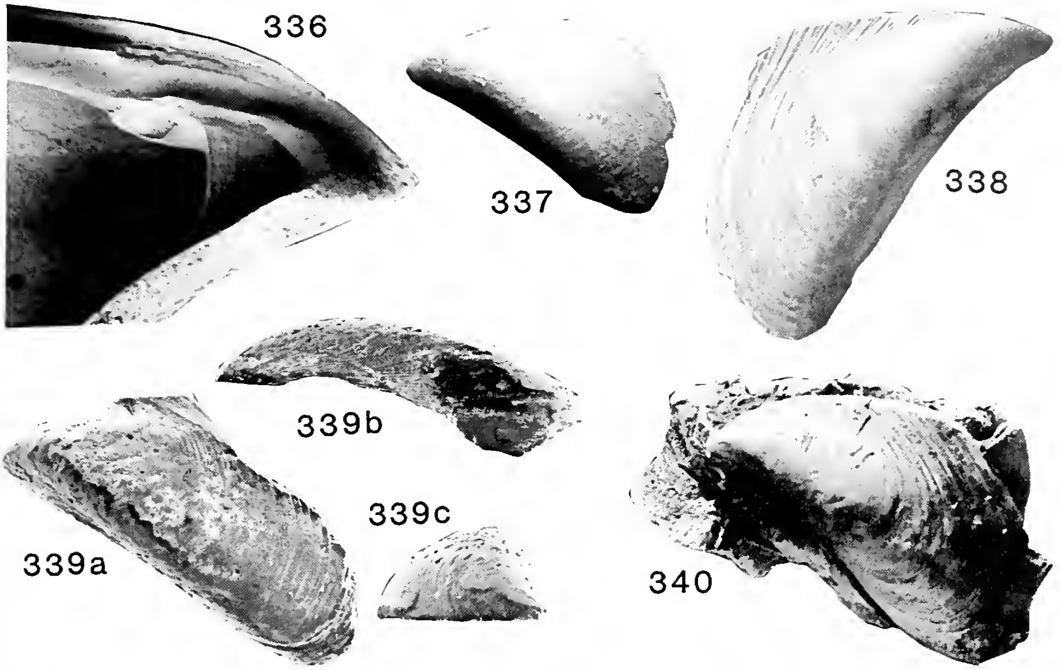
26 *et seqq.*; fig. 12c.

1983 *Mytilopsis sallei* (Recluz); Marelli & Gray: 189, figs 5, 6, 8.

TYPE MATERIAL. Types of *Dreissena sallei* Recluz not studied. Recent, Rio Dulce d'Izabel, Guatemala (Salle Colln; Recluz, 1849*a*).

Lectotype, selected herein, of *Dreissensia dalli* Clerc *in* Joukowsky & Clerc 1906, the shell originally figured as pl. 1, figs 4, 5. The three other specimens, the originals of pl. 1, figs 1, 2, 3, and over thirty unfigured specimens, are paralectotypes. All ? Late Oligocene (originally dated as Miocene or Pliocene), Bombacho, western Panama (Joukowsky Colln, Geneva N.H.M.)

?Syntypes of *Dreissenia americana* Dunker, 1855. Recent. Both Dunker and Reeve (1858) attributed the species to Recluz 'MS'. All three workers were almost certainly basing this species on the four shells in Cuming's Colln (BMZD



Figs 336–340 *Mytilopsis sallei* (Recluz). Pebasian; Peru and Colombia. **336–338**, Pichana; Peru; Hauxwell Colln. **336**, LL28097; left valve internal, showing septum and apophysis, × 12. **337**, LL28099; juvenile left valve, × 10. **338**, LL28098; juvenile right valve, × 10. **339**, LL27966; Puerto Nariño, Colombia; Weeda Colln. a, left valve external, × 10; b, side elevation of long diagonal anteroventral edge, × 10; c, front view, × 6. **340**, LL27915; Canamá, Peru; left valve, × 3; specimen found under holotype of *Dreissena acuta* Etheridge; Barrington Brown Colln.

1984237). They are so small that it is impossible to tell which shell Reeve figured. (*Mytilus americanus* d'Orbigny, 1846: 548 is not this species.)

OTHER MATERIAL STUDIED. Fossil: Late Caenozoic, Pebasian. LL27957, LL27933, LL28096–99, Pichana, Peru (Hauxwell Colln, extracted from matrix, 1982); LL27915, Canamá, found (in 1982) with holotype of *Dreissena acuta* Etheridge (see p. 285; Barrington Brown Colln); LL27966, Puerto Nariño, Colombia (Weeda Colln); LL28109–19, as *Congeria lamellata* Dall, Late Caenozoic; Caloosahatchee, Florida Sowerby & Fulton Colln, 1899).

Recent (All BMZD): Cuming Collection samples generally of three or four shells and including the specimens figured by Reeve (1858) of various nominal species. *M. sallei* Recluz, Central America' (BMZD 1984230); *M. rossmassleri* Dunker MS in Mus. Cum., United States' (BMZD 1984233); *M. morchiana* Dunker, unlocalized (BMZD 1984234); *M. riisei* Dunker, Vieque Island (BMZD 1984235). Numerous pecimens, 1.5 – 2.0 m depth, in scattered clumps, Quintana Roo, Laguna Bacalar, Mexico (Marelli & Berrend 1978) Marelli Colln; BMZD 1984231). Six shells, labelled '*M. allei*, Rio Dulce d'Izabel' (Cuming Colln; BMZD 1984232). Various other samples labelled 'Guatemala', including 3.2.4.2048–9. Specimens labelled *M. africana* (van Beneden), rom Senegal (BMZD 1984238) are possibly synonymous. See p. 284.

FURTHER RECORDS. Fossil: Upper Miocene, Cercado Formaion, Dominican Republic (Maury 1917). Late Caenozoic, Florida (Dall 1898). Raised beach, Venezuela (Weisbord 964). Late Caenozoic, Pebasian; Pebas, Peru (Boettger 878); Iquitos, Peru (de Greve 1938); Três Unidos, Peru Roxo 1924).

Recent. In the following entries, a specific name coupled with that of an author denotes that the reference is to the type locality of the nominal species: Guatemala (Fischer & Crosse 1894); Guatemala and Honduras (Dunker Colln, von Martens 1900); St Thomas Isle, W. I. (Dunker 1853, as *T. riisei*; Dunker 1855, as *D. morchiana*); Unare lagoon, Anzoategui State, Venezuela, 10° 10′ N, 65° W, (Escarbassiere & Almeida 1976); locks of Panama Canal (Jones & Rutzler 1975); Fiji (Hertlein & Hanna 1949, as *M. allyneana*); Visakhapatnam Harbour, Andhra Pradesh, India, introduced (Morton 1981; also BMZD 1984219). The records from Brazil (Dunker 1853, Dall 1898, Weisbord 1964) are not accepted; see discussion below, p. 285.

DISTRIBUTION. Oligocene, Panama; Miocene to Quaternary, United States and Caribbean; Late Caenozoic, Pebasian, Upper Amazon Basin. Recent, Florida, Caribbean widespread. Pacific coast of Panama, to ? northern Ecuador (possibly introduced). Presumably introduced to Panama Canal locks, India, ?West Africa, ?Fiji.

DIAGNOSIS. *Mytilopsis* with gently curved dorsal margin; diagonal ridge well rounded; apophysis elongate, lying adjacent to dorsal margin and partly under septum.

DESCRIPTION. Although the outline is of variable shape, it is generally regular, showing no gross changes in relative growth rates at different parts of the mantle edge, except in the region of the byssal notch. The umbonal ridge varies in strength, but is always well rounded, not angular. The apophysis is lanceolate. It is attached to and has its long axis parallel to the dorsal margin of the shell. Its pointed, anterior, end lies against or just under the dorsal edge of the septum. Its posterior, broad, end is frequently slightly barbed. Recent examples are sometimes tinged with purple or indigo,

Figs 341–344 *Mytilopsis sallei* (Recluz). Late Oligocene, Panama; originally described as *Dreissensia dalli* Clerc *in* Joukowsky & Clerc, from Bombacho, western Panama. Joukowsky Colln, Geneva NHM, all × 3. **341**, **lectotype** (herein selected), shell figured by Clerc (*in* Joukowsky & Clerc 1906: pl. 1, figs 4, 5). a, right side; b, front view. **342**, paralectotype, same details as Fig. 341 (originally figured as pl. 1, fig. 2); left side. **343**, paralectotype, same details as Fig. 341 (originally figured as pl. 1, fig. 3); right side. **344**, paralectotype, same details as Fig. 341 (originally figured as pl. 1, fig. 1); right side.

as in the type illustration (Recluz 1852) of *M. sallei* and in BMZD specimens from Mexico (Marelli & Berrend 1978). Other Recent shells are dirty white with a yellow-brown periostracum, as shown in Reeve's (1858) illustrations of *M. sallei*, *M. rossmassleri* and *M. morchiana*. Some specimens show dark purple concentric banding, which is normally more intense on the inner shell surface.

DIMENSION. In mm.	diag l	l	h	vbr	l/h
D. sallei Recluz 1852 (from type illustration)	22.2	21.0	17.0	–	1.24
M. sallei, shell fig'd Reeve, 1858: fig. 44.	17.5	16.7	14.5	4.4	1.15
M. rossmassleri, shell fig'd Reeve: 1858, fig. 45.	19.2	17.2	16.0	4.8	1.08
BMZD 93.2.4.2048, Guatemala	19.5	15.8	17.2	3.6	0.92
BMZD 93.2.4.2049, Guatemala	24.2	21.2	15.7	4.0	1.35
LL27915, Pebasian, Canamá.	17.2	15.0	13.2	4.0	1.14
LL27966, Pebasian, Puerto Nariño.	5.2	4.1	4.0	–	1.02
PIMUZ 804, *C. fragilis* Boettger, Iquitos; de Greve 1938: pl. 9, fig. 15.	11.9	10.5	9.0	3.8	1.17
PIMUZ 820, as above, var. II, fig. 24.	33.9	28.7	27.0	–	1.06
PIMUZ 821, as above, var. II, fig. 23.	32.5	33.8	27.9	8.6	1.20
PIMUZ 826, as above, var. III, fig. 26.	37.5	38.7	27.5	8.6	1.41

Note. The measurements of PIMUZ specimens are taken partly from de Greve's text and partly from his plates. The length measurements he gave in his text correspond to diagonal or maximum length.

REMARKS. In the small samples of nominal species, in the BMZD collections, variation in shell outline, convexity and strength of the diagonal ridge are sufficient to encompass all the references in the above synonymy. Comparisons with *M. scripta* are given under that species (p. 287) and with *M. leucophaetus* under the genus (p. 279). The synonymy published by Marelli & Gray (1983) is accepted here except for minor points and the addition of some extra Recent references, discussed below. They did not cover fossil taxa, which are also included here.

Marelli & Gray (1983: 190–191) argue that *M. domingensis* (Recluz, 1852) is a synonym of *M. sallei*. This seems reasonable: its apophysis is of the same type and it may be regarded as being typical of the species except for its relatively elongate shell. It seems virtually impossible to tell apart the BMZD shells which Reeve figured as *M. domingensis* from the Dominican Republic, from those he figured as *M. africana* (van Beneden, 1835: 167) from Senegal (Reeve, 1858: pl. 10, fig. 47). Both lots are Cuming collection. It may be suggested that *M. africana* could have been introduced to west Africa along the old slaving routes. The decision to retain *M. sallei* as the name for the species must therefore be regarded as provisional, but any change should await the examination of freshly collected Caribbean and west African material, as there is nearly always some doubt about the accuracy of locality data with samples from old collections. Furthermore, the whereabouts of van Beneden's collection is unknown. It is not in Bruxelles NHM (A. Dhondt, personal communication).

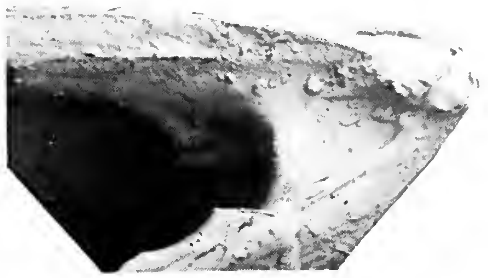
Marelli & Gray (1983) placed *M. americanus* (Recluz) in the synonymy of *M. leucophaetus* (Conrad). I suggest that the Cuming collection shells (BMZD) are the syntypical series of *americana* (p. 282). The apophysis is of the *sallei* type. Dunker, Recluz and Reeve all appear to have made use of Cuming's collection, with the result that their interpretations of the various nominal species are likely to be in accord. Although more research would be necessary to establish whether or not Cuming samples are the syntypes of these species, Reeve's (1858) illustrations of them may still be regarded as the best available interpretation of some of Dunker's unfigured species, such as *M. morchiana*, *M. riisei* and *M. rossmassleri*. Two of Dunker's species, *M. gundlachi* and *M. pfeifferi*, both from Cuba, are unrepresented in Cuming's collection and were not figured by Reeve. Marelli & Gray (1983) placed both in the synonymy of *M. sallei*, but no opinion on them is advanced here.

The living *M. trautwineana* (Tryon, 1866*b*), from the Rio San Juan of the Pacific coast of Colombia, has a semi-straight dorsal margin and its posterodorsal slope is also straight, with these two margins meeting in a very obtuse curve. The most distinctive features of this species are probably its well rounded umbones and exceptionally large septum. It seems reasonable to suppose that this species is distinct from *M. sallei*. Clessin (*in* Miller 1879) described *M. milleri* and *M. ecuadoriana* from Esmeraldas Province, northern Ecuador.

345a

345b

346



Figs 345–346 *Mytilopsis scripta* (Conrad). Pebasian; Pichana, Peru; Hauxwell Colln. **345**, LL27956; a, left valve, side; b, front view; both × 2.5. **346**, LL28100; left valve, details of interior showing septum and apophysis, × 20.

Both have been placed in the synonymy of *M. trautwineana* (Olsson 1961: 140; Keen 1971: 116).

The living *M. rossmassleri* (Dunker, 1853) was described as coming from Brazil, though Dunker had his doubts about the locality data, mentioning that the material was obtained from a trader. Both Dall (1898: 809) and Weisbord (1964) quoted its range as Florida to Brazil. Although comparatively trigonal in outline and with a straighter hinge line than usual, it cannot be considered as distinct from *M. sallei*, which is reported with confidence from Florida (Marelli & Gray 1983: 190), thus confirming that the ranges of this species and *M. leucophaetus* (Conrad) overlap. The Brazilian records of *Mytilopsis* all appear to stem from that of Dunker and are here dismissed. The nearest living occurrences are in Venezuela (Weisbord 1964; Marelli & Gray 1983). It is worth stressing that the genus is not recorded from Surinam by Vernhout (1914), nor in the very comprehensive work of Altena (1971).

The oldest known occurrence of *M. sallei* is its record from western Panama as *M. dalli* Clerc (*in* Joukowsky & Clerc 1906). Joukowsky, who collected the material and described the stratigraphy, thought that his locality was either Miocene or Pliocene. Like *M. trigalensis* Olsson, 1931 (see *M. scripta*, below), *M. dalli* occurs with an ampullinid, which Woodring (1959: 159) placed tentatively in the synonymy of *Ampullinopsis spenceri* (Cooke). Woodring also (1959: 160) mentioned Joukowsky's locality as being Late Oligocene.

The specimen figured by Maury (1917) as *M. domingensis* from the Miocene of the Dominican Republic is slightly deformed, but its almost alate posterodorsal region is typical of *M. sallei*, and thus there seems no reason to suppose that Maury's specimen is of an extinct species.

Mytilopsis scripta (Conrad, 1874) Figs 345–351

* 1874*a* *Dreissena (Mytiloides) scripta* (Conrad: 29; pl. 1, figs 12, 16.
*? 1878 *Dreissenia fragilis* Boettger: 497 (*pars*); pl. 13, figs 16a, b, 18; *non* figs 17a–c.
*v 1879 *Dreissena acuta* Etheridge: 82; pl. 7, fig. 1.
. 1897 *Congeria fragilis* (Boettger) Andrussov: 141 (Russian text); 30 (German text).
*. 1898 *Congeria lamellata* Dall: 809 (*pars*).
. 1924 *Dreissena acuta* Etheridge; Roxo: 44 (*pars*); Figs A3, A′3, A4, A′4; *non* figs A1, A′1, A2, A′2.
*v 1931 *Mytilopsis trigalensis* Olsson: 42 (138); pl. 1 (13), figs 3, 8, 9.
*. 1935 *Mytilopsis cira* Pilsbry & Olsson: 19; pl. 5, fig. 2.
. 1938 *Congeria scripta* (Conrad) de Greve: 56; pl. 9, figs 4, 5, 10, 12; text-figs 4, 5.
. 1938 *Congeria fragilis* (Boettger); de Greve: 49 (*pars*); pl. 9, figs 8, 9, 14; *non* fig. 15.
. 1938 *Congeria* cf. *fragilis* (Boettger) de Greve: 51; pl. 9, figs 19, 20.
. 1938 *Congeria* n. sp. aff. *fragilis* (Boettger) var. I de Greve: 53; pl. 9, figs 13, 16, 17.
. 1938 *Congeria* n. sp. aff. *fragilis* (Boettger) var. IV de Greve: 55; pl. 9, figs 18, 21, 22.
. 1944 *Mytilopsis scripta* (Conrad) Pilsbry: 152.
. 1968 *Mytilopsis scripta* (Conrad) Richards: 83.

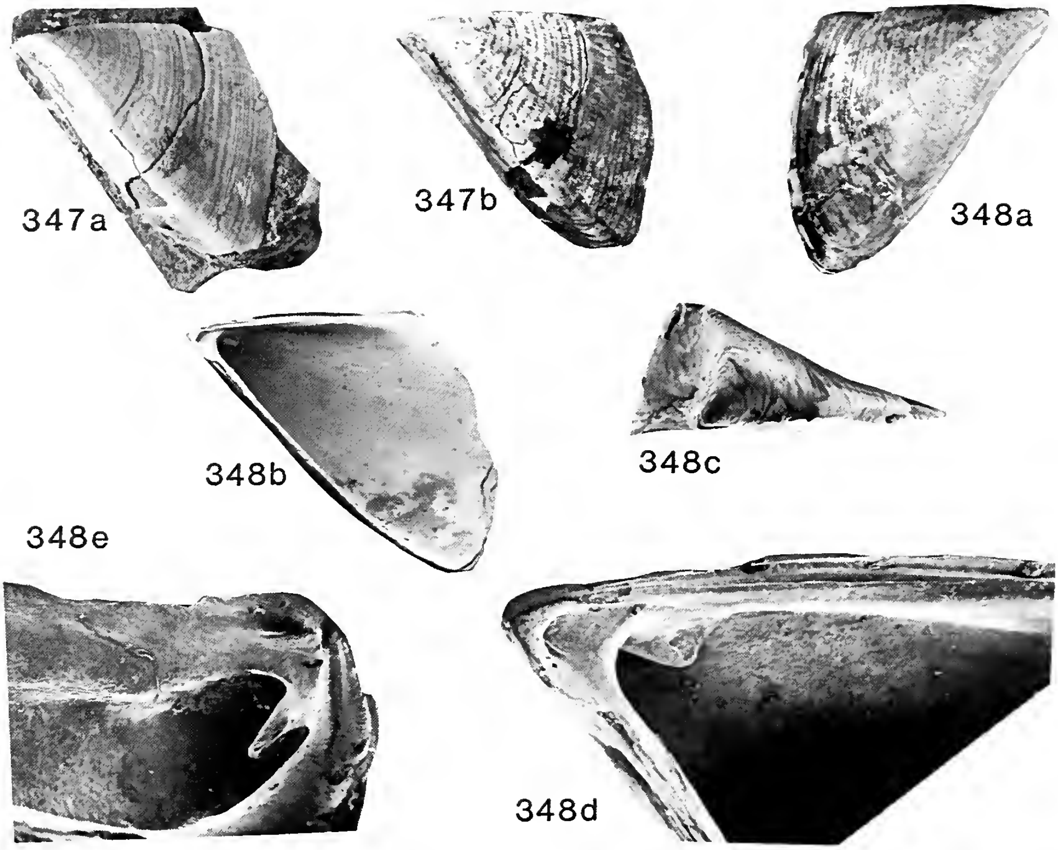
TYPE MATERIAL. Types of *Mytilopsis scripta* Conrad not studied. Conrad (1874*a*) figured several syntypes, one fully grown shell (pl. 1, fig. 16) and three juveniles (pl. 1, fig. 12). His specimens came from either Pebas, Old Pebas or Pichana. Pilsbry (1944) wrote of revealing the myophore on the underside of the septum when cleaning Conrad's type specimen. Richards (1968: 83) listed a possible paratype as being in ANSP (not registered).

Holotype of *Dreissena acuta* Etheridge, BMPD LL27913, Late Caenozoic; Canamá (C. Barrington Brown colln). Etheridge (1879) stated that he had only the one figured specimen, and in view of this the two others found with it cannot be regarded as paratypes. One, LL27914, is this species; the other, LL27915, is now identified as *M. sallei* (Recluz); see p. 283.

Holotype of *Mytilopsis trigalensis* Olsson (1931 : pl. 1, fig. 3; PRI 1927) and paratype (1931: pl. 1, fig. 8; PRI 1932), both ? Late Oligocene, Quebrada Boca Pan, western Peru.

OTHER MATERIAL STUDIED. All late Caenozoic. BMPD LL27911-2, LL27956, LL28100–4, Pebasian; Pichana, Peru (Hauxwell Colln, 1870), extracted from matrix, 1981); LL27901-2, Loc. 33, 570–670 cm, La Tagua, Colombia (Eden Colln); LL28120–9, as *Congeria lamellata* Dall, Caloosahatchee Formation; Florida (Sowerby & Fulton Colln, 1899) (Figs 352–354).

FURTHER RECORDS. Type locality of *Mytilopsis cira* Pilsbry & Olsson (1935), originally given as either late Oligocene or early Miocene, but redated as ? Miocene herein. La Cira Formation, Rio Oponcito area, near Guanabanas, Magdalena Valley, Colombia (fairly common; Pilsbry & Olsson 1935); Late Caenozoic, Pebasian: Pebas (Boettger 1878); Iquitos (de Greve 1938); Três Unidos (Roxo 1924).



Figs 347–348 *Mytilopsis scripta* (Conrad). Pebasian; Canamá, Peru; originally described as *Dreissena acuta* Etheridge; Barrington Brown Colln. **347**, LL27913 (*ex* BMPD 97730); holotype of *Dreissena acuta* Etheridge, figured by Etheridge (1879: pl. 7, fig. 1); a, b, left valve, × 3. **348**, LL27914; right valve found with LL27913, but not mentioned by Etheridge; a, side view, × 5; b, front view, × 8; c, interior, × 5; d, interior, detail showing septum and apophysis, × 20; e, umbonal region viewed from posterior end of shell showing apophysis hanging below dorsal margin of septum, × 20.

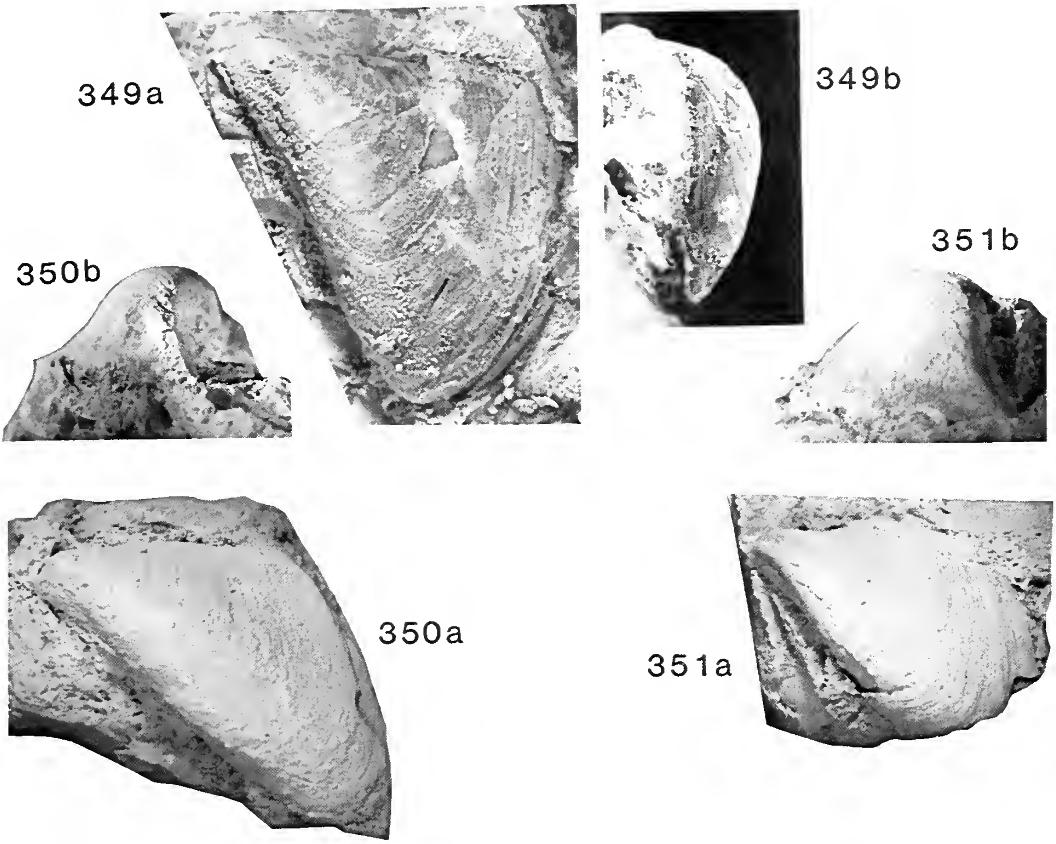
DISTRIBUTION. Late Oligocene, western Peru; ?Miocene, Magdalena Valley, Colombia; Late Caenozoic, La Tagua; Late Caenozoic, Pebasian (Pebas, Pichana, Iquitos, Canamá, Três Unidos).

DIAGNOSIS. *Mytilopsis* with a straight dorsal margin and prominent umbonal ridge; shell outline often markedly trigonal, but sometimes less regular; apophysis similar to that of *M. sallei*, relatively lanceolate, adjacent and parallel to dorsal margin of shell. Colour patterning variable, but sometimes prominent.

DESCRIPTION. The dorsal margin is almost straight and is usually about two-thirds of the total shell length, though sometimes, as in the case of Conrad's type illustration (1874*a*: pl. 1, fig. 16), it is much shorter. The outline is rather variable. At one extreme there are specimens such as LL27956, rather similar to Conrad's type illustration; at the other, the shell is much more triangular as in the holotype of *D. acuta* Etheridge, the type illustration of *M. cira* Pilsbry & Olsson and the two La Tagua specimens. Intermediate stages occur. Examples from Iquitos covering the whole range of variation are illustrated by de Greve (1938: pl. 9). The umbonal angle is also variable. In anterior view, the posterodorsal and anteroventral slopes meet at about right angles to form a prominent umbonal ridge. The ridge itself is sometimes well rounded but often angular. The byssal gape is not easily seen. The septum and apophysis can be seen in LL27914 from Canamá and in several juveniles (e.g. LL27912) from Pichana. Unfortunately, neither the muscle scars nor pallial line are visible enough to be described. The shell is thin. Colour patterning may be seen on some specimens and is variable, consisting either of concentric rays, or of broad zigzag bands, or of radiating patterns of lines or blotches.

DIMENSIONS. In mm.	diag. l	l	h	vbr	l/h
Conrad's type illustration 1874*a*: pl. 1, fig. 16): proportions only, no scale given.	22	17	17	–	1
LL27956, Pichana.	20.8	16.0	18.4	–	0.87
LL27902, Loc. 33/570–670, La Tagua.	7.2	6.1	6.0	–	1.02
LL27913, holotype of *D. acuta* Etheridge, Canamá.	14.3	10.7	10.6	–	1.01
LL27914, *D. acuta* Etheridge, Canamá.	9.6	6.8	7.4	1.8	0.92
M. cira, from Pilsbry & Olsson, 1935: 19.	16.75	–	14	4.25	–
M. cira, from Pilsbry & Olsson, 1935: 19.	18.25	–	16.5	6.25	–

Note. Pilsbry & Olsson (1935) did not indicate which of their measured specimens was the type and gave no scale for their type illustration.



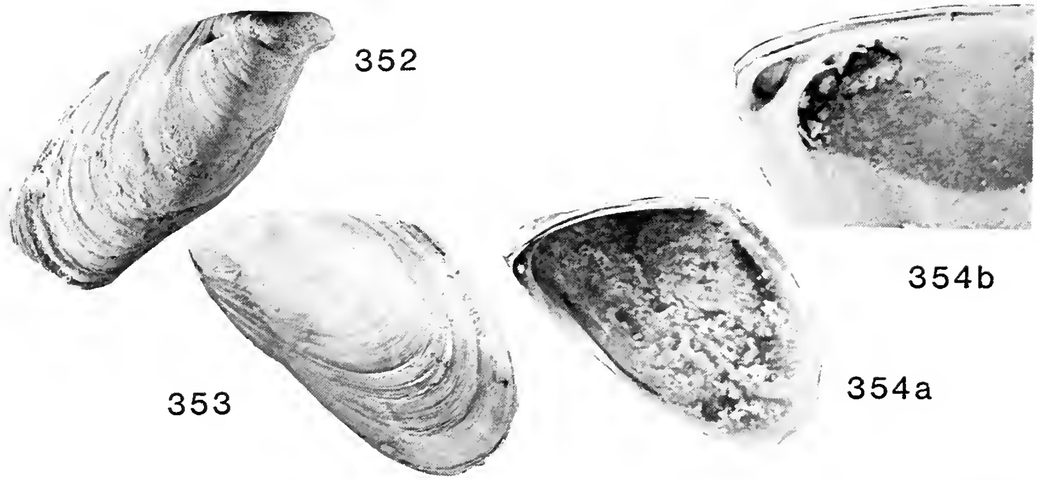
Figs 349–351 *Mytilopsis scripta* (Conrad). Late Caenozoic; La Tagua, and from Pacific coastal area of Peru (originally described as *M. trigalensis* Olsson). **349**, *Mytilopsis scripta* (Conrad), LL27902; Late Caenozoic; La Tagua, Loc. 33/570–670; Eden Colln. a, left valve, side, × 8; b, elevation of anteroventral side. × 5. **350**, PRI 1927; holotype of *Mytilopsis trigalensis* Olsson, figured by Olsson (1931: pl. 1, fig. 3); Late Oligocene; Quebrada Boca Pan, western Peru. a, left valve, side; b, anterior; both × 3. **351**, PRI 1932; paratype of *M. trigalensis*, same details as holotype, originally figured by Olsson (1931: pl. 1, fig. 8). a, left valve, side; b, anterior; both × 3.

REMARKS, *M. scripta* may be easily distinguished from other species of *Mytilopsis* by the straightness of its dorsal margin, coupled with the angularity of its diagonal umbonal ridge. The dorsal margin of *M. leucophaetus* (and its probable synonym, *M. jamaicensis* Woodring, 1925) may be straight, but its umbonal ridge is not so prominent and its apophysis is different from those of both *M. sallei* and *M. scripta*. In *M. sallei*, the dorsal margin is curved to some extent and it merges fairly gradually, with less of an angulation, with the posterior margin of the shell. In *M. scripta*, however, the straight dorsal side and the high, angular, diagonal ridge are strongly reminiscent of the living European *Dreissena polymorpha* (Pallas). Some Recent samples in BMZD, previously identified as *M. rossmassleri* (Dunker) which is now synonymized with *M. sallei*, have comparatively straight hinge lines and strong posterior angulations, but they lack the prominent umbonal ridge of *M. scripta*. In contrast, *M. trigalensis* Olsson (1931) from the Oligocene of Peru resembles *M. rossmassleri* in outline, but is here placed in *M. scripta* because it is strongly ridged. *M. trigalensis* also has some resemblance to the living Pacific drainage species *M. trautwineana* (Tryon), but the latter may be distinguished by its blunter beak and weaker umbonal ridge. Unfortunately, the internal characters of *M. trigalensis*, preserved in hard limestone, are unknown, so no comparison is possible with the unusually large septum of *M. trautwineana*.

Conrad (1874*a*) referred to the colour patterning of zigzag brown lines on his specimens. Similar markings are also present on an Iquitos shell (de Greve, 1938: pl. 9, fig. 12). A few BMPD shells from both Pichana and Canamá show such markings, whilst the colour patterning on a La Tagua specimen (LL27901) consists only of concentric bands. It would thus appear that although such clear-cut colour patterning has not been seen in living species of *Mytilopsis*, it is not an essential feature of *M. scripta*.

When describing *D. fragilis* from Pebas, Boettger (1878) was clearly unaware of Conrad's earlier description of *D. scripta*. The identity of Boettger's species is uncertain. He figured three specimens (1878: pl. 13, figs 16–18). Only fig. 17 was sufficiently complete to be recognizable, and as its hinge line is moderately curved, it is assigned with some confidence to *M. sallei* (Recluz). His fig. 16 lacks the hinge line, whilst his fig. 18 could be either a dorsal or ventral view of a bivalved specimen lacking the umbones. De Greve (1938: 50; pl. 9, fig. 9) figured a shell which he referred to as the original of Boettger's 'pl. 14' (*sic*), fig. 18. De Greve's figure is of a left valve, including the umbo, of a specimen exhibiting the straight hinge line of *M. scripta*: it is certainly not one of Boettger's figured syntypes.

The characters used by de Greve (1938) to separate *M. fragilis* (Boettger) from his 'cf. *fragilis*' and the 'varieties I to IV' of his 'nov. sp. aff. *fragilis*' appear from his illustrations to



Figs 352–354 *Mytilopsis lamellata* (Dall). Plio-Pleistocene, Florida. **352**, LL28109; specimen referred herein to *M. sallei* (Recluz), with *M. sallei*-type apophysis and with external shape resembling its junior synonym, *M. domingensis* (Recluz). Sowerby & Fulton Colln. Right valve, × 2.5. **353**, LL28120/1; specimen herein referred to *M. leucophaetus* (Conrad), same sample as Fig. 352; left valve exterior, × 2.5. **354**, LL28120/2; specimen herein referred to *M. leucophaetus* (Conrad); same sample as Fig. 352. Right valve interior, a × 2.5, b × 10.

be inconsistent. In the present paper, those with straight hinge lines are placed in *M. scripta*, whilst the remainder seem to fall within the range of variation encountered in living *M. sallei*.

The figure of the holotype of *M. cira* Pilsbry & Olsson (1935) shows that its posterodorsal region is damaged, but earlier growth lines indicate that it was correctly described as having a straight dorsal margin. This specimen has a rather trigonal outline and a sharply angled umbonal ridge. Pilsbry & Olsson did not compare their species with any other, but it clearly seems to be synonymous with *M. scripta*.

M. trigalensis Olsson (1931) was omitted by Weisbord (1964: 206–211) from his list of western hemisphere *Mytilopsis*. It was described from the small fauna of the Punta Brava Grits of the Mancora Formation of the Pacific coastal region of northern Peru. Both the Mancora and the overlying Heath Formation were thought by Olsson to be Oligocene. In his account of the stratigraphy (1931: 12), he seemed sure that the Trigal locality underlay the Heath Formation. Eames (*in* Morley Davies 1973: 296), however, suggested that the Mancora Formation was early Miocene on the grounds that it contained *Ampullinopsis spenceri* (Cooke) and also was believed to be the equivalent of horizons in southern Peru and southern Ecuador containing the age-diagnostic benthonic foraminifera *Miogypsina gunteri* and *Miolepidocyclina ecuadoriensis*. Eames gave neither names nor localities for these horizons and offered no supporting evidence for his correlation. Bristow (1975: 128–129), writing without knowledge of Eames' work, quoted the views of other workers who supported an Oligocene dating. *Ampullinopsis spenceri* (Cooke) also occurs at the Panamanian type locality of *Mytilopsis dalli* Clerc, *in* Joukowsky & Clerc, but Olsson's determination of this species was not accepted as definite in the synonymy of that species given by Woodring (1959: 159). Thus, on present evidence, there seem to be no compelling reason for rejecting an Oligocene age for *M. trigalensis*, which along with *M. dalli* (placed here in *M. sallei*) are probably the oldest *Mytilopsis* in the western hemisphere.

Order **MYOIDA** Stoliczka, 1870
Superfamily **MYACEA** Lamarck, 1809

[*nom. transl.* Gill (1871: 18), *ex* Myaires Lamarck (1809: 319; 1818: 423, 459); Myacea (family) Goldfuss (1820: 613)]

Family **CORBULIDAE** Lamarck, 1818

[*nom. correct.* Gray (1840: 150) *ex* Corbulidées Lamarck (1818: 423, 493); Corbuladae Fleming (1828: 425)]

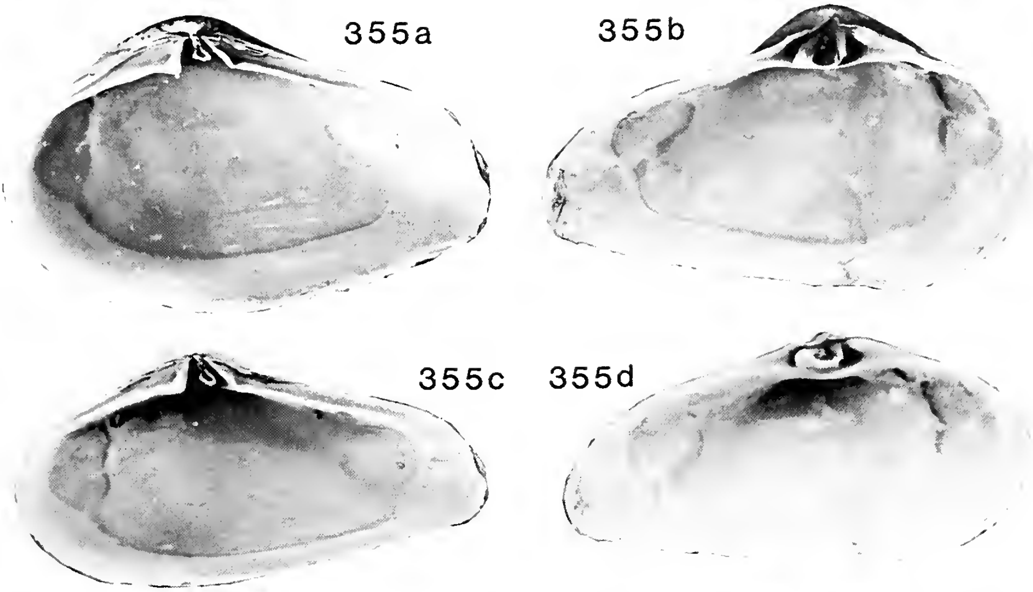
Subfamily **PACHYDONTINAE** Vokes, 1945

[Pachydontinae Vokes (1945: 6)]

Keen *in* Moore (1969: N692) credited Broderip (1839) with latinizing 'Corbulidées' Lamarck as Corbulidae. I have been unable to trace this reference: the earliest use of the family name Corbulidae I have been able to find is that by Gray (1840).

Vokes (1945), in his revision of the Corbulidae, proposed what he described as a tentative new classification, with the erection of several new subfamilies, including the Pachydontinae. In this he placed only two genera, *Pachydon* Gabb, 1869, from the late Tertiary of the Upper Amazon Basin and *Tiza* de Gregorio, 1890, from the Vicksburg Oligocene of Mississippi.

In the present paper, it is suggested that *Tiza* is unlikely to be closely related to *Pachydon* and should therefore be removed from the Pachydontinae. Three other genera, *Pebasia* gen. nov. (p. 315) and *Ostomya* Conrad (1874*a*), both occurring in the same deposits as *Pachydon*, and the living *Guianadesma* Morrison (1943) from the Guyanas, are now assigned to the Pachydontinae. Most previous authors have considered *Guianadesma* to be a junior synonym of *Ostomya*, usually placed in the Lyonsiidae. Most of the reasons for proposing these chages in the classification are given below,



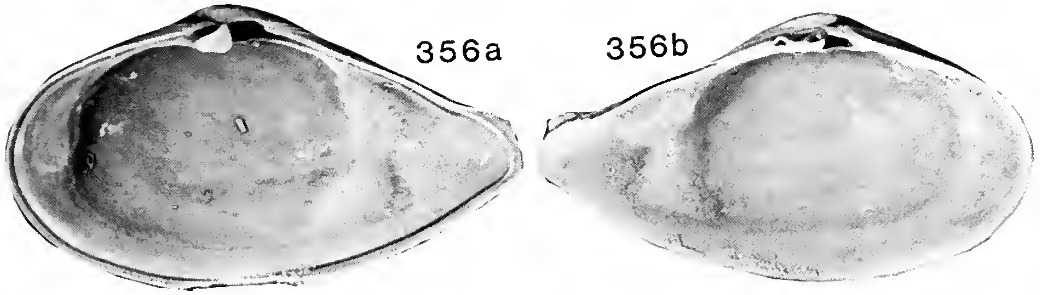


Fig. 355 *Erodona mactroides* (Bosc). BMZD 1854.12.4.754; Recent; specimen identified by d'Orbigny as *Azara labiata* (Maton) from sample labelled 'Buenos Aires and Montevideo'; d'Orbigny colln. a–d, left and right valve internal, normal and slightly tilted views, × 3.

Fig. 356 *Corbula (Caryocorbula) ovulata* Sowerby. BMZD 1984227; Recent; Pacific Coast of Mexico; Cuming Colln. a, b, left and right internal views, × 3.

though a few points are more appropriately dealt with in the remarks following the diagnosis of a particular genus.

Vokes (1945: 6), whose study was based mainly on type species of genera, defined the Pachydontinae as follows: 'Valves tending to be distorted, with the ligamental area so twisted that the resilium was attached to the lateral, rather than to the dorsal face of the condrophore.' Other features of *Pachydon* which should be taken into account in recognizing the subfamily are that the shell is almost smooth and that there are no abrupt changes in post-neanic shell characters as in many other members of the Corbulidae (Cox *in* Moore 1969: N100, fig. 83). The right cardinal tooth is unusual in that in many species its anterior surface is visible from the outside. In species with very incurved umbones, including the type species *Pachydon obliquus* Gabb, this tooth is not in contact with the outside world, but a small lunule-like swelling is present. The hinge plate anterior to the cardinal tooth is either reduced or lacking in the subfamily. Recent *Corbula* and *Erodona* are illustrated for comparison with *Pachydon* (Figs 355–356).

I have not examined specimens of *Tiza*, but Vokes' illustrations (1945: pl. 4, figs 16–22) show that the right cardinal tooth is not close to the outside world and that a substantial area of anterior hinge plate exists. Although *Tiza*, like *Pachydon*, is comparatively smooth and its commissure is twisted, it appears unlikely that the two genera are closely related. It seems much more plausible that *Pachydon* developed independently in the non-marine environment widespread in the Tertiary of northern South America.

Vokes (1945: 27), in a section on names he was rejecting from the Corbulidae, dealt with *Ostomya*, which Conrad (1874*a*) had described from the Pebasian deposits. Vokes placed in its synonymy the living South American *Himella* H. Adams, 1860 (*non* Dallas, 1852, Hemiptera), *Anticorbula* Dall, 1898 – which had been proposed as a replacement name for *Himella* Adams – and *Guianadesma* Morrison, 1943. These genera are each monotypic. Adams described his species *Himella fluviatilis* as a member of the Corbulidae and wrote that it came from the River Marañón. Conrad thought that his *Ostomya papyria* was a member of the Anatinidae (now Laternulidae). Morrison collected his new genus and species *Guianadesma sinuosum* live in Guiana. He interpreted it as an aberrant member of the Lyonsiidae which had lost its ligamental ossification. Vokes' synonymy is the same as that given by Pilsbry (1944), with whom he had been in correspondence on the matter. Pilsbry, however, accepted *Ostomya* as a member of the Corbulidae whilst Vokes, in rejecting it as such, thought that it was probably a member of the Lyonsiidae as suggested by Morrison. Keen *in* Moore (1969: N847) has also followed the same synonymy and placed *Ostomya* in the Lyonsiidae, but her diagnosis, perforce following that of Conrad (1874*a*), has the hinge structures of the two valves transposed.

In the present paper *Himella fluviatilis* is regarded as a *nomen dubium*. The types of both *Himella fluviatilis*, which Adams did not figure, and of *Ostomya papyria* are lost. The material upon which Adams based his description of *H. fluviatilis* was in the Cuming Collection and had been obtained from the naturalist Bates who collected from both the Guianas and the Amazon Region. There is no trace either of these specimens or of any other material bearing this name in BMZD. All subsequent authors' opinions about these two genera have been based on Conrad's rather poor figure and on specimens in ANSP identified as *Himella fluviatilis* and eventually figured by Pilsbry (1944). Pilsbry, however, does not explain how they came to be so identified and no connection with Adams' type material can be found. These specimens are clearly conspecific with *Guianadesma sinuosum* Morrison. Because of the complete lack of authenticated material neither the genus *Anticorbula* Dall not the species *fluviatilis* H. Adams can be defined except by reference to the type series of *Guianadesma sinuosum* Morrison. I have therefore decided to use the name *Guianadesma sinuosum* Morrison here rather than to follow either Altena (1971: 82), who referred to *Anticorbula sinuosum*, or Pilsbry (1944), who used *Ostomya fluviatilis* Adams; both the latter are regarded here as *nomina dubia*. Confidence in ever establishing the true identity of *Anticorbula fluviatilis* is further undermined by doubts about the locality data. Both Adams' and Pilsbry's shells were said to come from the River Marañón. There is a strong probability that Pilsbry's were mislocalized for, as has been said, they clearly belong to *G. sinuosum*, a species so far known living only in the Guianas. If Adams was correct in stating that his species came from the fresh-water Marañón, it might be expected that it would be distinct from the brackish-water *G. sinuosum*, living 2000 km further to the east.

The type locality of *Ostomya papyria* could be any one of the three fossil localities visited by Steere (*in* Conrad, 1874*a*: 26–27), Pebas, Old Pebas or Pichana. These lie within 25 km of each other and have yielded very similar faunas. They are thought to be of the same geological deposit and are certainly of very similar age and facies. Newly extracted specimens from the matrix of Hauxwell's collection from Pichana are almost certainly of *O. papyria*, and are indeed from one of the possible type localities. They resemble Conrad's figure closely and cannot easily be confused with other known species in the fauna. They also agree with the original description, bearing in mind that Conrad also confused the left and right valves of two other species of bivalves he described in the same paper, *Pachydon* (*Anisorhyncus* ?) *dispar* – now the type species of *Pebasia* – and *P. (A.) cuneiformis* (1874*a*: 26, 27). Pilsbry (1944: 147–149) clearly did not have Conrad's material for study when discussing *Ostomya*, though in the same paper (1944: 149–150) he went on to redescribe *Pachytoma tertiana* and *Tropidobora eborea*, both of which were also originally described by Conrad (1874*a*). These were both listed by Richards (1968), who does not record *O. papyria*.

The hinge structures of *Ostomya* and *Pachydon* show strong similarities; that of *Guianadesma* is one of the same general type, but is reduced. A feature common to all three is the lanceolate resilifers disposed in different planes in the two valves, and the twisting of the ventral commissures. The shells of the Lyonsiidae are always predominantly nacreous (Taylor *et al*. 1969, 1973, Prezant 1981). Morrison (1943: 50) described the shell of *Guianadesma* as nacreous-porcellanous within. I have examined under the binocular microscope (at ×30 and ×100) all the available material of *Guianadesma*, *Ostomya* and *Pebasia*, along with numerous specimens of *Pachydon* and both Recent and fossil *Corbula*, including the rather porcellanous *Bicorbula gallica* (Lamarck) from the Eocene of France. The shell of all of these appears to be very similar, consisting of crossed lamellar and complex crossed lamellar structure. Nacre has not been observed.

Morrison (1943) also described the inner and outer branchiae of *Guianadesma* as subequal and (1943: 50) as eulamellibranchiate. He gave no indication that the branchiae were distinctively unusual as in *Lyonsia* and *Pandora* (Ridewood 1903: 151–152, text-figs 1B, 2J; Cox *in* Moore 1969: N20, fig. 20). In fact, Morrison did not base his reasons for placing *Guianadesma* in the Lyonsiidae on either shell structure or gill type.

It is clear that neither *Ostomya*, *Guianadesma* nor *Pebasia* belong to the Lyonsiidae and the features they share with *Pachydon* are sufficient grounds for placing them all in the Pachydontinae. The possibility remains, however, that *Guianadesma* and *Ostomya* may be descended from some other corbulid ancestor which independently invaded brackish and possibly fresh water environments in South America during the Tertiary. So far, *Ostomya* is known only by its type species *O. papyria* Conrad. All other records of that genus are here rejected, some being of *Guianadesma*. The presumed earliest record of *Guianadesma* is *G. colombiana* (Pilsbry & Olsson, 1935) – originally described as *Ostomya* – from the ? Late Oligocene or early Miocene La Cira Formation, in which *Pachydon cebada* (Anderson) also occurs. It seems possible that these genera both originated at about the same time. *Guianadesma* is of special interest as the sole surviving possible member of the Pachydontinae.

Genus ***PACHYDON*** Gabb, 1869

[= *Anisothyris* Conrad (1871*b*: 196), an unjustified substitute name for *Pachydon*; = *Pachydon* (*Anisorhynchus*) Conrad (1874*a*: 28; type species by monotypy *Pachydon* (*Anisorhynchus*) *cuneiformis* Conrad 1874a: 28), Late Caenozoic, Pebasian; Peru.]

TYPE SPECIES. *Pachydon obliquus* Gabb, 1869, by subsequent designation of Dall (1872: 91) and independently by Meek (1876: 240). Late Caenozoic; Pebas, Peru.

DIAGNOSIS. Small to large Pachydontinae, up to 50 mm in length; surface often almost porcellanous, with weak growth lines; weak concentric ribbing mainly on later growth stages and posterior slope; umbones often strongly incurved and prosogyrous; sometimes equivalve but normally with right valve more convex than left; commissure often markedly twisted; right valve margin often grooved for reception of left valve with posterodorsal portion of groove sometimes developing into elongate posterolateral socket; right cardinal tooth massive and adjacent to outside world in most species; lunule-like protuberence often present in front of umbones; right posterior resilium pit trigonal and deep, arising at umbo and sloping in a posteroventral direction, thus partly obscured by cardinal tooth; resilifer lanceolate and forming shallow groove slightly posterior to the centre of the socket; left valve with deep trigonal cardinal socket, separated by weak postero-

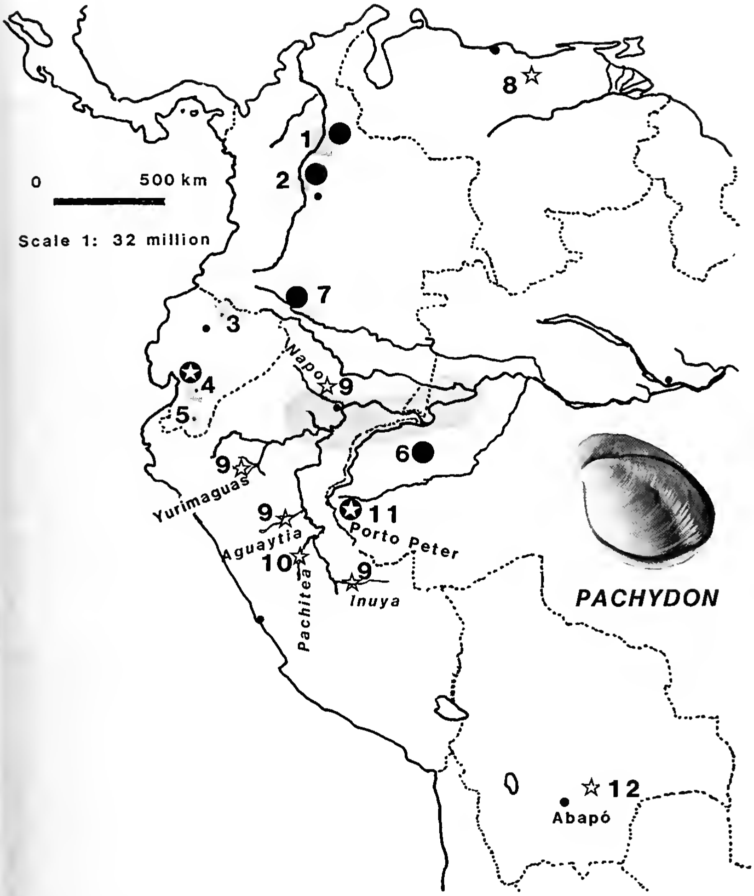


Fig. 357 Neogene distribution of the extinct genus *Pachydon*. Key as for Fig. 6 (p. 177) with additions: 8, Venezuela (Rutsch 1951); 9, Peruvian localities of Bassler (Willard 1966); 10, Pachitea River as *Corbula arcana* (Pilsbry 1944); 11, Porto Peter, Brazil as *Anisothyris acreana* (Maury 1937); 12, Taterenda Formation, Bolivia, as *Tellina* sp. (Mather 1922). Inset: *P. obliquus* Gabb, Pichana. × 1.5. Black circles, = authenticated records; white stars, = doubtful records; white stars in black circles, = discredited records.

dorsal septum from overlying resilifer; resilifer lanceolate, lying almost in plane of commissure and subparallel to hinge, bordered dorsally by elongate process which functions as posterolateral tooth; mantle cavity rather small, with pallial line some distance from commissure; pallial sinus very shallow, normally only a truncation of the pallial line in front of posterior adductor scar; anterior and posterior pedal or byssal muscle scars situated at dorsal margins of anterior and posterior adductor scars respectively; other scars situated either just above the first anterior pedal (or byssal) or on anteroventral surface of hinge plate and also under hinge plate. Shell structure, outer layer crossed lamellar; inner layer within pallial line, complex crossed lamellar.

Other species assigned. *Pachydon tenuis* Gabb, 1869 (= *Pachydon ovata* Conrad, 1871*b*, = *Anisothyris hauxwelli* Woodward, 1871, unjustified replacement name for *P. tenua* Gabb); *Tellina amazonensis* Gabb, 1869; *Pachydon carinatus* Conrad, 1871*b*; *Pachydon erectus* Conrad, 1871*b* (= *Pachydon alta* Conrad, 1871*b*, = *Corbula canamaensis* Etheridge, 1879); *Anisothyris erecta elongata* Boettger, 1878; *Pachydon cuneatus* Conrad, 1871*b* (= *Anisothyris tumida* Etheridge, 1879); *Corbula (Anisothyris?) ledaeformis* Dall, 1872; *Corbula hettneri* Anderson, 1928; *Corbula cebada* Anderson, 1928 (= *Corbula abundans* Pilsbry & Olsson, 1935, = *Corbula magdalensis* Pilsbry & Olsson, 1935); *Anisothyris iquitensis* de Greve, 1938; *Pachydon trigonalis* sp. nov. (p. 309); *Pachydon ovalis* sp. nov. (p. 305).

Doubtful species. *Anisothyris acreana* Maury (1937: 4), Late Caenozoic; Valley of Rio Juruá, Acre Province, Brazil. This species is based on internal moulds and the type illustrations (1937: figs 1–4) show no characters diagnostic of *Pachydon*. The age of the type locality was reviewed by Simpson (1961), who concluded that it was probably Pleistocene, if not younger, and quoted the opinion of D. W. Taylor that the species might belong to the Corbiculacea. Both *?Ostomya terminalis* Pilsbry, 1944 and *?Corbula arcana* Pilsbry, 1944 were described from the Pachitea River Red Beds of imprecisely known Tertiary age. Neither species is generically determinable from their type illustrations. None of these doubtful species have been examined in the course of the present study.

Distribution. Unknown living. Widespread during the late Caenozoic of northern South America, particularly in Pebasian deposits of the Upper Amazon Valley of easternmost Peru and adjoining regions of Colombia and Brazil. Now also recognized in the following deposits, all thought to be Miocene: La Tagua Beds, Caqueta River, Colombia; La Cira Beds, Middle Magdalena Valley, Colombia; Santa Teresa Formation (*ex* Guaduas Beds of Anderson, 1928), Upper Magdalena Valley, Colombia. Recorded from ill-defined horizons and localities in Venezuela (Rutsch 1952). The genus is unknown in Ecuador (Cuenca Basin, etc.); the record of *Erodona iquitensis* (de Greve, 1938) in Bristow & Parodiz (1982:31) appears to be based on a misidentified specimen, BMPD LL27817, of *Corbicula cojitamboensis* Palmer, *in* Liddle & Palmer 1941. See p. 315.

REMARKS. The distribution of this genus provides some of the most important palaeontological evidence on the Neogene palaeogeography of northern South America, and is discussed in more detail in a later section, especially p. 353.

The first designation of a type species, *Pachydon obliqua* Gabb, by Dall (1872 : 91) has been generally overlooked: fortunately the later, but usually accepted, designation by Meek (1876: 240) was of the same species, which also has the merit of being common.

Vokes (1945) was correct in retaining Gabb's original name *Pachydon*. He pointed out that although *Pachyodon*, first used by von Meyer, 1838, for a mammal, is a valid name, this was no reason for adopting, as most authors have, Conrad's substitute name *Anisothyris*. Conrad's own usage was peculiar: in spite of the fact that he proposed this unjustified substitute name, he always described (1871*b*, 1874*a*) the numerous species he dealt with under *Pachydon*.

The lengthy diagnosis and discussion given here is warranted by the wide variation in morphology exhibited by the genus and the fact that Vokes' views were based largely on his study of the type species only, which happens to be one of the most inequivalve so far discovered. In sorting over 1000 specimens from Pichana in the Hauxwell Collection (BMPD), it became clear that six apparently sound species occurred together. Most of the specimens were individual shells, but the presence of several blocks provided some confirmation of co-occurrence. Individual specimens may be assigned to species with confidence and shells showing characters intermediate between species have not been found. Material from other localities supports this view. The collection from Pichana is dominated by large numbers of *P. obliquus* Gabb and *P. tenuis* Gabb; most of the other species are comparatively rare.

Dall (1872) argued at some length that there were no hard and fast reasons for separating *Pachydon* – for which he used the name *Anisothyris* – from *Corbula*, but finally concluded that subgeneric separation was desirable. He wrote (1872: 91) that 'there is a general physiognomy which is somewhat peculiar, though valueless when subjected to rigid criticism; and the following characters are especially emphasized in most of the species. The beaks are usually (but not always) more oblique and more posterior and more spiral than in most *Corbula*, and the external surface is usually smoother, though often like that of typical *Corbula* . . .' His views must still command some support. Within the genus, the wide variation in shell shape, which is possibly due to different species adopting different attitudes within the substrate, may be linked with differences in the hinge regions. Thus the shapes and attitudes and positioning of the right cardinal tooth, of the various sockets, resilium pits and resilifers, of the umbones and the adductor muscles, and also the presence or absence of lateral teeth have all varied in order that the two valves might articulate correctly. The genus includes the highly gibbous *P. erectus* Conrad, with a truncated anterior and rather alate posterior, and the slim *Paphia*-shaped *P. amazonensis* Gabb: both of these are virtually equivalve. There are also several moderately inequivalve species, such as *P. tenuis* Gabb, and the very inequivalve *P. obliquus* Gabb, with cornuate umbones reminiscent of *Glossus*. Examination of the very large number of specimens available suggests that there is no justification in erecting separate genera for equivalve and inequivalve species. *Pachydon*, therefore, must be recognised on a variety of features which are not constant for all species but, taken together, are unusual for the Corbulidae, and provide justification for Vokes' Subfamily Pachydontinae.

The first valid use of *Anisorhynchus* was by Schönherr (1842) for Coleoptera. *Anisorhynchus* Conrad (1874*a*: 28) was described as a subgenus of *Pachydon*, but is here regarded as being synonymous. It was based on what Conrad described as a single right valve – now lost – of its type species, *P.* (*A.*) *cuneiformis* Conrad (1874*a*: 28), but his inadequate figure (pl. 1, fig. 19) is of a left valve. It appears to be a typical *Pachydon*: no dimensions were given. On the previous page (1874*a*: 27) Conrad described another, very different species, as *P.* (*Anisorhynchus* ?) *dispar*, again confusing the two valves. This is here made type species of the new genus *Pebasia*. Other molluscan usages of *Anisorhynchus* were reviewed by Vokes (1945: 15, 16) under his substitute name *Ursivirus* for a very different Cretaceous taxon.

The name *Pachydon*, meaning 'thick tooth', is derived from the Greek word οδούς, a tooth, which is masculine. Trivial names which are adjectives have been inflected to agree where necessary.

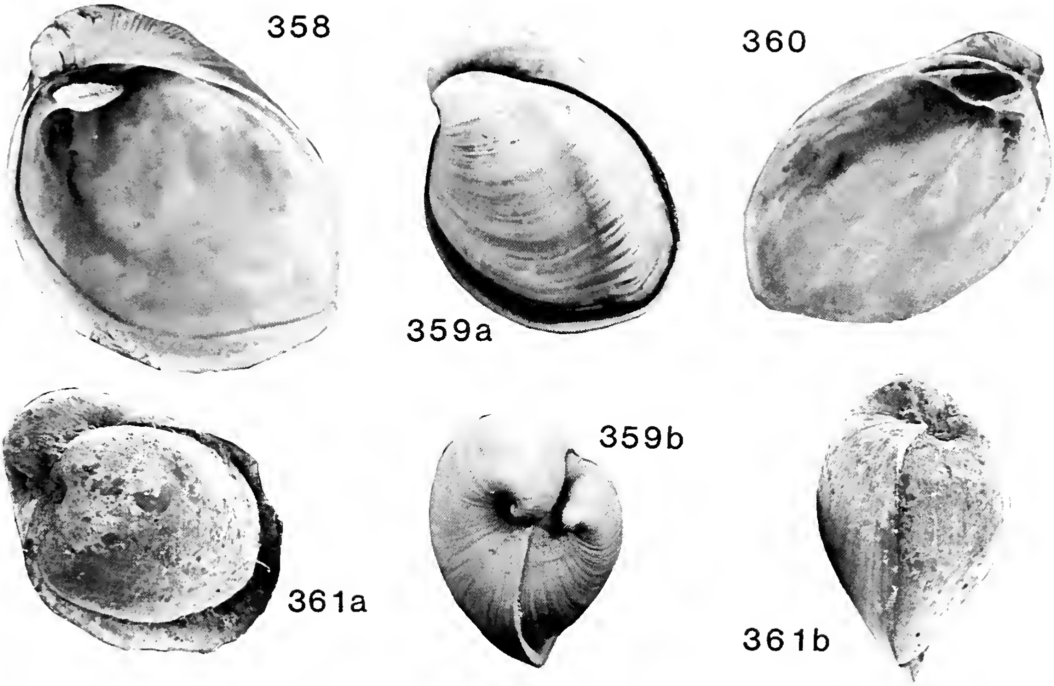
Pachydon obliquus Gabb, 1869 Figs 358–361

* 1869 *Pachydon obliqua* Gabb: 99; pl. 16, figs 5a–e.
. 1871*b* *Pachydon obliquis* Gabb (*sic*); Conrad: 196; pl. 10, fig. 15.
v. 1871 *Anisothyris (Pachydon) obliqua* (Gabb) Woodward: 106; pl. 5, figs 5a, b.
. 1872 *Corbula (Anisothyris) obliqua* (Gabb) Dall: 91.
. 1878 *Anisothyris obliqua* (Gabb); Boettger: 501; pl. 14, figs 18–22.
. 1878 *Anisothyris obliqua* (Gabb)–*A. carinata* (Conrad), transitional form; Boettger: 501; pl. 14, figs 16, 17.
. 1887 *Corbula (Anisothyris) obliqua* (Gabb); Fischer: 1124.
. 1906 *Pachydon obliquus* Gabb; Clarke: 133.
. 1938 *Anisothyris obliqua* (Gabb); de Greve: 40; pl. 7, figs 5, 9, 12, 14, 23.
. 1945 *Pachydon obliqua* Gabb; Vokes: 21; pl. 4, figs 11–15.
. 1966 *Anisothyris obliqua* (Gabb); Willard: 65–69; pl. 57, figs 2, 3.
. 1969 *Pachydon obliqua* Gabb; Keen *in* Moore: N697, fig. E158, 7a–e.

TYPE MATERIAL. Not Studied. Late Caenozoic; Pebas, Peru (Gabb 1869). (ANSP, lost, not mentioned by Richards, 1968).

MATERIAL STUDIED. All late Caenozoic, Pebasian. L27749 (figured Woodward, 1871: pl. 5, figs 5a, b), Pichana, Peru, Hauxwell colln; L27750–2; L27703–11 (details as above, about 300 specimens). LL28008/1–7, Canamá, Brazil, juvenile valves, extracted from matrix, 1984 (C. Barrington Brown colln).

FURTHER RECORDS. Pebas (Gabb 1869, Boettger 1878, de Greve 1938, Willard 1966); Pichana (Conrad 1871*b*); Iquitos (de Greve 1938). Rio Marañon, 10 km upstream from Iquitos; 30 km north of Iquitos; Negro Urca, 200 km north of



Figs 358–361 *Pachydon obliquus* Gabb. Pebasian; Pichana, Peru; Hauxwell Colln. **358**, L27703; right valve internal, × 4. **359**, L27705; a, b, bivalved specimen viewed from left and front, × 3. **360**, L27704; left valve internal, × 4. **361**, L27706; a, b, juvenile specimen viewed from left side and front, × 15.

Iquitos; Rumi Tuni, on Rio Napo, 225 km north of Iquitos; 100 km south of Contamana on Rio Ucayali (all Willard 1966). Late Caenozoic, Pebasian, Upper Amazon Basin only.

DIAGNOSIS. Moderate-sized *Pachydon* with very incurved, prosogyrous umbones; generating curve oval; both valves *Glossus*-shaped, but with weak posterior ridges; highly inequivalve, with left valve much the smaller and right valve margin overlapping left; cardinal tooth of right valve very large, hooked, elongate, with correspondingly shaped socket in left valve; cardinal tooth not visible from outside when valves are closed; umbonal cavities present under hinge plates in both valves.

DESCRIPTION. The right valve is very tumid, the left valve has about half its convexity. The umbones, particularly that of the right valve, are prominent and very strongly incurved. Growth lines suggest that the right valve describes about one and a half whorls and the left only one whorl during growth to maximum convexity. Both figures are very high for bivalves in general. Lunule-like swellings occur under and anterior to the umbones in both valves, and the anterior surface of the cardinal tooth is not visible from the outside as it is in several other species assigned to the genus. Two posterior ridges are developed in each valve, those in the left being much the stronger. One ridge marks the posterior angulation, the other lies dorsal to it on the posterior area and is so weak that it can be seen only with difficulty. The highly polished shell surface is smooth, except for growth lines which give rise to some wrinkling. The commissures are curved and the right valve overlaps the left to a varying extent. The margin of the smaller left valve rests in a groove lying just inside the edge of the right valve. Both muscle scars and the pallial line are clearer in the less convex left valve. The pallial line is a broad, indistinct, band which lies comparatively far from the valve margins. The umbonal cavities under the hinge plates are very deep. The pedal muscle scars are difficult both to see and to interpret. In the right valve one, often deeply pitted, scar lies at the posterodorsal edge of the anterior adductor scar. This is probably the anterior pedal retractor scar. One, or sometimes two, deep scars lie just behind it on the buttress of the huge cardinal tooth. This may mark the pedal elevator. Scars are situated in similar positions in the left valve, within the anterior adductor scar and on the underside of the hinge plate underneath the anterior half of the cardinal socket. No distinct part of the posterior adductor scar can be recognized as the site of the posterior pedal retractor scar. The resilium pits are falciform or lanceolate. That in the right valve lies along the posterodorsal margin of the socket behind the cardinal tooth. The left resilifer is situated in a groove running parallel to the valve margin and lies dorsal to a somewhat angular ridge marking the posterodorsal edge of the cardinal socket.

DIMENSIONS. In mm.	rv l	rv h	rv br	lv l	lv h	lv br	both valves br
L27749, fig'd Woodward, 1871: pl. 5, fig. 5	16.5	15.2	–	–	–	–	11.3
L27750	18.5	14.8	–	–	–	–	11.2
L27751	18.9	15.5	8.5	15.2	11.4	5.2	10.7
L27752	18.3	14.2	8.5	15.6	11.5	5.1	10.7

All specimens listed above are from Pichana (Hauxwell Colln).

Note. The sum of the breadth of the left and right valves is greater than that of the shell breadth measured with the two valves fitted together: this is because of the curvature of the commissure.

REMARKS. In this species the pallial line is comparatively far away from the valve margins. The umbonal cavities are, however, relatively large. This suggests that the mantle cavity is of normal volume with much of the available space for the soft parts lying in the umbonal cavities themselves.

Pachydon obliquus is one of the more inequivalve members of the genus. It is most similar to *P. carinatus* (Conrad), from which it may be distinguished by its highly incurved umbones. In addition, the latter is more elongate, more inequivalve and also has stronger and truly angular posterior ridges as well as a more strongly curved commissure.

Boettger (1878: pl. 14, figs 16, 17) figured a shell from Pebas that he considered to be transitional between *P. obliquus* and *P. carinatus*. From his illustration, it appears to lie within the normal range of *P. obliquus*, and there are no transitional forms between these two species in the large BMPD series from Pichana. *P. tenuis* Gabb and *P. cuneatus* Conrad resemble *P. obliquus* in having fairly smooth oval outlines, so incomplete specimens of these three species might be confused. However, the less incurved umbones of the two former species are an immediate distinction. In addition, *P. tenuis* is much more elongate-oval and far less inequivalve. *P. cuneatus* is equivalve and with a distinctly attenuated posterior. *P. obliquus* is the most common species of the genus in the Hauxwell Collection from Pichana.

The species was not previously recorded from Canamá: the specimens cited here were all obtained from washings of matrix mainly surrounding specimens of *Mytilopsis*. The specimen (L27749) figured by Woodward (1871) is deformed by growth halts in both valves accompanying a slight change of direction of growth. Other shells are figured herein: internal features are illustrated by valves from different specimens as it proved impossible to find a suitably well preserved conjugate individual.

Pachydon tenuis Gabb, 1869 Figs 362–367

*. 1869 *Pachydon tenua* Gabb: 199; pl. 16, figs 6, 6a.
. 1871*b* *Pachydon tenuis* Gabb; Conrad: 196; pl. 10, figs 1, 1a.
*v 1871*b* *Pachydon ovatus* Conrad: 197; pl. 10, fig. 4.
*v 1871 *Anisothyris hauxwelli* Woodward: 105; pl. 5, figs 7a–d.
v. 1871 *Anisothyris hauxwelli* var.α *distorta* Woodward: 105.
v. 1871 *Anisothyris hauxwelli* var.β *crassa* Woodward: 105.
. 1872 *Corbula (Anisothyris) tenuis* (Gabb) Dall: 91.
? 1874*b* *Pachydon tenuis* Gabb; Conrad: 83; pl. 12, fig. 5.
. 1878 *Anisothyris tenuis* (Gabb) Boettger: 499; pl. 14, figs 1–8 [see text, not *A. cuneatus* as indicated in plate explanation].
1879 *Anisothyris tenuis* (Gabb); Etheridge: 83.
1879 *Anisothyris hauxwelli* Woodward; Etheridge: 83.
. 1906 *Pachydon tenuis* Gabb; Clarke: 133.
v. 1906 *Pachydon ovatus* Conrad; Clarke: 133.
. 1924 *Anisothyris hauxwelli* Woodward; Roxo: 44.
. 1938 *Anisothyris tenuis* (Gabb); de Greve: 32; pl. 6, figs 1–3, 5, 9–15.
1966 *Anisothyris hauxwelli* Woodward; Willard: 66.
. 1966 *Anisothyris* cf. *hauxwelli* Woodward; Willard: pl. 57, fig. 4.
1966 *Anisothyris tenuis* (Gabb); Willard: 68.
. 1966 *Anisothyris* cf. *tenuis* (Gabb); Willard: pl. 58, fig. 1.
. 1968 *Pachydon tenuis* Gabb; Richards: 89.

HOLOTYPE of *P. tenuis* Gabb, ANSP 20061; Late Caenozoic, Pebasian; Pebas, Peru, Orton colln. (Richards, 1968: 89; not seen, since lost).

Holotype of *P. ovatus* Conrad, NYSM 8966; Late Caenozoic, Pebasian; Pichana, Peru, Hauxwell colln.

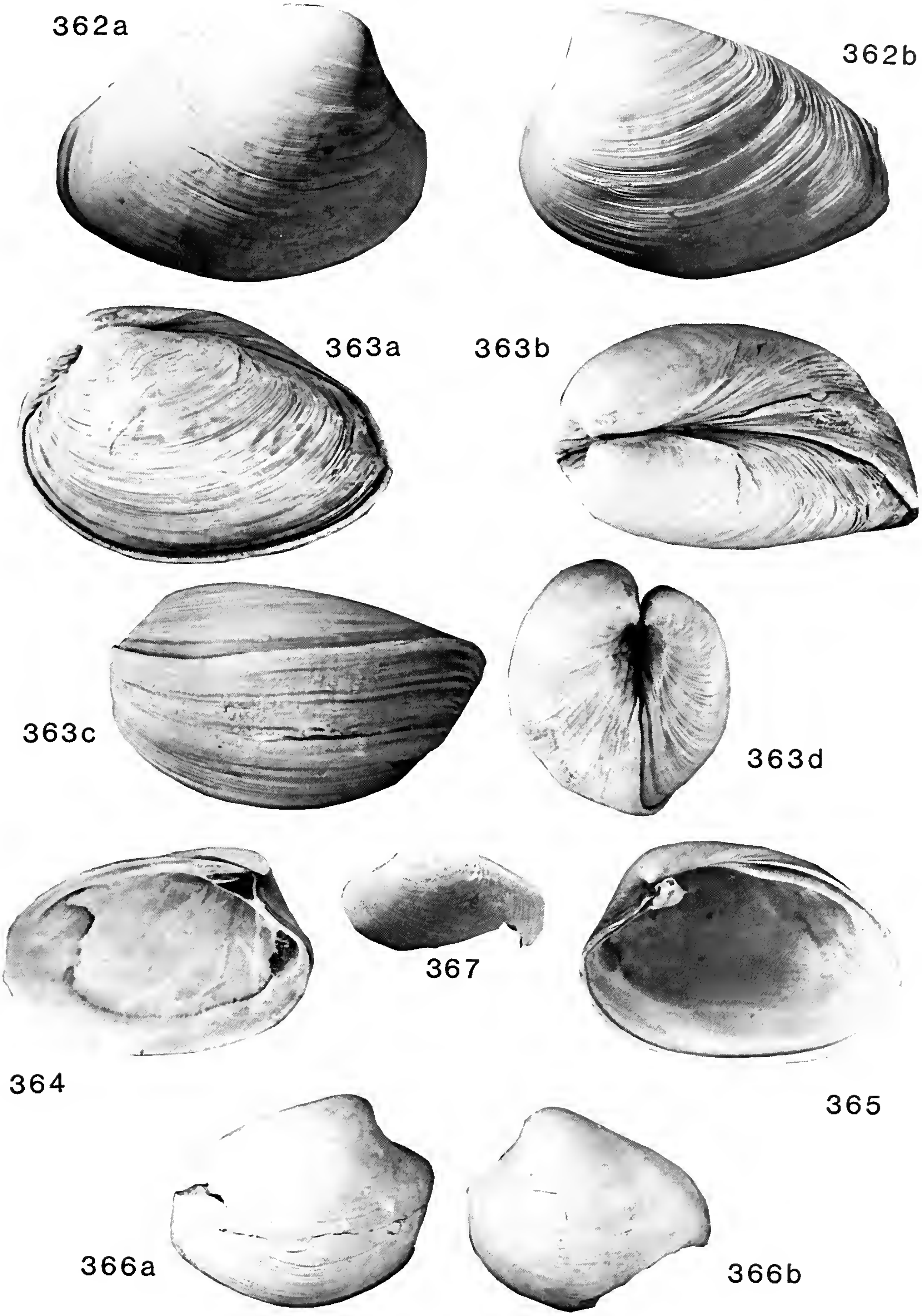
OTHER MATERIAL STUDIED. All Late Caenozoic, Pebasian; Pichana, Peru, Hauxwell colln. BMPD L27730, both valves of shell figured by Woodward (1871: pl. 5, figs 7a–d) as *Anisothyris hauxwelli* nom. nov. for *Pachydon tenua* Gabb; L27712–19; L27732–5 (about fifty specimens). LL27959/1–3, three broken juvenile valves, Puerto Nariño, Weeda colln.

FURTHER RECORDS. All Late Caenozoic, Pebasian; Pebas (Gabb 1869, Boettger 1878, Willard 1966: 68); Canamá (Etheridge 1879); Três Unidos (Roxo 1924); Iquitos (de Greve 1938, Willard 1966: pl. 58, fig. 1); on Rio Marañon, 10 km upstream from Iquitos (Willard 1966: pl. 57, fig. 4). Unlocalized (Conrad 1874*b*). Late Caenozoic, Pebasian only, Upper Amazon Basin.

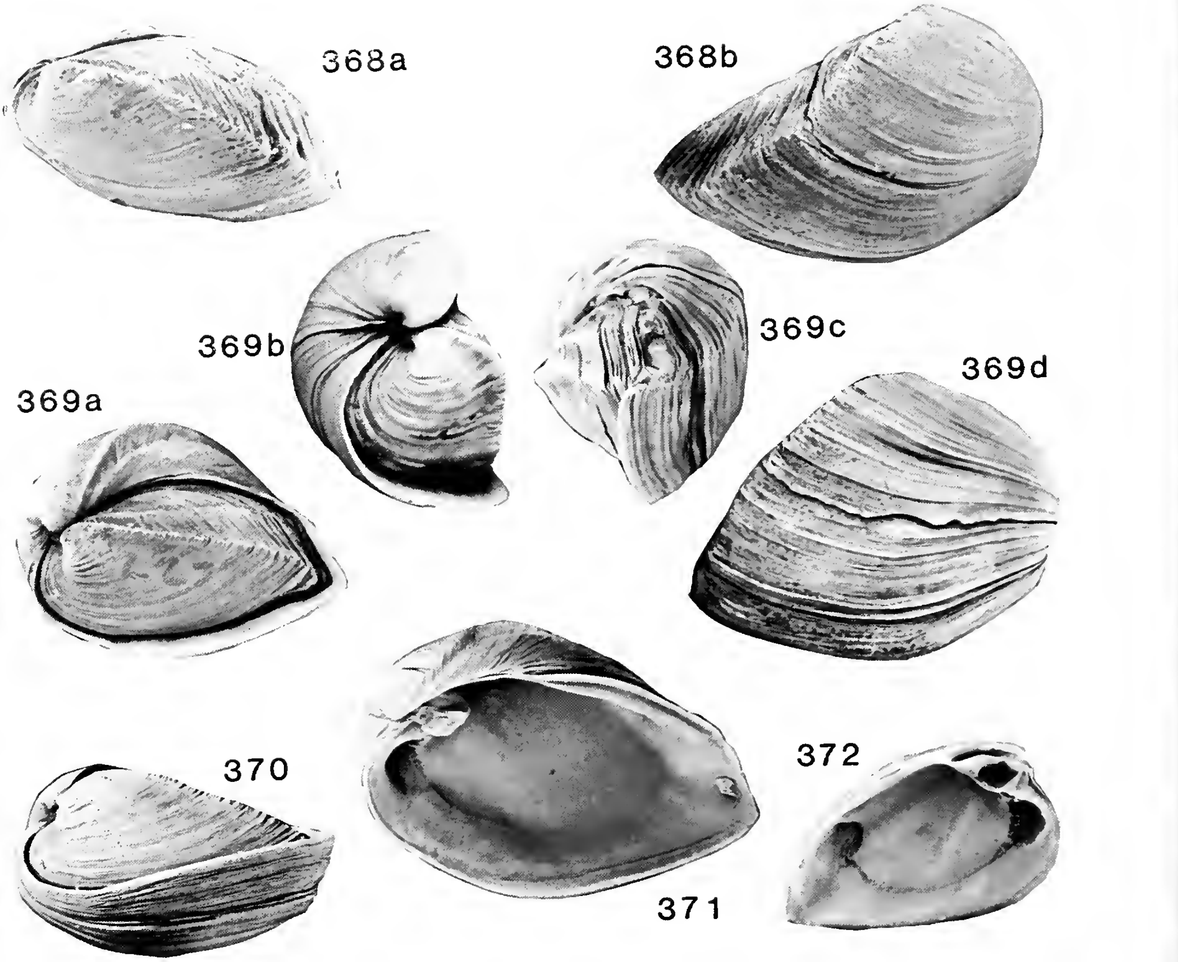
DIAGNOSIS. Large inequivalve *Pachydon* with smoothly elongate oval outline; commissure sinuous; left valve only just overlapped by rim of right valve; anterior surface of cardinal tooth visible from outside when viewed from front.

DESCRIPTION. The shell surface is shiny and smooth except for growth lines. There are few traces of radiating sculpture. There is a faint ridge running from the umbo to the most anterior point of the left valve. In the right valve there is a groove marking the edge of the lunule and also two ridges running posteriorly from the umbo; the latter are in the same position as those in *P. carinatus* (p. 296) but very faint, not forming an angulation isolating a posterior area or corselet. The internal features are broadly similar to those of *P. obliquus* (p. 292), with the left hinge plate attached to the dorsal margin of the valve, but with the pallial line lying nearer the ventral margin in both valves. A pair of anterior retractor scars are situated behind and above the anterior adductor scar in the right valve. In the left valve the retractor scars are at the ventral surface of the anterior end of the hinge plate. The pedal elevator scars are best seen in rather small, less tumid shells in which much of the umbonal cavity is visible; they leave a line of small scars underneath the central and rear part of the hinge plate in the left valve. In the right valve a single, larger and deeper, scar is present underneath that part of the hinge plate underlying the ligamental socket behind the cardinal tooth. The posterior pedal retractor scar coalesces with the anterodorsal margin of the posterior adductor.

DIMENSIONS. In mm. (All Pichana).	rv l	rv h	rv br	lv l	lv h	lv br	br both valves
L27730, figured Woodward, 1871: pl. 5, fig. 7.	40.8	30.0	15.5	39.6	29.0	12.4	27.8
L27712	30.0	21.2	–	–	–	–	18.4
L27713	26.0	18.0	10.0	–	–	–	–
L27714	–	–	–	25.0	17.5	7.1	15.0
Holotype of *P. ovatus*, NYSM 8966	27.6	22.9	–	25.9	22.1	–	–



Figs 362–367 *Pachydon tenuis* Gabb. Pebasian. **362–366**, Pichana, Peru; Hauxwell Colln. **362**, L27730; shell figured by Woodward (1871: pl. 5, fig. 7) as *Anisothyris hauxwelli* nom. nov.; a, b, left, right valve, × 1.5. **363**, L27712; a–d, left, dorsal, ventral, front views, × 2. **364**, L27714; left valve internal, × 2. **365**, L27713; right valve internal, × 2. **366**, NYSM 8966; holotype of *Pachydon ovatus* Conrad. a, b, left, right valves, × 1.5. **367**, LL27954/1; Puerto Nariño, Colombia; Weeda Colln. Broken left valve with umbonal region tilted towards camera to show early stages of shell; × 4.



Figs 368–372 *Pachydon carinatus* Conrad. Pebasian; Pichana, Peru; Hauxwell Colln; all × 2. **368**, L27720; specimen figured by Woodward (1871: pl. 5, fig. 6); a, b, left, right valves. **369**, L27722; a–d, viewed from left, front, rear, and right. **370**, L27721; ventral view. **371**, LL28136; right valve internal. **372**, L27723; left valve internal.

REMARKS. *P. tenuis* is rather similar in general shape to *P. carinatus* Conrad but lacks the posterior angulation and has virtually obsolete radiating ribs. *P. cuneatus* Conrad is equivalve and its umbones are much nearer the anterior. A comparison with *P. obliquus* Conrad is given under the latter, p. 294. *P. tenuis* is the largest species of *Pachydon* with the exception of *P. erectus* Conrad, and is plentifully represented in the BMPD collections from Pichana. Woodward (1871) proposed the name *Anisothyris hauxwelli* as a replacement for *P. tenuis* Gabb, on the unjustified grounds that Gabb's specific name was inappropriate and therefore misleading. Woodward's 'varieties' *distorta* and *crassa* do not appear to merit separation from *P. tenuis*, s.str., and are not figured herein. *P. ovatus* Conrad is clearly the same as *P. tenuis*. Although Etheridge (1879) recorded this species as occurring at Canamá, no specimens from there were ever acquired by BMPD: some doubt must exist about his record. The specimen figured by Willard (1966: pl. 58, fig. 1) does not show the specific characters clearly, though his other illustration as *A.* cf. *hauxwelli* (pl. 57, fig. 4) undoubtedly belongs to *tenuis*.

Pachydon carinatus **Conrad, 1871** Figs 368–373

* 1871*b* *Pachydon carinatus* Conrad: 196; pl. 10, fig. 7.
v. 1871 *Anisothyris carinata* (Conrad) Woodward: 106; pl. 5, fig. 6.
. 1872 *Anisothyris carinata* (Conrad); Dall: 89.
. 1878 *Anisothyris carinata* (Conrad); Boettger: 501; pl. 14, figs 23–27.
1879 *Anisothyris carinata* (Conrad); Etheridge: 83.
. 1906 *Pachydon carinatus* Conrad; Clarke: 132.
1924 *Anisothyris carinata* (Conrad); Roxo: 44.
. 1938 *Anisothyris carinata* (Conrad); de Greve: 43; pl. 9, figs 1–3, 6, 7.
? 1966 *Anisothyris carinata* (Conrad); Willard: 65, 67, 68.
. 1966 *Anisothyris cuneata* (Conrad); Willard: pl. 57, fig. 1.

TYPE MATERIAL. Late Caenozoic, Pebasian; Pichana, Peru, Hauxwell colln (NYSM; Clarke 1906). Not studied.

MATERIAL STUDIED. L27720, figured Woodward (1871: pl. 5, fig. 6); L27721–3, L27727–9 (about 20 specimens), LL28136–40; all late Caenozoic; Pichana, Peru, Hauxwell colln.

FURTHER RECORDS. All late Caenozoic. Pebas (Boettger 1878); Canamá (Etheridge 1879); Três Unidos (Roxo 1924); Iquitos (de Greve 1938). Rumi Tuni (Willard 1966: pl. 57, fig. 1, as *A. carinata*). Other unfigured records from the Iquitos area (Willard 1966) are doubtful. Late Caenozoic, Upper Amazon Basin only.

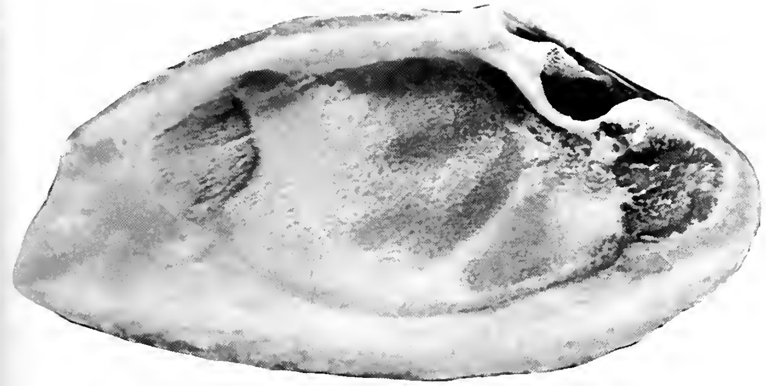


Fig 373 *Pachydon carinatus* Conrad. Pebasian; Pichana, Peru; Hauxwell Colln. LL28137; left valve interior showing row of pits, interpreted as pedal elevator scars, lying along junction between hinge plate and floor of valve; × 4.

Diagnosis. Moderately large *Pachydon* with strong carina separating flank from posterior area in both valves; secondary carina on posterior areas also present; inequivalve, with ventral margin of smaller left valve resting inside strongly curved rim of right valve; umbones prosogyrous, incurved and pointed; anterior surface of cardinal tooth barely visible from outside; outline elongate oval but with angular junction between ventral and posterior margins; deep umbonal cavity formed in tumid right valve; no umbonal cavity in left valve.

Description. The commissure of the right valve is strongly twisted along all margins, but that of the left valve, which sits within the right valve, is less so. The posterior area or corselet of the right valve is so curved that it is barely visible in side view. The pallial line runs in a curve between the inner and ventral margins of the two adductor scars. The posterior pedal retractor scar is just visible above the posterior adductor scar. The anterior pedal retractor scar in the right valve occurs low on the buttress below the cardinal tooth, fairly close to the anterior adductor scar. In the left valve, two or three irregular and pock-marked scars are situated on the ventral surface of the hinge plate in front of the cardinal socket. No umbonal cavity is present in the left valve; instead, the hinge plate is attached to the floor of the valve rather than being suspended from its dorsal margin as in the right valve. Thus, in the left valve a series of up to a dozen small, sometimes coalescing, scars may be seen along this junction of hinge plate and valve floor. These are interpreted as pedal elevator scars. No such scars can be seen in the more tumid and incurved right valve.

Dimensions. In mm. (All Pichana).	rv			lv			br both valves
	l	h	vbr	l	h	vbr	
L27720, fig'd Woodward, 1871.	27.6	19.0	12.4	23.8	13.1	6.4	13.2
L27721	23.0	14.2	–	–	–	–	12.5
L27722	25.5	18.2	–	–	–	–	14.0
L27723	–	–	–	20.0	12.3	5.8	–

Remarks. Differences between this species and *P. obliquus* are given under the latter, p. 294. Differences in their muscle scar pattern are probably because the left valve of *P. carinatus* is comparatively flat.

Pachydon erectus Conrad, 1871 Figs 374–384

*v 1871*b* *Pachydon erectum* Conrad: 197; pl. 10, fig. 16 (two figures).
*v 1871*b* *Pachydon altus* Conrad : 197; pl. 11, fig. 1.
v. 1871 *Anisothyris erecta* (Conrad) Woodward : 107; pl. 5, figs 9a, b.
. 1874*a* *Pachydon altus* Conrad; Conrad : 28; pl. 1, figs 4, 18.
. 1878 *Anisothyris erecta* (Conrad); Boettger : 500; pl. 14, figs 12, 13.
*v 1879 *Corbula canamaensis* Etheridge : 84; pl. 7, figs 3, 3a.
v. 1906 *Pachydon altus* Conrad; Clarke : 132.
v. 1906 *Pachydon erectus* Conrad; Clarke : 133.
. 1938 *Anisothyris erecta* (Conrad); de Greve : 36, pl. 8, figs 1–3, 8.
. 1938 *Anisothyris erecta* (Conrad)–*Anisothyris tenuis* (Gabb); de Greve: pl. 7, figs 1, 6.
. 1966 *Anisothyris erecta* (Conrad); Willard : 65–69 (*pars*); pl. 58, fig. 2.
v. 1982 *Anisothyris erectus* (Conrad); Nuttall *in* Bristow & Parodiz: 20.

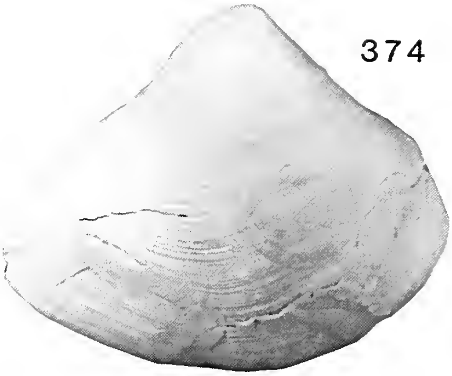
Holotype of *P. erectus* Conrad, 1871, NYSM 8964, the right valve figured by Conrad 1871: pl. 10, fig. 16, right figure, an external view. Late Caenozoic; Pichana, Peru (Hauxwell colln). The left figure is an internal view of a left valve, apparently of the same specimen; it has not been seen and its whereabouts are unknown. Conrad stated that he had only one specimen of this species and that the valves were much less unequal than in *P. obliquus* Gabb.

Holotype of *Pachydon altus* Conrad, 1871, NYSM 8961. Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell colln).

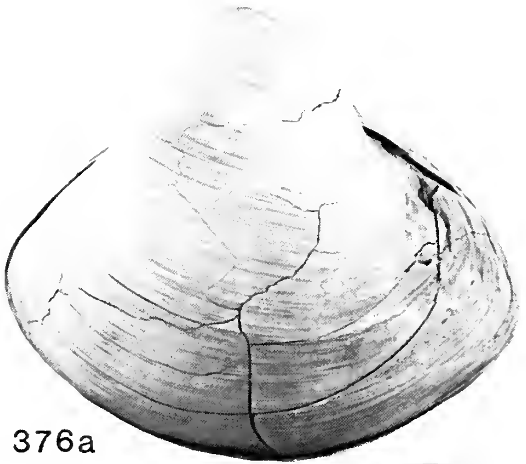
Lectotype, selected herein, of *Corbula canamaensis* Etheridge, 1879: BMPD LL27853, the specimen figured by Etheridge (1879). The accompanying unfigured shells, LL27854–6, 3 left and 1 right valves are paralectotypes. All Late Caenozoic, Pebasian; Canamá (C. Barrington Brown colln).

Other material studied. BMPD L27740, specimen figured by Woodward (1871: pl. 5, figs 9a, b) and the accompanying unfigured specimens, L27736–9, LL27844, LL28072; all Late Caenozoic, Pichana (Hauxwell colln); LL28080–5, Pichana, as above, but extracted from matrix 1982. LL27888, Loc. 33/480–560 cm; LL27890–6, Loc. 33/570–670 cm; LL27873, LL40802,

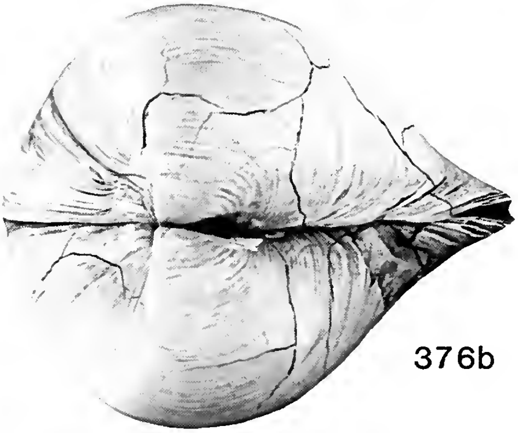
374



375

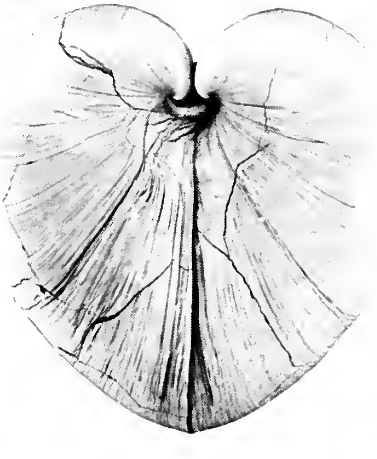


376a

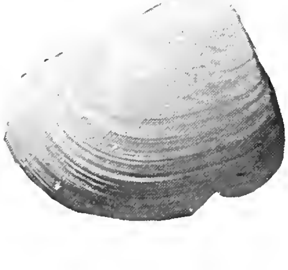


376b

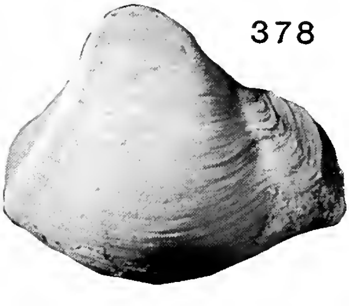
376c



377



378



Figs 374–378 *Pachydon erectus* Conrad. Pebasian; Peru. **374–377**, Pichana; Hauxwell Colln. **374**, NYSM 8964; holotype of *Pachydon erectus* Conrad, figured by Conrad (1871: pl. 10, fig. 16); single right valve, × 1.5. **375**, NYSM 8961; holotype of *Pachydon altus* Conrad, figured by Conrad (1871: pl. 11, fig. 1); right valve, × 1.5. **376**, L27740; shell figured by Woodward (1871: pl. 5, fig. 9) as *Anisothyris erecta*; a–c, left, dorsal and front views, × 1.5. **377**, LL27844; juvenile shell, right valve, × 2.5. **378**, LL27853; **lectotype** (herein selected) of *Corbula canamaensis* Etheridge, figured by Etheridge (1879: pl. 7, fig. 3); Canamá, Barrington Brown Colln. Left valve, × 2.5.

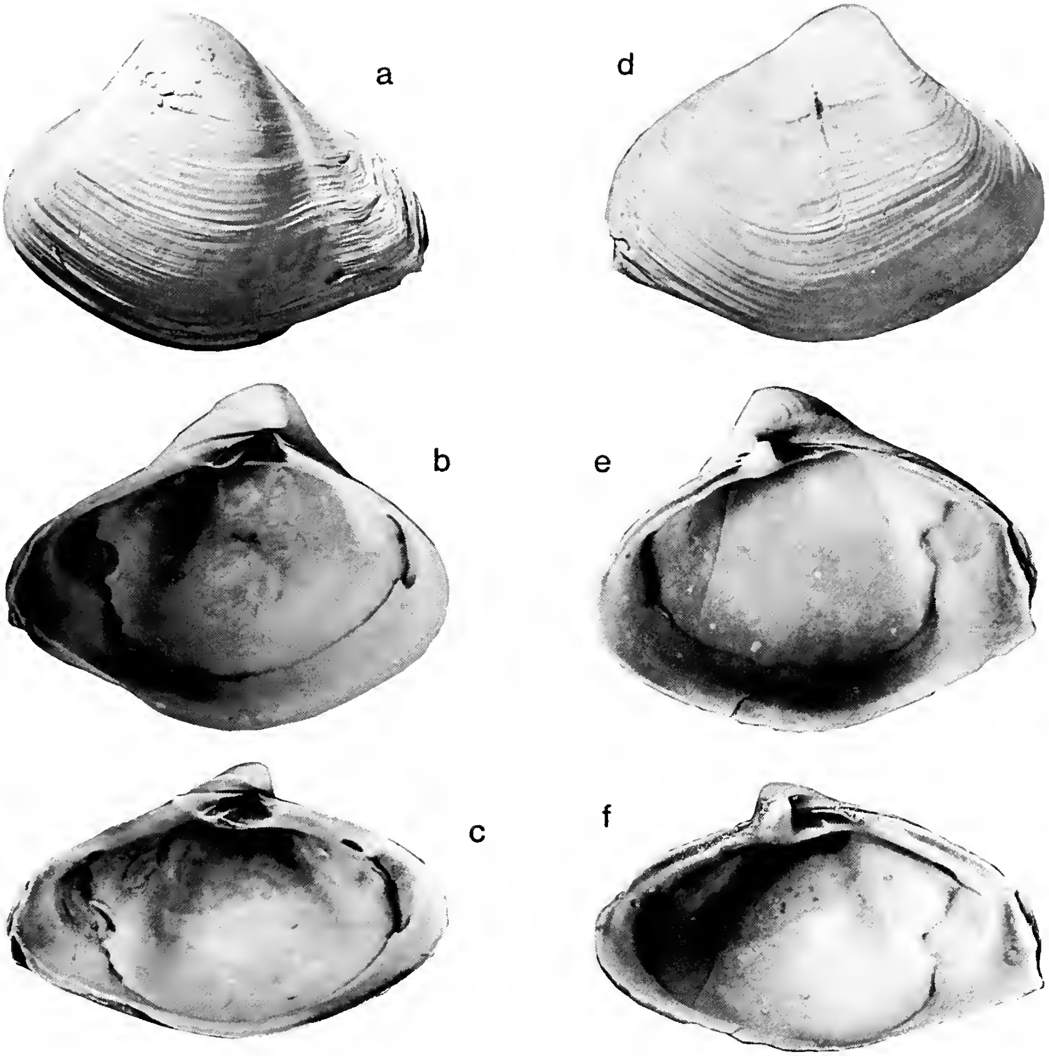


Fig. 379 *Pachydon erectus* Conrad. L27738; Pebasian; Pichana, Peru; Hauxwell Colln. a–f, left and right valves, external, internal normal and oblique views, × 2.5.

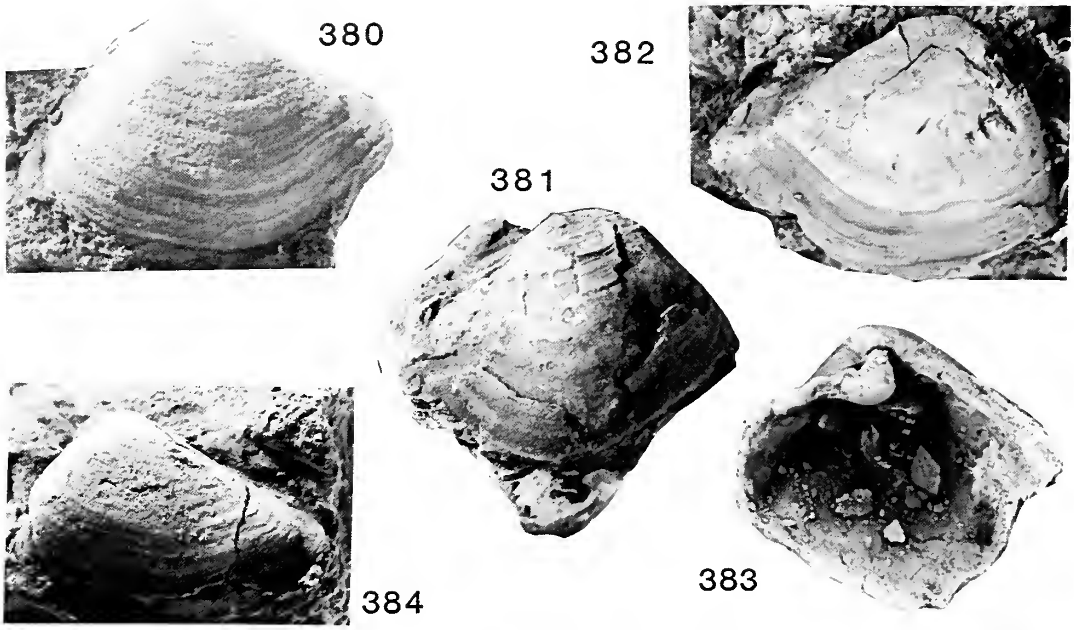
Loc. 45; LL27874–8, Loc. 54; all Late Caenozoic, La Tagua (Eden colln).

FURTHER RECORDS. Pebas (Conrad 1874*a*, Boettger 1878, de Greve 1938); Iquitos (de Greve 1938); Pebas, Iquitos, Rumi Tuni and Rio Aguaytia 25 km from confluence with Rio Ucayali (Willard 1966).

DISTRIBUTION. Late Caenozoic, Pebasian; Upper Amazon Valley. Late Caenozoic; La Tagua, Colombia.

DIAGNOSIS. Large, tumid, equivalve *Pachydon*; subtrigonal with short anterior, posterior alate, slightly upturned; corselet crassatelliform; umbones very prominent and strongly curved; front of cardinal tooth external.

DESCRIPTION. In smaller, slim, specimens, such as those from La Tagua, the anterior appears comparatively elongate with the anterodorsal margin sloping forward and downward in a mildly convex curve. In very tumid adults, such as those figured by Conrad (1871*b*) and Woodward (1871), this margin forms a concave curve and the shell will balance on this broad flattened area. The change of appearance can be explained as a result of normal spiral growth of a shell with large, strongly incurved, prosogyrous umbones, producing an abnormally high angular displacement of the earlier-formed parts of the shell compared with the majority of bivalves. Internal views show that the generating curves in this species are similar in shape regardless of shell size. The ventral margin may be either evenly convex or drawn out into an elongate posterior extension which is differentiated weakly from the main flank of the shell by a broad, shallow, sulcus. The posterodorsal margin tends to be crassatelliform to a varying extent. The zone nearest to this margin is vaguely distinct from the rest of the shell but is rarely separated as a corselet by a radiating ridge. The most anterior and posterior extremities of the shell lie well below mid-height and the umbones lie forward of mid-length. The lowest point of the ventral margin is slightly posterior to mid-length of the shell and corresponds with a slight fold in the commissure of the right valve and sulcus in the left. The adductor scars are subcircular with identations on their inner margins marking the separation into 'quick' and 'catch' attachment scars (Cox, *in* Moore 1969: N35). Anterior and posterior pedal retractor scars are situated



Figs 380–384 *Pachydon erectus* Conrad. Late Caenozoic; La Tagua, Colombia; Eden Colln. **380**, LL27890; Loc. 33/570–670, left valve, × 5. **381**, LL27893; Loc. 33/570–670, right valve, × 3. **382**, LL27877; Loc. 54, right valve, × 3. **383**, LL27874; Loc. 54, right valve internal view, × 5. **384**, LL40802; Loc. 45, latex cast of internal mould of left valve, × 4.

immediately dorsal to the adductors and in some specimens the anterior scar can be seen to have two parts, the one nearer the umbo being the larger. The pallial sinus is notched posteriorly, meeting the posterior adductor at its forward lower margin.

DIMENSIONS. In mm.	l	h	br	l/h	br/l
Lectotype of *P. erectus* Conrad. NYSM 8964, Pichana	40.0	32.8	15.3 (sv)	1.22	0.77
Lectotype of *P. altus* Conrad. NYSM 8961, Pichana	–	38.5	32.0	–	–
Shell figd. Woodward, 1871: pl. 5, fig. 9. L27740, Pichana	49.0	44.2	39.3	1.11	0.80
Lectotype of *Corbula canamensis* Etheridge. LL27853, Canamá	19.5	15.5	7.8 (sv)	1.25	0.80
L27736, Pichana	35.7	26.8	12.6 (sv)	1.33	0.71
L27737, Pichana	23.2	18.3	7.5 (sv)	1.27	0.65
LL27844, Pichana	15.7	13.3	6.0 (sv)	1.18	0.76
LL27877, Loc. 54, La Tagua	16.3	12.3	–	1.33	–
LL27890, Loc. 33/570–670, La Tagua	9.8	6.9	–	1.42	–

Note. (sv) = single valves only.

REMARKS. The reasons for regarding NYSM 8964 as the holotype of *P. erectus* are given above. Conrad also appears to have had only one specimen of *P. altus*. In his description of it, he said the shell was silicified, and that the internal mould was of indurated ferruginous clay. The posterior of NYSM 8961 is missing, thus revealing the infilling matrix and the apparently normal but worn aragonitic shell, which probably explains Conrad's reference to the internal mould and his belief that the shell was silicified.

P. erectus is the largest species of the genus known. Features distinguishing it from other almost equivalve species such as *P. cuneatus* Conrad, *P. hettneri* (Anderson) and *P. trigonalis* sp. nov. (p. 309) are its both erect and strongly incurved umbones, its alate posterior and its crassatelliform corselet. *P. iquitensis* (de Greve 1938: 46; pl. 5, figs 38–41), known only from a single right valve from Iquitos, is fairly similar but has a lower and less incurved umbo and also lacks the crassatelliform corselet typical of *P. erectus*.

Study of type material of *P. altus* Conrad and *P. canamaensis* (Etheridge) shows that both are synonyms of *P. erectus*. De Greve (1938: pl. 7, figs 1, 6) illustrates a left valve from Iquitos which he named as '*Anisothyris erectum* Conrad – *Anisothyris tenuis* Dall'. It is a typical *P. erectus* and shows no features characteristic of *P. tenuis*.

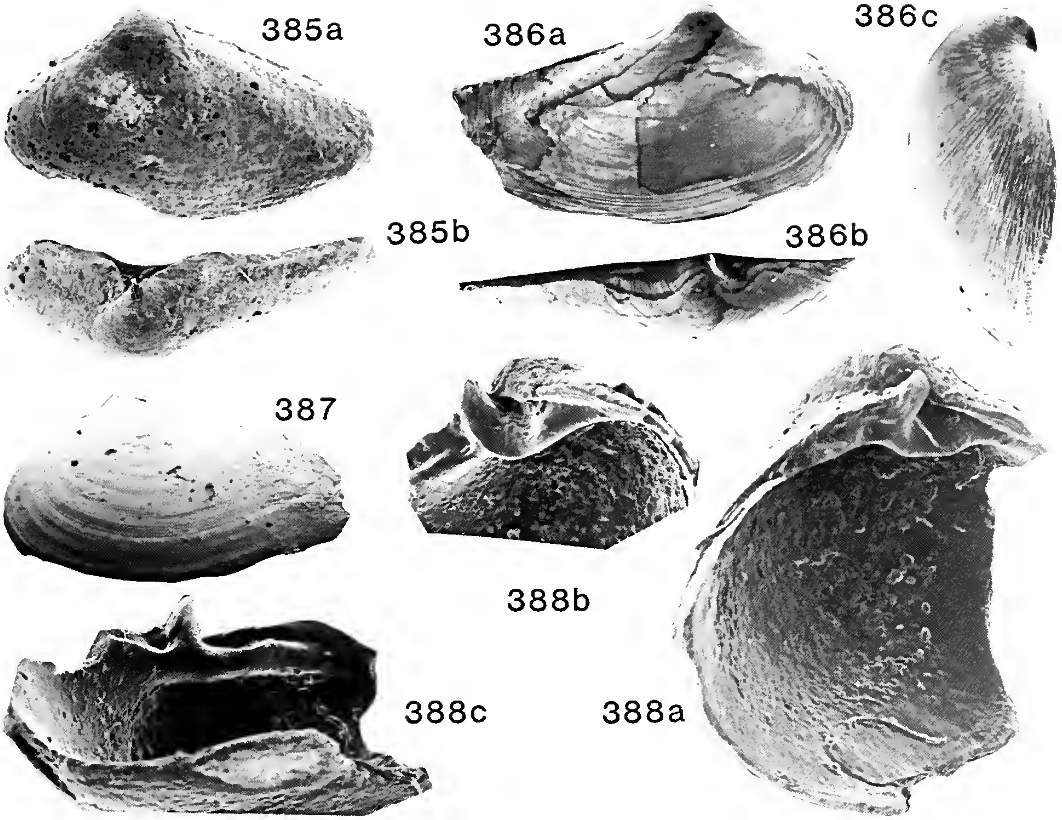
Some doubt exists about Willard's (1966) records. He figured two shells, both from Pebas. His pl. 58, fig. 2 is correctly identified, but his pl. 58, fig. 3, the interior of a right valve, is of a different, unidentifiable species.

Pachydon erectus elongatus (Boettger, 1878)

Figs 385–388

* 1878 *Anisothyris erecta* (Conrad) var. *elongata* Boettger: 500; pl. 14, figs 14, 15.
. 1938 *Anisothyris erecta* (Conrad) var. *elongata* Boettger; de Greve: 38; pl. 7, fig. 13; pl. 8, figs 4, 5.

LECTOTYPE (selected de Greve 1938: 40). The specimen figured by Boettger (1878: pl. 14, fig. 14) and again by de Greve (1938: pl. 7, fig. 13; pl. 8, fig. 5). The original of Boettger's (1878) pl. 14, fig. 15, refigured by de Greve (1938: pl. 8, fig. 4), is a paralectotype. Both Late Caenozoic, Pebasian;



Figs 385–388 *Pachydon erectus elongatus* (Boettger). Pebasian; Pichana, Peru; Hauxwell Colln. **385**, LL28083; a, b, left valve, side and dorsal views, × 10. **386**, LL28081; a, right valve, side, × 10; b, dorsal view, × 10; c, front, × 20. **387**, LL28080; left valve, × 10. **388**, LL28082; a–c, internal views of broken right valve, all × 30.

either Pebas or Pichana, Peru (Hauxwell colln). In Senckenburg Museum, Frankfurt (not studied).

Material studied. BMPD LL28080–5, Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell colln, extracted from matrix, 1982). No further records.

Distribution. Restricted to Pebasian. Pebas or Pichana (Boettger 1878); Iquitos (de Greve 1938); probably Pichana (herein).

Diagnosis. Differing from *Pachydon erectus* Conrad, s.str., in being very small and elongate, with a length to height ratio of more than 1.5:1.

Dimensions. In mm.	l	h	br	l/h
Lectotype, Boettger's (1878) pl. 14, fig. 14, ? Pebas or Pichana.	5.6	3.6	–	1.59
Paralectotype, Boettger's (1878) pl. 14, fig. 1, ? Pebas or Pichana.	7.0	4.4	–	1.56
Iquitos (de Greve 1938: 40).	20.3	11.8	3.0 (sv)	1.72
Iquitos (de Greve 1938: 40).	18.9	11.1	4.4 (sv)	1.70
Iquitos (de Greve 1938: 40).	16.9	9.6	2.9 (sv)	1.76
LL28080, Pichana.	2.5	1.5	–	1.67
LL28081, Pichana.	6.2	2.5	1.15 (sv)	2.48

Note. The above measurements of Boettger's figured specimens are calculated from de Greve's illustrations. In his text (1938: 40), de Greve quotes a length of 7.5 mm and height of 4.5 mm for the lectotype. (sv) = single valve.

Description. The shell is small, apparently not exceeding 8 mm in length. The umbones are situated well anterior to mid-length of the shell. Outline crassatelliform, with a corselet separated from the main flank of the shell by a comparatively weak diagonal ridge of variable strength. The posterior tends to be truncated to some extent. The shell is virtually equivalve, and the commissure straight, as far as can be ascertained. In vertical view, the shell is rather stout.

Remarks. Unfortunately, there is no good, continuous, growth series of *P. erectus* available for study. However, the impression gained from the Hauxwell Collection is that there are a few small shells which are distinctly too elongate to be assigned to typical *P. erectus*. At the same time, they can be separated from the even more elongate *P. ledaeformis* (Dall) which is also noticeably slimmer in vertical view. *P. amazonensis* (Gabb) possesses much less prominent umbones. Boettger's decision, therefore, to regard his small specimens as representing a variety of *P. erectus* seems reasonable on the available evidence. Unfortunately, de Greve (1938) figured none of the distinctly larger Iquitos specimens, whose dimensions are repeated above.

Pachydon cuneatus Conrad, 1871 Figs 389–393

*v 1871*b* *Pachydon cuneatus* Conrad: 197; pl. 10, fig. 12.
v. 1871 *Anisothyris cuneata* (Conrad) Woodward: 107; pl. 5, figs 8a, b.

. 1874*a* *Pachydon cuneata* Conrad; Conrad: 28; pl. 1, fig. 3.
. 1878 *Anisothyris cuneata* (Conrad); Boettger: 500 (*pars*); pl. 14, fig. 11.
*v 1879 *Anisothyris* (*Pachydon*) *tumida* Etheridge: 83; pl. 7, fig. 2.
v. 1906 *Pachydon cuneatus* Conrad; Clarke: 133.
1924 *Anisothyris cuneatus* (Conrad); Roxo: 44.
. 1938 *Anisothyris cuneata* (Conrad); de Greve: 34; pl. 6, figs 4, 6–8, 16, 17; pl. 8, figs 18, 19.
1952 *Pachydon cuneatus* Conrad; Rutsch: 449.
? 1966 *Anisothyris cuneata* (Conrad); Willard: 66–68 (*pars*); pl. 59, figs 2, 3 (*non* fig. 1)

LECTOTYPE, selected herein, of *Pachydon cuneatus* Conrad, 1871: NYSM 8963, the right valve figured by Conrad (1871*b*). The unfigured left valve of another individual found with the lectotype is a paralectotype. Both Late Caenozoic, Pebasian; Pichana (Hauxwell colln).

Lectotype, selected herein, of *Anisothyris (Pachydon) tumida* Etheridge, 1879: BMPD LL27851, a left valve, probably that figured by Etheridge (1879). One complete bivalved shell and two separate right valves, LL27852/1–3, not figured, are paralectotypes. All Late Caenozoic, Pebasian; Canamá (C. Barrington Brown colln).

OTHER MATERIAL STUDIED. BMPD L27725, specimen figured by Woodward (1871: pl. 5, figs 8a, b) and accompanying unfigured specimens, L27724, L27726/1–2, LL27845; all Late Caenozoic, Pebasian; Pichana (Hauxwell colln); LL28078–9, two good left valves, and LL27857/1–4, three left and one right valves (all damaged); Late Caenozoic, Pebasian; Puerto Nariño, Colombia (Weeda colln).

FURTHER RECORDS. Late Caenozoic, Pebasian: Pebas, Peru (Boettger 1878, Willard 1966); either Pebas, Old Pebas or Pichana (Conrad 1874*a*); Iquitos, Peru (de Greve 1938); Negro Urca and ? Rumi Tuni, Peru (Willard 1966); Três Unidos, Peru and Tracaos on Rio Quixitos, Brazil (Roxo 1924). ? Yucales Formation, Santa Ines Group: State of Monogas, Guarico and Aragua, Venezuela (Rutsch 1952).

DISTRIBUTION. Late Caenozoic, Pebasian Basin of Upper Amazon Valley and ? Late Caenozoic of Venezuela.

DIAGNOSIS. Virtually equivalve *Pachydon* with almost plane commissure; high, prosogyrous umbones placed well forward, above anterior adductor; outline subtrigonal, with posterodorsal and ventral margins forming comparatively smooth curves; cardinal tooth very prominent.

DESCRIPTION. Both the greatest height and greatest breadth are very close to the anterior, and in dorsal view the anterior of the shell appears very foreshortened. The large cardinal tooth is strongly hooked, directed forwards at about 45°, and its anterior surface has a prominent callosity which is exposed to the outside world. A comparatively strong right posterior lateral tooth is present. The right anterior lateral is no more than a weak ridge lying parallel to the anterior extension of the hinge plate. The pallial line is slightly truncated below the posterior adductor scar, but no definite sinus is formed.

DIMENSIONS. In mm.	l	h	br (sv)	l/h	br/l
Lectotype, NYSM 8963, Pichana	26.0	22.5	11.2	1.16	0.86
L27725, shell fig'd Woodward (1871: pl. 5, fig. 8), Pichana	30.0	24.8	24.0	1.21	0.80
L27724, Pichana	28.4	23.8	11.9	1.19	0.84
L27726/1, Pichana	24.8	21.4	10.0	1.15	0.81
L27726/2, Pichana	29.2	24.8	12.0	1.18	0.82
Lectotype of *Anisothyris tumida* Etheridge, LL27851, Canamá	17.9	14.5	6.2	1.23	0.69
LL28078, Puerto Nariño	14.9+	13.7	6.0	1.09+	0.81
LL28079, Puerto Nariño	10.8	9.4	3.5	1.15	0.62

Note. Breadth measurements are of single valves (sv). This is doubled for br/l calculations.

REMARKS. This is a very uncommon species, represented in BMPD collections by eight specimens from Pichana, five from Canamá and six from Puerto Nariño. The forward position of the umbones immediately distinguishes it from other almost equivalve species of *Pachydon*. The outline of *P. tenuis* Gabb, 1869, most closely resembles that of *P. cuneatus*, but its umbones are further back and it is inequivalve. In the very inequivalve *P. obliquus* Gabb, 1869, the umbones are even further forward.

A. (*P.*) *tumida* Etheridge, 1879, is clearly identical to *P. cuneatus* Conrad: Etheridge, however, gave no comparison between the two. Boettger's (1878) explanation of his plate 14 lists figs 1–11 as *A. cuneata*. This appears to be a misprint as his text (1878: 499, 500) shows that he rightly identified figs 1–8 as *A. tenuis* (Gabb). I consider that his figs 9 and 10 are probably juvenile *P. tenuis*, leaving only pl. 14, fig. 11 as *P. cuneatus*.

Willard's (1966) records need interpreting with some care. For example, the specimen from Rumi Tuni figured (his pl. 57, fig. 1) as *A. cuneata* is clearly *P. carinatus* Conrad: he lists both these species from this locality. On the other hand, his pl. 59, fig. 2 and probably fig. 3, from Pebas and Iquitos respectively, are correctly identified as *Anisothyris cuneata*. However, the latter figure is a posterodorsal and not an anterior aspect as stated and, in addition, in his text (1966: 65) he did not list the species as occurring at Iquitos.

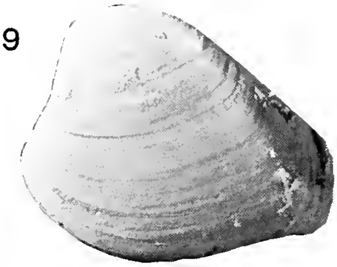
Rutsch (1952) expressed some doubts about his identification of *P. cuneatus* from Venezuela.

Pachydon hettneri (Anderson, 1928) Figs 394–402

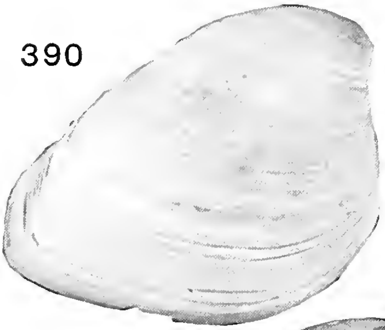
*v 1928 *Corbula hettneri* Anderson: 24; pl. 1, figs 11–14; text-figs 10, 11.
v. 1982 *Anisothyris* sp. Nuttall *in* Bristow & Parodiz: 20.

LECTOTYPE, selected herein: CAS 2698, specimen figured by Anderson, 1928: pl. 1, figs 11, 12 and text-figs 10, 11, 'from near base of Guaduas Group of brackish water beds, near San Juan de Rio Seco'. This locality was originally thought to be Eocene, but is here redated as probably Miocene, Santa Teresa Formation (Porta 1966), possibly located near km 106 on Bogotá–Cambao Highway (Butler 1939, 1942). Downs McCloskey and Thomas Wark colln. Specimen CAS 2699,

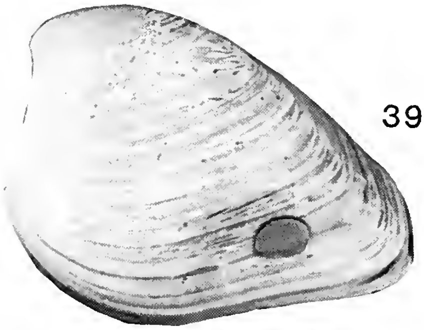
389



390



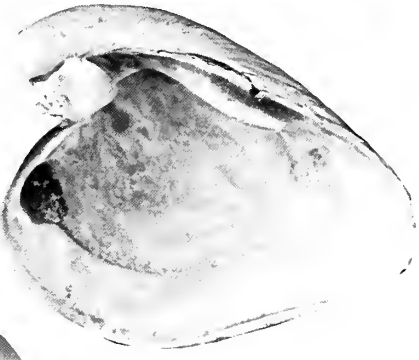
391a



391b

391c

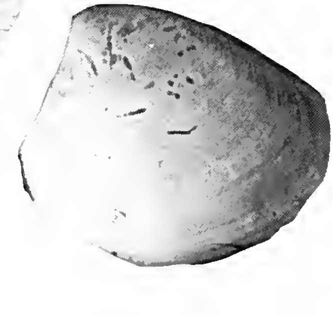
391d



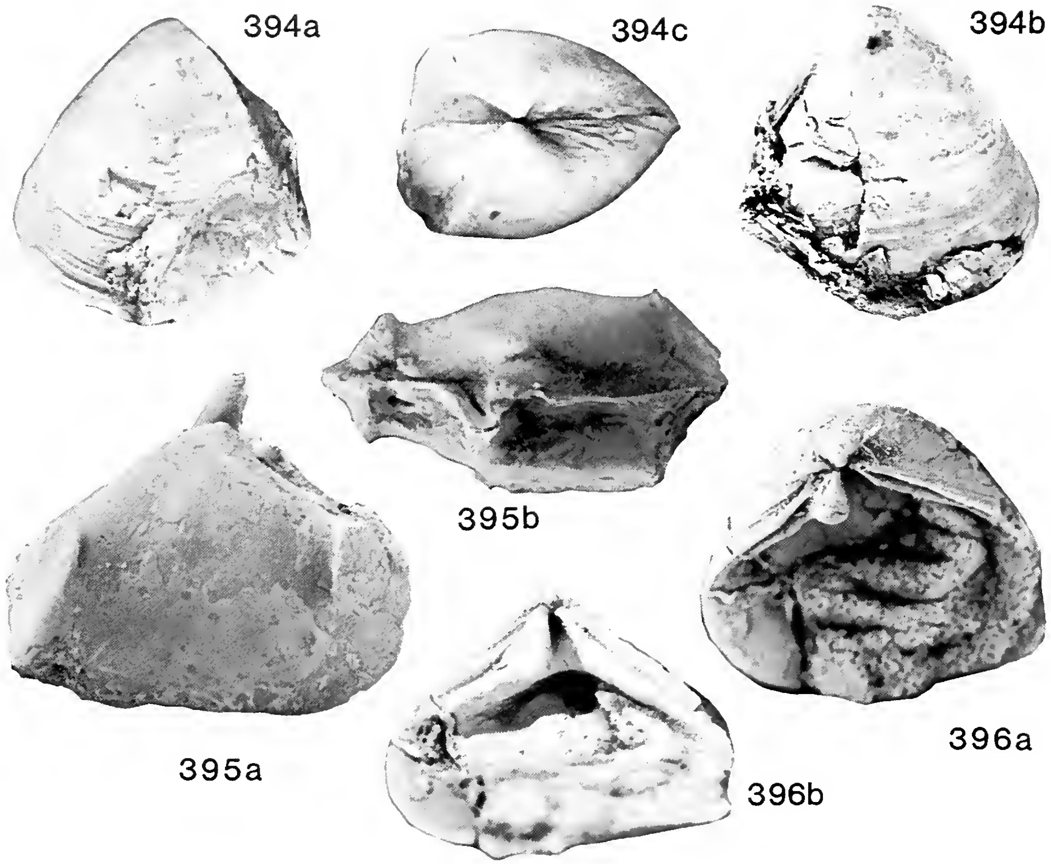
391e

392

393



Figs 389–393 *Pachydon cuneatus* Conrad. Pebasian. **389**, LL27851; **lectotype** (herein selected) of *Anisothyris tumida* Etheridge, probably figured by Etheridge (1879: pl. 7, fig. 2); Canamá, Peru; Barrington Brown Colln. Left valve, × 2.5. **390**, NYSM 8963; **lectotype** (herein selected) of *Pachydon cuneatus* Conrad, figured by Conrad (1871: pl. 10, fig. 12); Pichana, Peru; Hauxwell Colln. Right valve, × 1.5. **391**, L27725; shell figured as *Anisothyris cuneata* Conrad by Woodward (1871: pl. 5, fig. 8); Pichana, Peru; Hauxwell Colln. a–d, left and right valves, internal and external views, × 2; e, front view, × 2. **392**, **393**, LL28078–9; Puerto Nariño, Colombia; Weeda Colln. Left valves, both × 4.



Figs 394–396 *Pachydon hettneri* (Anderson). ? Miocene, probably Santa Teresa Formation; 'from near San Juan de Rio Seco', near km 106, Cambao to Bogotá Highway, Colombia. **394**, CAS 2698; **lectotype** (herein selected) of *Corbula hettneri* Anderson, figured by Anderson (1928: pl. 1, figs 11, 12; text-figs 10, 11); a–c, left valve, right valve, and dorsal view, all × 3. **395**, CAS 61359a; a, right, and b, dorsal views of internal mould, × 4. **396**, CAS 61359b; a, b, two slightly tilted internal views of dissection of right valve, × 4.

figured by Anderson, 1928: pl. 1, figs 13, 14, and CAS 2700–2705 (unfigured), all from same locality and collection as the lectotype, are paratypes.

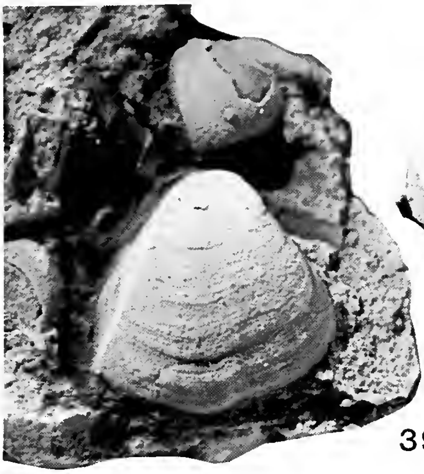
Other material studied. CAS 31695, more than fifty other specimens from the type locality. These are not regarded as paralectotypes as there is no indication that they were actually studied by Anderson. CAS 61359, two specimens re-registered from CAS 31695 (all same collection as type material). BMPD LL27897–9, LL28086–9, Loc. 33/570–670; LL27884–7, Loc. 33/480–560; LL27903–5, Loc. 33/560; LL4804, Loc. 44; LL4803, Loc. 45; LL27879, Loc. 54; all Late Caenozoic, La Tagua (Eden colln). No further records.

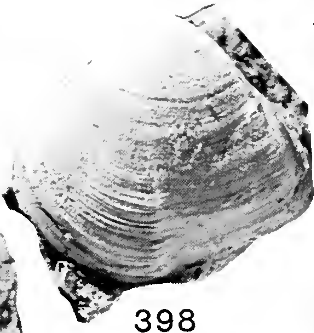
Distribution. Santa Teresa Formation and La Tagua Beds, Colombia.

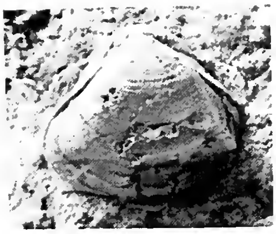
Diagnosis. Tumid, nearly equivalve *Pachydon*; outline equilateral and subtrigonal, often higher than long; umbones at about shell mid-length; corselet broad, extremely truncated, bordered by angular ridge marking maximum breadth of shell.

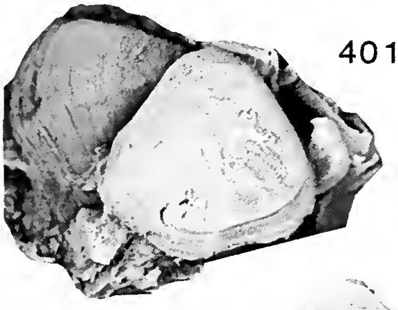
Description. The anterodorsal and posterodorsal margins of the shell are almost straight in outline, but the ventral margin is evenly rounded. There is a marked flexure at the middle of the ventral margin of some of the La Tagua shells. The umbones are small, in contact, slightly prosogyrous and only moderately incurved. The corselet is clearly differentiated from the flank by an angular ridge, and is divided by a much weaker ridge which is seen commonly in shells from La Tagua, but rarely in the more distorted and less well preserved shells from the Magdalena Valley. In dorsal

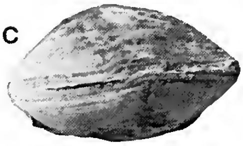
Dimensions. In mm.	l	h	br	l/h	br/l
Lectotype, CAS 2698, San Juan de Rio Seco.	14.1	14.6	10.2	0.97	0.72
CAS 2699, figured paralectotype, San Juan de Rio Seco (distorted).	13.1	13.5	–	–	–
LL27903, La Tagua, 33/570–670	8.2	7.2	5.0	1.14	0.61
LL27884, r.v., La Tagua 33/480–560	7.5	7.5	–	1	–
LL27879, l.v., La Tagua Loc. 54	5.5	4.7	–	1.17	–
LL27897/1, r.v., La Tagua 33/570–670	5.2	5.5	–	0.95	–
LL27898, l.v., La Tagua 33/570–670	7.5	7.9	–	0.95	–
LL27897/2, l.v. La Tagua 33/570–670	5.3	5.7	–	0.93	–

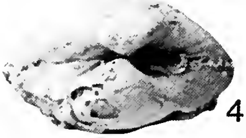


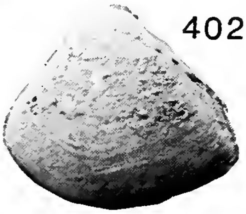












Figs 397–402 *Pachydon hettneri* (Anderson). Late Caenozoic; La Tagua, Colombia; Eden Colln; all × 4. **397**, **398**, LL27898, LL27897; Loc. 33/570–670, right and left valves. **399**, LL40804; Loc. 44, latex cast of internal mould of left valve. **400**, LL40803; Loc. 45. **401**, LL27884; Loc. 33/480–560, left valve. **402**, LL27903; Loc. 33/560; a–e, left, dorsal, ventral, rear and oblique view from above left.

view, the posterior of the shell appears almost flattened because the corselets of the two valve meet each other at almost 180°.

The right cardinal tooth lies dorsoventrally. It is fairly large, tear-drop shaped, and pointed dorsally: it is not visible externally. Both the posterior and anterior lateral teeth are strong and lie parallel to the shell margin at the edge of a fairly broad, weakly grooved hinge plate which acts as a socket for the reception of the left valve margin.

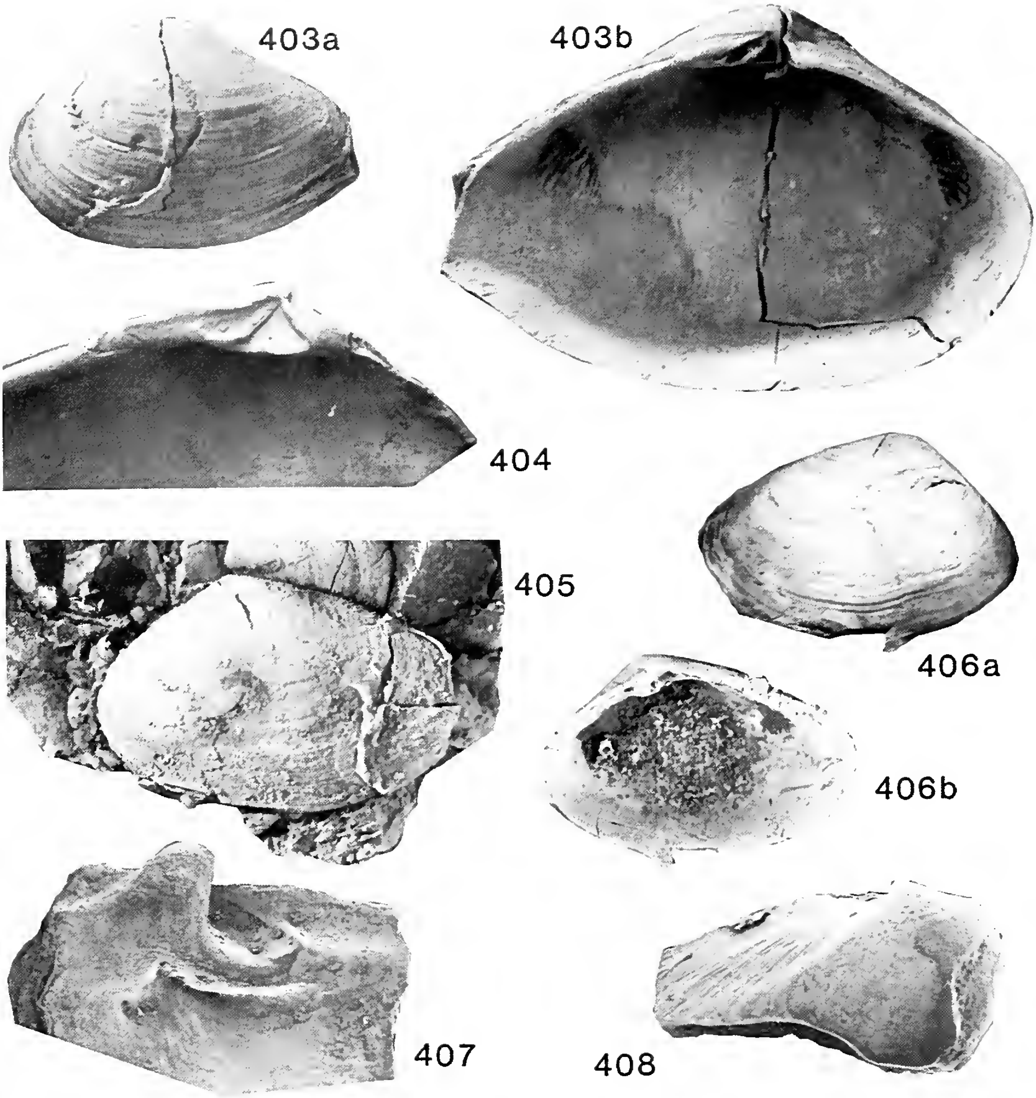
REMARKS. Anderson described both of his figured specimens, CAS 2698 and 2699, as syntypes, and the unfigured ones, CAS 2700–5, as paratypes. The opportunity is therefore now taken to designate CAS 2698, his most complete and least distorted figured specimen, as lectotype. CAS 2699 becomes a paralectotype along with CAS 2700–5. As in the case of *Pachydon cebada* (Anderson), p. 312, described from the same locality, it seems unsafe and unnecessary to regard the numerous specimens from CAS 31695 as paralectotypes.

The specimens from La Tagua are assigned to this species with only slight doubt. They differ in being smaller, and also have the extra minor angulation on the corselet and show flexure in the ventral commissure. The shell surfaces of Anderson's material are too poorly preserved in too coarse a sediment for such features to be seen. A possibly important difference is that the right cardinal tooth in the La Tagua shells appears to be swollen in an anteroventral direction rather than almost dorsoventrally, but unfortunately it has not been possible to reveal all the internal features of specimens from either locality for full comparison.

This species most clearly resembles *P. trigonalis* sp. nov., (p. 309), from Puerto Nariño, which is also almost equilateral, and has a rather similar hinge except that the resilium pit is shallower. It may be distinguished from *P. hettneri* in lacking the prominent corselet and carinate ridge and in being relatively longer.

Pachydon ovalis sp. nov. Figs 403–408

HOLOTYPE. BMPD LL27872, a left valve; late Caenozoic, 1.5 km upstream from La Tagua (Weeda colln). The following



Figs 403–408 *Pachydon ovalis* sp. nov. Late Caenozoic; La Tagua, Colombia. **403**, LL27872, **holotype**, a left valve; 1.5 km upstream from La Tagua; Weeda Colln. a, external, × 3; b, internal, × 5. **404**, LL28092, paratype, left valve; same locality as holotype; internal view, × 10. **405**, LL27881, paratype, left valve; Loc. 33/480–560, × 4. **406**, LL27880, paratype, right valve; Loc 54; Eden Colln. a, external; b, internal, × 4. **407**, LL28094, paratype; from type locality; internal view of right valve fragment showing cardinal tooth and resilium pit on hinge plate with pedal retractor scars below, × 15. **408**, LL28093, paratype; from type locality; fragment of left valve of juvenile specimen, × 10.

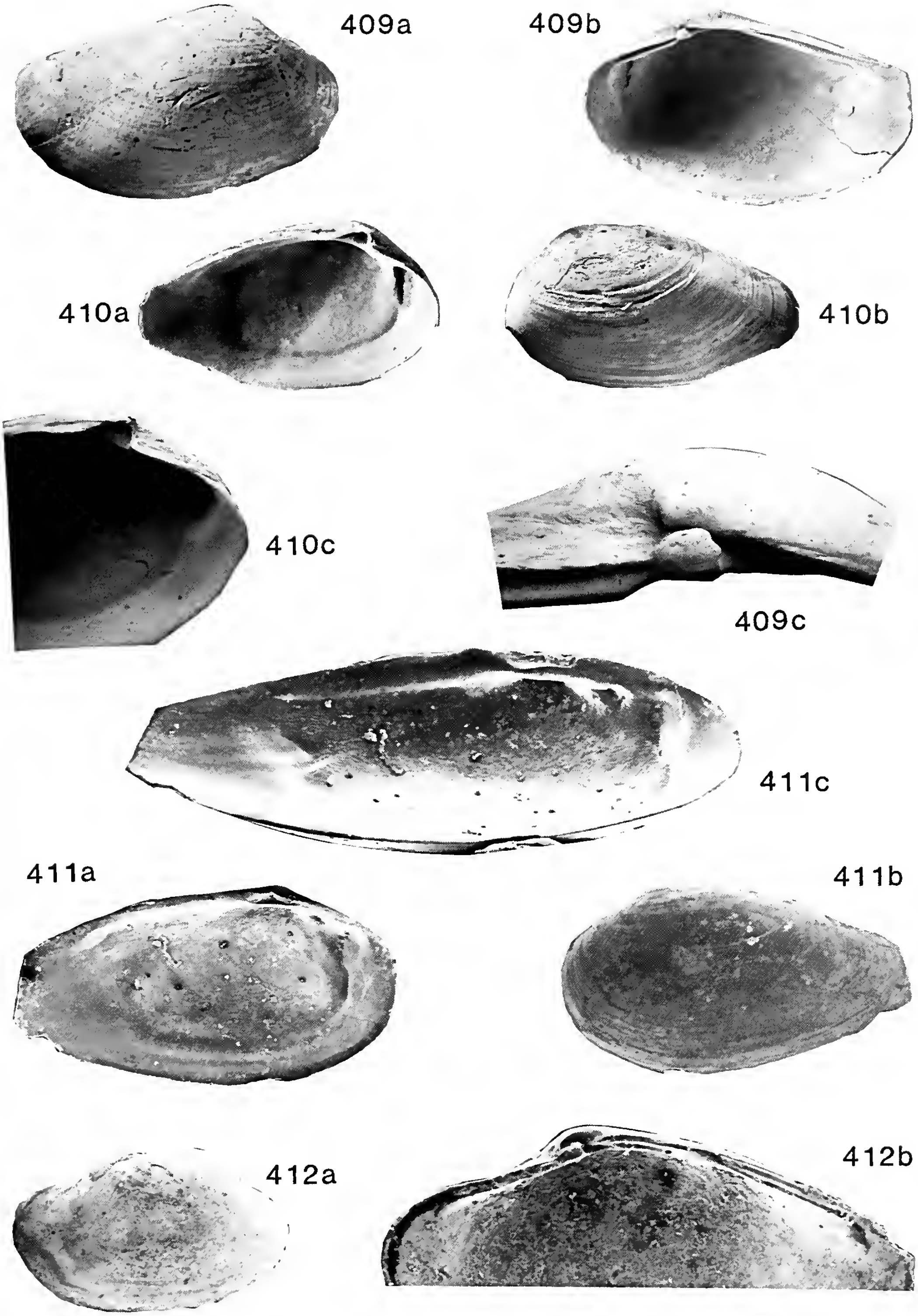
are paratypes; all Late Caenozoic of La Tagua district: LL28090–5, from type locality. Remainder all Eden colln; LL27880, Loc. 54; LL27881-3 (block), Loc. 33/480–560 cm; LL27906 (block), Loc. 33/560 cm.

NAME. 'Egg-shaped, oval.'

DIAGNOSIS. Small, oval, almost equivalve *Pachydon*; umbones not prominent, slightly anterior to mid-length; dentition comparatively weak: pallial sinus deep.

DISTRIBUTION. Late Caenozoic, La Tagua Beds; La Tagua, Colombia, only.

DESCRIPTION. The description is based on single, dissociated valves, but it is clear that the species is virtually equivalve and the ventral commissure shows signs of only a weak flexure. The oval growth lines are modified posterodorsally by a weak, somewhat crassatelliform truncation, but no corselet is differentiated. The slightly prosogyrous umbones are neither prominent nor strongly curved. Internal features of the left valve are known from the holotype, and the paratype LL28092 from the type locality: those of the right valve are known only from paratype LL27880. In this specimen the cardinal tooth is damaged, but appears to lie in a dorsoventral plane. A long anterior lateral tooth lies parallel to and separated from the shell margin by a narrow socket. No true posterior lateral tooth can be seen in this specimen but the posterodorsal shell margin is greatly thickened in the damaged region where a lateral tooth might have been expected. The hinge plate in the left valve is typical of the genus but relatively thin in cross section. Pedal muscle scars are seen just behind the anterior adductor scar, as an anterior extension to the dorsal margin of the posterior adductor scar. Four pits are visible under the hinge plate of paratype



Figs 409–412 *Pachydon amazonensis* (Gabb). Pebasian; Pichana, Peru; Hauxwell Colln. **409**, LL27907; a, b, right valve external and internal, × 4; c, umbonal area from above, × 15. **410**, LL28062; a, b, left valve, external and internal, × 4; c, cardinal socket, × 6. **411**, LL28064; a, b, left valve, external and internal, × 10; c, inside of valve viewed obliquely from below, × 15. **412**, LL28065, right valve; a, external, × 10; b, internal, × 20.

LL28092. There is a broad, invaginated pallial sinus, stretching from the anterior of the posterior adductor scar half-way to a point below the umbo.

Dimensions. In mm.		l	h	br	l/h	br/l
Holotype, LL27872, 1.5 km upstream from La Tagua	actual	16.0	10.7	4.0	1.54	0.51
	est.	16.5				
Paratype LL27881, La Tagua, 33/480–560		11.2	8.0	–	1.40	–
Paratype LL27880, La Tagua, Loc. 54		11.0	c. 7.5	c. 2.8	1.47	c. 0.51

Note. The above ratios are calculated on estimated dimensions, with shell breadth estimated as twice valve breadth. Other specimens are too fragmentary to measure.

Remarks. This species is briefly discussed under *P. cebada* (Anderson), p. 312, from which it is distinguished by its more oval, less crassatelliform, outline and its greater size. *P. ovalis* strongly resembles *P. amazonensis* (Gabb). The latter, however, is more elongate, its hinge is lighter and is pallial sinus is a truncation of the pallial line. *P. ovalis* is the only species of *Pachydon* in which such a deep pallial sinus is known, but its other features and its resemblance to *P. amazonensis* suggest that generic separation would be unjustified.

Pachydon amazonensis (Gabb, 1869) Figs 409–412

- * 1869 *Tellina amazonensis* Gabb: 198; pl. 16, fig. 4.
- . 1878 *Anisothyris amazonensis* (Gabb) Boettger: 499; pl. 13, figs 19a, b, 20a–c, 21a, b.
- 1924 *Tellina amazonensis* Gabb; Roxo: 44.
- . 1938 *Anisothyris amazonensis* (Gabb); de Greve: 30; pl. 6, figs 18, 19; pl. 7, figs 2–4, 7, 8, 10, 11.
- ? 1966 *Anisothyris amazonensis* (Gabb); Willard: 66–68; pl. 58, figs 4, 5.

Type material. Gabb's material, described from Pebas, is not listed as being in ANSP (Richards 1968).

Material studied. BMPD LL27907–9, LL28060–7; Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell colln, extracted from matrix, 1981).

Occurrences. All Late Caenozoic. Type locality, Pebas, Peru (Gabb 1869, Boettger 1878); Três Unidos, Peru, and Cachoera das Tracoás, Brazil (Roxo 1924); ?Rumi Tuni, Negro Urca and confluence of Rio Mazan and Rio Napo, all Peru (Willard 1966). Late Caenozoic, Pebasian of Upper Amazon Basin only.

Diagnosis. Small, rather tumid, virtually equivalve *Pachydon*; outline resembling *Paphia*, elongate-oval with posterior sometimes truncated.

Description. The elongate-oval shell tapers towards the posterior end, which may be either rounded or truncated and somewhat crassatelliform. The lowest point of the ventral margin is well behind the umbones which are situated between a third and a quarter of the length of the shell from the anterior. The umbones are slightly prosogyrous, low, and not strongly incurved. The right cardinal tooth is hooked, and lies in the plane perpendicular to the hinge line with its anterior surface in contact with the outside world. The resilium pit is subparallel to the dorsal commissure, sloping ventrally at a shallow angle. The anterior adductor scar is strongly pitted and deeply impressed, particularly dorsally. In the right valve LL27907/1, two deep pedal muscle scars are situated side by side just behind the anterior adductor scar. In the best preserved left valve LL27907/2, a single deep pedal muscle scar lies behind the anterior adductor. The posterodorsal region of the adductor scar is very deeply impressed and may well be a pedal muscle attachment. Two other small muscle scars can be seen, one underneath the posterior end of the hinge plate, and the second just above the posterior adductor scar, which is not strongly impressed. The pallial line is truncated, but not invaginated posteriorly beneath the anterior margin of the posterior adductor scar. Ample space is thus left to accommodate retracted siphons. The commissure is plane except for a weak flexure in the ventral margin.

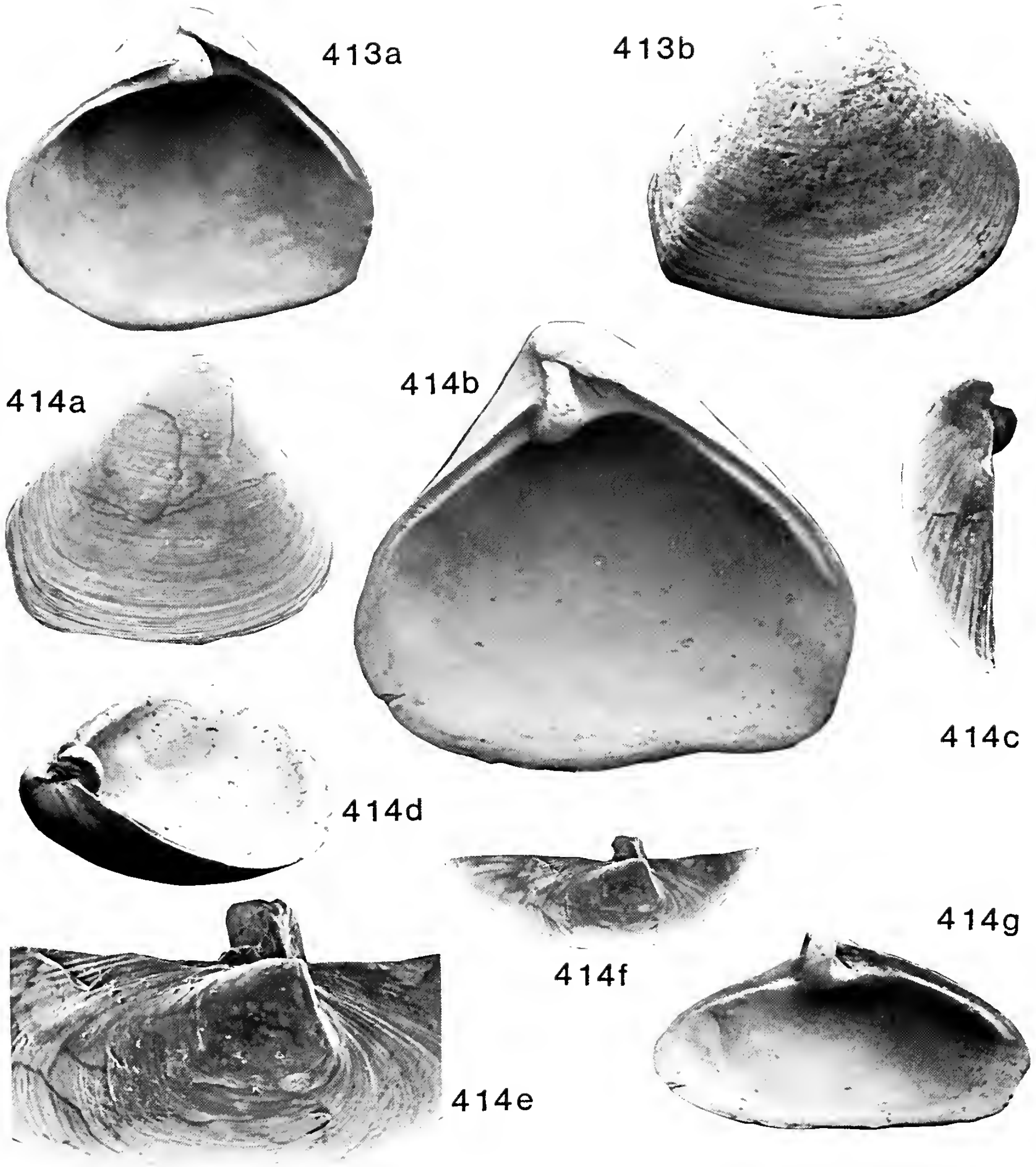
Dimensions. In mm.	l	h	br	l/h	br/l
LL27907/1, r.v., Pichana, Peru	13.1	7.4	3.4	1.77	0.52
LL28062, l.v., Pichana, Peru	11.8	6.6	2.8	1.79	0.48
LL28064, l.v., Pichana, Peru	6.3	3.5	1.3	1.80	0.42
LL28065, r.v., Pichana, Peru	4.3	2.5	1.0	1.72	0.44
PIMUZ 717A, r.v., Iquitos	14.5	7.7	–	1.88	–
Fig'd Boettger 1878: pl. 13, fig. 19; Pebas	4.4	2.3	–	1.90	–
Fig'd Boettger 1878: pl. 13, fig. 20; Pebas	11.5	7.0	–	1.64	–
Fig'd Boettger 1878: pl. 13, fig. 21; Pebas	11.8	6.6	–	1.79	–

Note. Dimensions of Iquitos and Pebas shells calculated from de Greve (1938: pls 6, 7). Breadth measurements are of single valves; br/l ratios take shell breadth to be double valve breadth.

Remarks. Gabb's type material from Pebas cannot be found in ANSP (Mary A. Garback, ANSP, personal communication). The dimensions he gave were of a small shell (l, 0.25″; 'w', 0.15″; h, single valve, 0.04″) (l, 6.4 mm; h, 3.8 mm; br, 1.0 mm), but he had fragments indicating the presence of a shell twice the size, and his illustration (1869: pl. 16, fig. 4) shows a more elongate shell than his dimensions would suggest (l/h, 1.9 as opposed to 1.7).

The material described by Boettger (1878) came from either Pebas or Pichana and there are no grounds for doubting that the specimens that he figured, which were subsequently refigured by de Greve, are correctly identified. Willard's illustration shows a shell whose outline is not quite typical of the species and whose hinge is not clearly shown. It would appear that the shell might not have been orientated normally for photography, and there must therefore be some doubt about this identification.

For what appears at first to be a small, delicate, species, the shell is surprisingly tumid and the muscle scars remarkably strong. The species is discussed also under *P. cebada* (Anderson), p. 312, and *P. ovalis* sp. nov. (above).



Figs 413–414 *Pachydon trigonalis* sp. nov. Pebasian; Puerto Nariño, Colombia; Weeda Colln; right valves. **413**, LL27860, **holotype**; a, b, external and internal views, × 6. **414**, LL27861, paratype; a, external, × 10; b, internal, × 15; c, front, × 10; d, front oblique view of umbo and cardinal tooth, × 10; e, f, dorsal views showing cardinal tooth, × 40 and × 10; g, internal view obliquely from below, × 10.

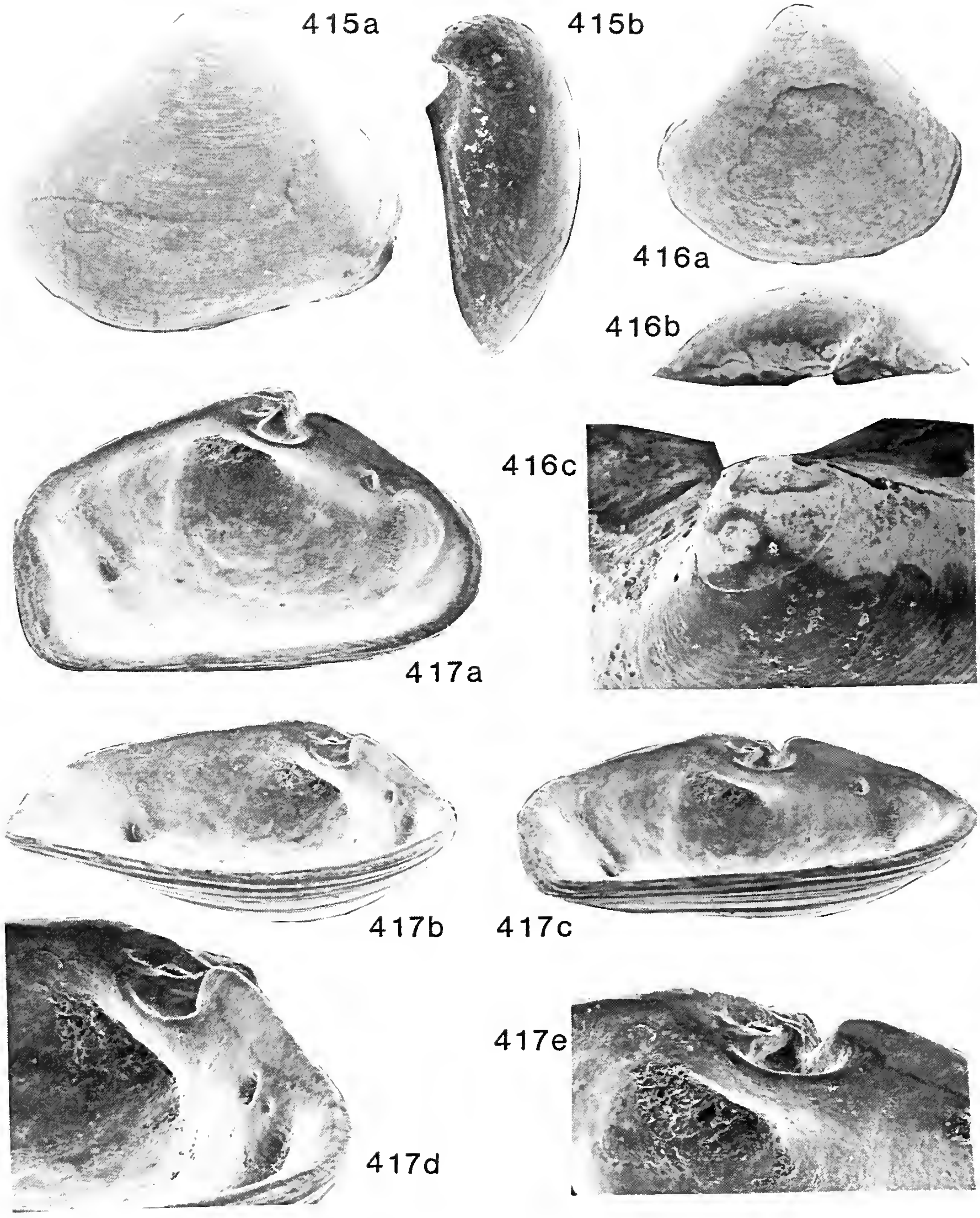
Pachydon trigonalis sp. nov. Figs 413–419

HOLOTYPE. A right valve, LL27860; Late Caenozoic; Puerto Nariño, Colombia (Weeda colln). Paratypes LL27861–70, over thirty separate valves and two complete juveniles, locality and horizon as holotype; and LL28007, six juvenile shells, Canamá, extracted in 1984 from matrix of Barrington Brown colln.

NAME. 'Triangular'.

DIAGNOSIS. Subtrigonal, crassatelliform in outline, almost equivalve *Pachydon*: umbones erect, at about mid-length.

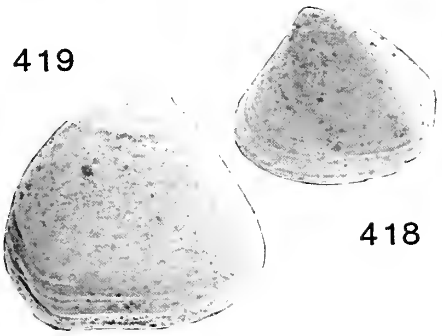
DESCRIPTION. The anterodorsal and posterodorsal margins slope downwards at almost the same angle. The anterior of the shell is well rounded. Posteriorly, a crassatelloid corselet is separated from the flank by a weak, well-rounded ridge. The ridge bordering a region analogous to an escutcheon is also very weak. The ventral margin is barely convex and its deepest point is in front of the umbones. The ventral commissure is also virtually straight and the two valves are of the same convexity. The centrally placed umbones are slightly prosogyrous and touching. The cardinal socket and tooth are comparatively strong but narrow and vertical. The front of the tooth is exposed to the outside world underneath the anterior of the umbones. A shallow pallial sinus is present.



Figs 415–417 *Pachydon trigonalis* sp. nov. Pebasian; Puerto Nariño, Colombia; Weeda Colln; left valves, all paratypes. **415**, LL27862; a, b, external and front views, both × 10. **416**, LL27865; a, b, external and dorsal views, × 10; c, detail of umbonal region, × 40. **417**, LL27863; a–e five internal views; a–c, × 10; d, e, × 20.

DIMENSIONS. In mm.	l	h	br/2	l/h	l/br
LL27860, holotype, r.v., Puerto Nariño.	8.6	7.5	2.7	1.23	1.65
LL27861, r.v., Puerto Nariño.	7.0	6.0	2.3	1.16	1.52
LL27862, l.v., Puerto Nariño.	6.4	5.5	2.0	1.16	1.48
LL28007/1, l.v., Canamá.	3.2	2.9	–	1.10	–
LL28007/2, r.v., Canamá.	3.4	3.1	–	1.10	–

REMARKS. The distinctions between this species and *P. hettneri* (Anderson) are discussed under the latter, p. 305. Both are easily distinguished from other species of *Pachydon* by their trigonal shape. There is some resemblance to *P. erectus* (Conrad), which differs in having more prosogyrous and forwardly positioned umbones and a strongly alate posterior.



Figs 418–419 *Pachydon trigonalis* sp. nov. Pebasian; Canamá, Peru; Barrington Brown Colln. Paratypes, both × 10. **418**, LL28007/1; left valve. **419**, LL28007/2; right valve.

Pachydon cebada (Anderson, 1928) Figs 420–425

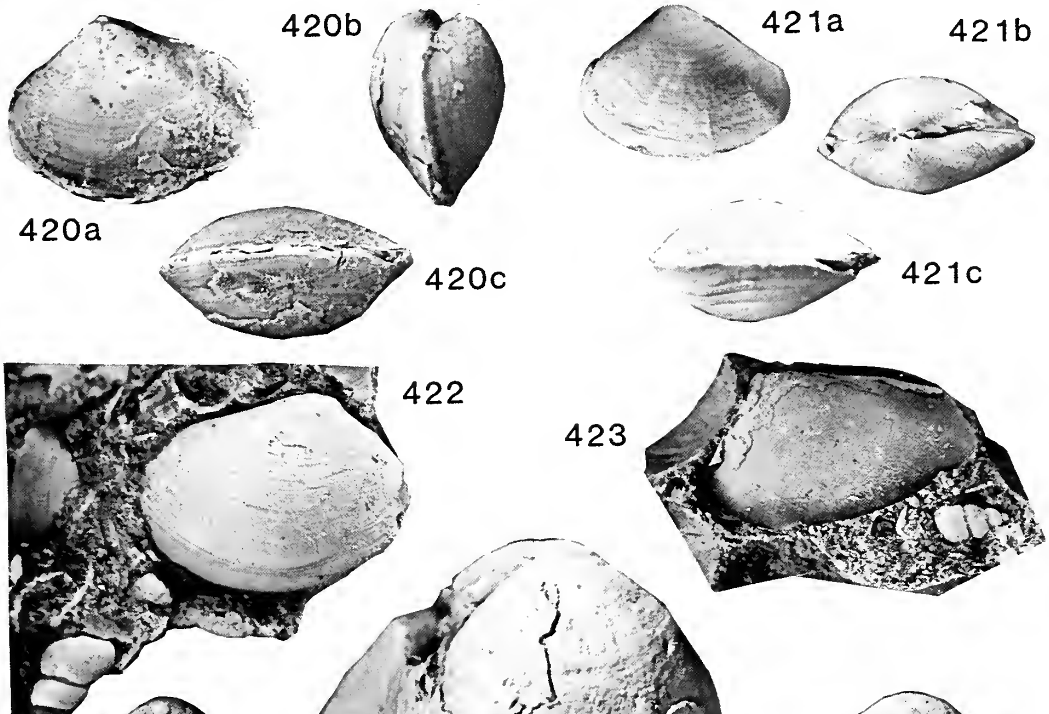
*v 1928 *Corbula cebada* Anderson: 24; pl. 1, fig. 15, text-figs 6, 7.

*v 1928 *Corbula scheibi* Anderson: 25 (*pars*); pl. 1, figs 16, 17 (*non* fig. 18); (*non* text-figs 8, 9).

*v 1935 *Corbula* (*Corbula*) *abundans* Pilsbry & Olsson: 19; pl. 2, figs 13, 14.

*v 1935 *Corbula* (*Erodona* ?) *magdalensis* Pilsbry & Olsson: 20; pl. 4, fig. 8.

HOLOTYPE of *Corbula cebada* (Anderson), CAS 2706, and unfigured paratypes, CAS 2707–14, 'from near San Juan de Rio Seco, eastern border of the Upper Magdalena Valley, Colombia, from near the base of the Guaduas Group, not far above the horizon of the coal veins' (Anderson 1928). Originally dated as Eocene, this locality is here redated as



Figs 420–425 *Pachydon cebada* (Anderson). Probably all Neogene; Colombia. **420**, CAS 2706, holotype of *Corbula cebada* Anderson; figured by Anderson (1928: pl. 1, fig. 15; text-figs 6, 7), probably Santa Teresa Formation; from near San Juan de Rio Seco, probably near km 106, Cambao to Bogotá Highway. a–c, left, front and ventral views, × 5. **421**, ANSP 13077a, **lectotype** (herein selected) of *Corbula abundans* Pilsbry & Olsson; figured by Pilsbry & Olsson (1935: pl. 2, figs 13, 14); Miocene; La Cira Formation, Zopffs, near La Cira, Colombia. a–c, left, dorsal, and ventral views, × 5. **422**, ANSP 13077, previously unfigured paralectotype of *Corbula abundans*, same details as lectotype; right valve, × 8. **423**, ANSP 13075, left valve of the almost entirely decorticated **lectotype** (herein selected) of *Corbula magdalensis* Pilsbry & Olsson, figured by Pilsbry & Olsson (1935: pl. 4, fig. 8), from same locality as *Corbula abundans*; × 5. **424**, CAS 2717, right valve of holotype of *Corbula scheibi* Anderson; same locality as holotye of *C. cebada*; × 5. **425**, CAS 2716, paratype of *C. scheibi* Anderson, same locality as holotype of *C. cebada*; a, b, left and right sides, × 5. (See discussion, p. 312, on unclear original type designations of this species).

Miocene, Santa Teresa Formation (Porta 1966); probably at km 106, Bogotá to Cambao Highway (Butler 1939, 1942) (Downs McCloskey & Thomas Wark colln).

CAS 2716, one of the paratypes of *Corbula scheibi* Anderson, is from the same locality, horizon and collection. See below.

Lectotype, selected herein, of *Corbula abundans* Pilsbry & Olsson, 1935: ANSP 13077a, the specimen originally figured (1935: pl. 2, figs 13, 14). ANSP 13077 is two unfigured paralectotypes. All from Zopffs, near La Cira, middle Magdalena Valley, Colombia; La Cira Formation, originally dated (Pilsbry & Olsson 1935: 8, Wheeler *in* Pilsbry & Olsson 1935: 34–35) as Upper Oligocene or Lower Miocene, but here redated as Miocene.

Lectotype, selected herein, of *Corbula magdalensis* Pilsbry & Olsson, 1935: ANSP 13075, the specimen figured by them (1935: pl. 4, fig. 8), and an unfigured paralectotype on the same block, are from the same locality as *Corbula abundans*. Several other possible paralectotypes are associated with ANSP 13074, on blocks from the same locality bearing the type series of *Potamopyrgus laciranus* Pilsbry & Olsson, 1935, (*Dyris*, herein): see p. 195.

Other material. CAS 31695, several other specimens of *Corbula cebada* Anderson, in three small samples of grey mudstone from the type locality, have been examined. These are not regarded as paratypes as there is no indication that they were studied by Anderson. The species is further recorded from many other localities near La Cira in the La Cira Formation (Pilsbry & Olsson 1935): not seen. Miocene; Santa Teresa and La Cira Formations, Magdalena Valley, Colombia.

Diagnosis. Small, almost equivalve *Pachydon*; oval with weak crassatelliform corselet developed; umbones slightly anterior to mid-length and not prominent.

Description. The left valve is slightly more tumid than the right. The ventral commissure is curved so as to form a weak central sinus in the left valve. The anterior of the shell is evenly rounded and the posterior is truncated to a varying extent but never strongly. A weak corselet is present; in some shells, however, it can be seen only with difficulty. The slightly prosogyrous umbones are neither prominent nor strongly curved.

Internal features are known from only one specimen, CAS 2716, a paratype of *Corbula scheibi* Anderson, in which part of the right hinge is exposed. It is worn so that neither the exact shape of the cardinal tooth nor the position of the resilifer in relation to the resilium pit can be made out. The anterior of the massive cardinal tooth is exposed to the outside world and slopes at about 45° towards the antero-dorsal commissure, where its base merges with the posterior end of a rather ill-defined elongate anterior lateral tooth. This is separated by a shallow depression from the sharp bordering ridge forming the commissure. The rear margin of the cardinal tooth is cut off vertically by the side of the deep resilium pit. The posterior part of the shell, where a posterior lateral tooth might be expected to lie, is broken away. Muscle scars are not exposed.

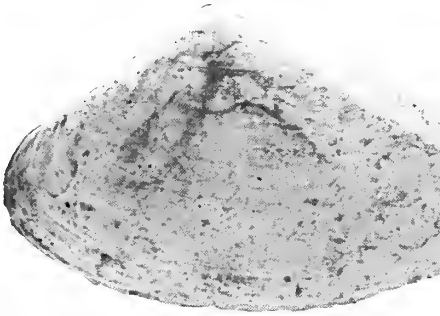
Dimensions. In mm.	l	h	br	l/h	br/l
Holotype of *C. cebada*, Anderson, 1928, CAS 2706, San Juan de Rio Seco.	7.1	5.1	3.6	1.4	0.51
Lectotype of *C. abundans*, Pilsbry & Olsson, 1935, ANSP 13077a, Zopffs.	5.8	3.6	3.0	1.6	0.52
Lectotype of *C. magdalensis*, Pilsbry & Olsson, 1935, ANSP 13075, Zopffs.	7.5(e)	5.0(e)	–	*c.* 1.5	–

Remarks. *Pachydon hettneri* (Anderson) (p. 302) was described from the same locality as *P. cebada*, and the differences between the two are obvious.

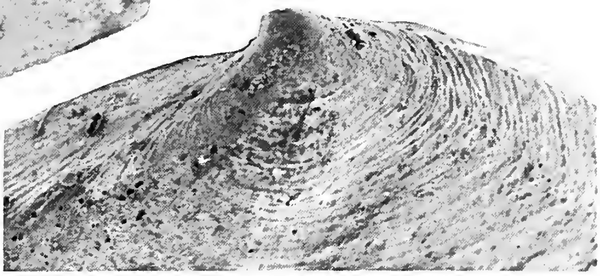
P. abundans and *P. magdalensis* were originally separated by Pilsbry & Olsson (1935) because the latter was crassetelloid in shape and was also described as having the umbones relatively far forward with the posterior part of the shell three times the length of the anterior. The type series of both species come from the same locality (Zopffs), occurring in a hard dark brown mudstone crowded with shells. With the exception of the holotype of *P. abundans*, all are damaged, often partly decorticated and, like the holotype of *P. magdalensis*, partly buried in matrix. In the original illustrations this matrix has been completely blocked out, resulting in a highly distorted representation of the true shape. In fact it would appear that all the shells seen from Zopffs are conspecific. Moreover, the measurements quoted by Pilsbry & Olsson (1935) cannot be reconciled with those now made. However, Pilsbry & Olsson (1935: 20) acknowledged the similarity between their *C. abundans* and *C. cebada* Anderson. They separated the two on the grounds that *C. cebada* had a less plump convex (i.e. right) valve, lacked the concentric wrinkles (greatly accentuated in their heavily retouched type illustrations) of *C. abundans*, and was larger. But the difference in convexity of valves between the two is slight, and some specimens of *C. cebada* show traces of concentric wrinkling. Furthermore, the size difference seems too slight for specific distinction: the dimensions they quoted for the holotype of *C. cebada* Anderson (length, 6.8 mm; height, 5.3 mm; breadth, 3.7 mm) are also inaccurate: see above.

It is difficult to make a proper assessment of *C. scheibi* Anderson (1928: 25; pl. 1, figs 16–18) from the same locality as *cebada*. In the text and his plate description, Anderson referred to two 'syntypes', CAS 2716 and 2717, as well as paratypes CAS 2718–20. The explanation of his text-figures 8 and 9, however, refers to the 'holotype'. He gave no registration number for it, but the dimensions he quotes show that it can only be CAS 2717, which is also illustrated as his pl. 1, fig. 18. This specimen was subsequently curated at CAS as the holotype of *scheibi* and must be accepted as such, and all the other specimens as paratypes. Unfortunately, CAS 2717 is too badly preserved to be used as a yardstick for the determination of other specimens. The figured paratype CAS 2716 (1928: pl. 1, figs 16, 17) is a rather deformed *C. cebada*, and provides some information on the internal features of that species: see above. None of the other paratypes (CAS 2718–29) are specifically determinable.

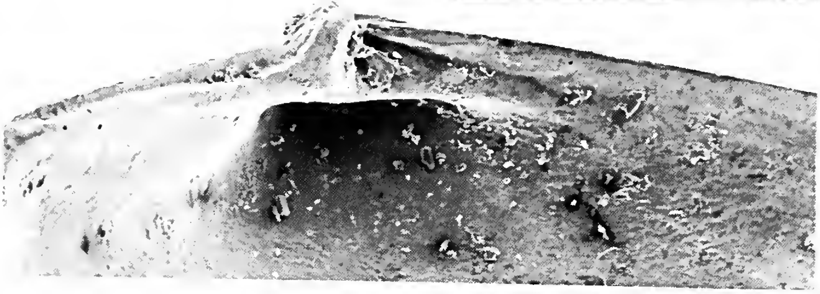
P. cebada (Anderson), *P. amazonensis* (Gabb), *P. iquitensis* (de Greve) and *P. ovalis* sp. nov. (p. 305) form a group of small, relatively equivalve, thin-shelled *Pachydon* species with weak umbones. *P. iquitensis* is *Cuspidaria*-shaped with an attenuated and upturned posterior end. *P. amazonensis* from Pebas (Gabb 1869, Boettger 1878, de Greve 1938), Iquitos (de Greve 1938), and Pichana (BMPD, Hauxwell colln) is distinguished by its more forwardly placed umbones, less curved ventral margin, shallower pallial sinus, and by being usually more elongate (l:h usually 1.7–1.9:1, exception-



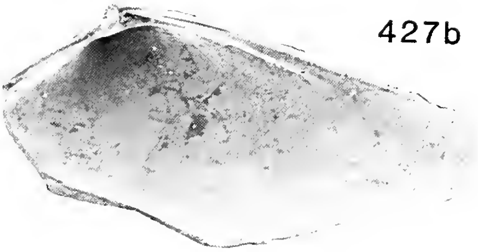
426a



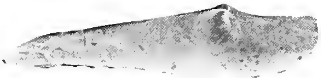
426b



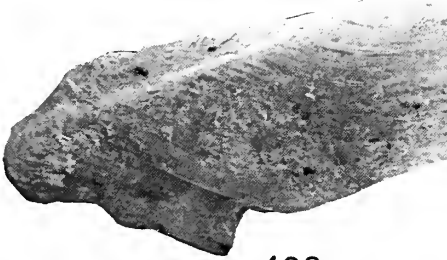
427a



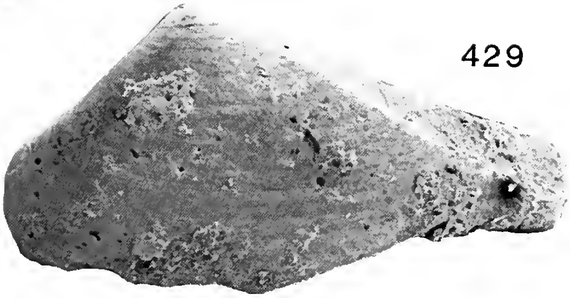
427b



428b



428a



429

Figs 426–429 *Pachydon ledaeformis* Dall. Pebasian; Pichana, Peru; Hauxwell Colln. **426**, LL28068; a, left valve, × 15; b, details of umbo, × 50. **427**, LL28071; a, right valve, internal oblique view into umbonal cavity, × 50; b, internal normal view, × 15. **428**, LL28070; a, right valve, × 15; b, dorsal view, × 6. **429**, LL28069; left valve exterior, × 15. Note: LL28069 (Fig. 429) and LL28070 (Fig. 428) were found separately but may well be the two valves of the same individual.

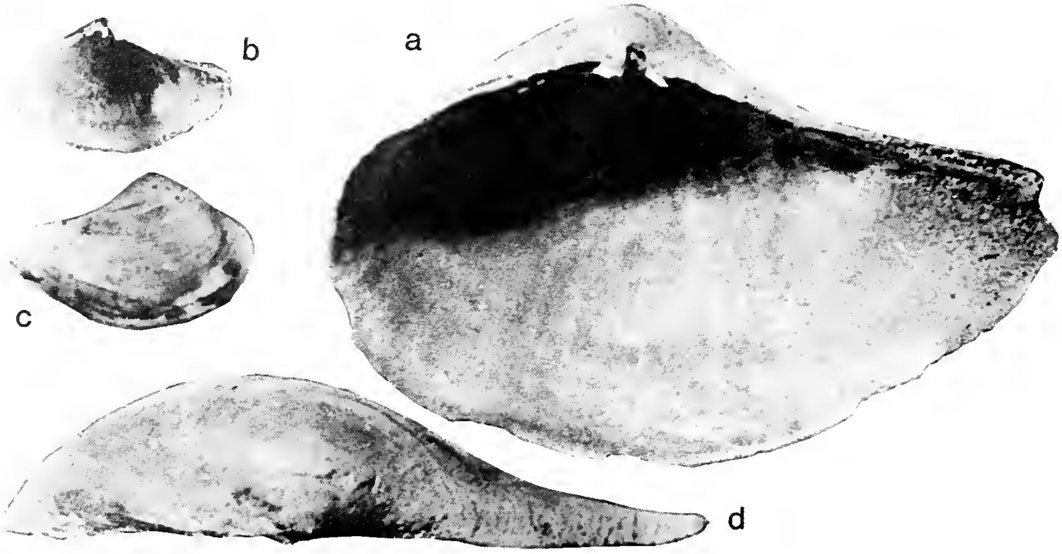


Fig. 430 *Pachydon iquitensis* (de Greve). Pebasian; Iquitos, Peru. Copies of original illustrations of holotype, the only known specimen, a right valve, of *Anisothyris iquitensis* de Greve (1938: pl. 5, figs 38–41). a, internal view, × 6 (fig. 38); b, internal view, × 1.85 (fig. 39); c, external view, × 2 (fig. 40); d, dorsal view, × 6 (fig. 41). Note: de Greve gave no dimensions in his text.

ally 1.4:1; see de Greve, 1938: pl. 7, figs 10, 11, a re-illustration of one of Boettger's Pebas shells).

P. erectus elongatus (Boettger) from Pebas was also refigured by de Greve (1938) and may be readily recognized by its prominent, erect, umbones. The specimen figured by Willard (1966: pl. 56, fig. 3) from 'El Salad', north of Iquitos, as *Corbula abundans* Pilsbry & Olsson is misidentified.

Anderson's trivial name *cebada* is of uncertain meaning, though the Spanish word for 'barley' could be intended. It is taken as a noun is apposition and not an adjective, and therefore not inflected.

Pachydon ledaeformis (Dall, 1872) Figs 426–429

*. 1872 *Corbula (Anisothyris) ledaeformis* Dall: 92; pl. 16, figs 14, 15.

Type material. USNM, not studied. Upper Amazon Basin, unlocalized, presumed Pebasian (Orton colln, see Remarks).

Material studied. BMPD LL28068–71, Late Caenozoic, Pebasian; Pichana, Peru (Hauxwell colln, extracted from matrix, 1982).

Diagnosis. Small crassatelliform *Pachydon*; elongate with length about twice height; umbones situated at about one third of length from anterior of shell, posterior rostrate.

Description. The material is fragile and no completely undamaged shell outlines are available in the material at hand. The umbones are not large, but are sufficiently produced to make both the anterodorsal and posterodorsal margins appear slightly concave when the shell is viewed externally. From inside, these margins, which form the two halves of the hinge, appear virtually straight. The shell outline has a slightly truncated, convex anterior, and an almost straight, only slightly convex ventral margin, whilst the posterior of the shell is alate. Careful examination of the growth lines shows that the most posterior point of the shell coincides with the ridge separating the corselet from the main flank of the shell. Damage to all the specimens seen gives the false first impression that the posterior is abruptly truncated. The growth lines, though not strong, are clearly visible and appear to be the same strength on all parts of the shell. The shell is fairly compressed. Although the material consists entirely of dissociated and incomplete valves extracted from washings, it seems that two of them (LL28069, 28070) are likely to be from the same individual: enlarged photographs of the two are exact mirror images. If this deduction is correct, the species appears to be equivalve, apart from the minor differences in the rostrum, and the commissure is straight, or certainly not noticeably curved. The dentition is comparatively light, as in *Pachydon amazonensis* (Gabb), p. 308. Neither muscle scars nor the pallial line can be seen.

Dimensions. In mm.	l	h	l/h
LL28068 (l.v.)	5.8	3.2	1.8
LL28069 (l.v.)	3.9+	–	–
LL28070 (r.v.)	5.2	–	–
LL28071 (r.v.)	4.1+	–	–

Note. The dimensions given by Dall (1872) were: l, 0.3″ (7.6 mm); h, 0.14″ (3.6 mm); this gives a length to height ratio of 2.1.

Remarks. Dall gave no locality for this species. It was described at the end of a short paper discussing the relationship between Pebasian *Anisothyris* and *Corbula*. Dall stated that it was from Orton's collection. Orton, himself, had collected the material from Pebas described by Gabb (1869), the surviving parts of which are in ANSP. Orton also handled at least part of Hauxwell's collection, which came mainly from Pichana and was divided between several workers (Conrad 1871*a*, *b*, Woodward 1871, and, possibly a later collection, Boettger 1878). The BMPD material was extracted from Hauxwell's collection, mainly from Pichana: on balance, this is the more likely source of Dall's type material, particularly bearing in mind the date of his work and the fact that the Hauxwell collection was almost certainly much larger, and therefore more likely to have been widely distributed, than Orton's own collection.

This species, which Dall thought was the young of an undescribed species, has been neglected since its original description. However, it still cannot be matched with any other known species. *Pachydon erectus elongatus* (Boettger), p. 300, is much more tumid and has a more elongate and well rounded outline. *Pachydon amazonensis* (Gabb), p. 308, is also rather more tumid and lacks any trace of a posterior extension or rostrum.

Pachydon iquitensis (de Greve, 1938) Fig. 430

* 1938 *Anisothyris iquitensis* de Greve: 46; pl. 5, figs 38–41.

HOLOTYPE. PIMUZ 394, Pebasian, Iquitos (Peyer colln), a single right valve (not studied). No other material or records.

DIMENSIONS. De Greve gave no measurements. Calculated from his illustrations, however, we have: l, 12 mm; h, 7.8 mm; vbr, 3 mm; umbo situated 5 mm posterior to the most anterior point of shell.

REMARKS. This single right valve, which has not been reexamined, was well illustrated by de Greve and clearly merited description as a new species. It is comparatively small for the genus and may be grouped for comparative purposes with *P. amazonensis* (Gabb), *P. cebada* (Anderson), *P. erectus elongatus* (Boettger), *P. ledaeformis* (Dall) and *P. ovalis* sp. nov. (p. 305). Its cuspidariiform outline serves to distinguish it from all but *P. ledaeformis*, which is more elongate and has a corselet bordered by a definite diagonal ridge, whilst *P. erectus elongatus* has a somewhat similar outline but is much more truncated anteriorly. In vertical view, the swollen anterior coupled with the attenuated posterior of the present species give an outline not seen in other species of *Pachydon*.

The single rather poorly preserved specimen, LL27817 (Fig. 451), from the Miocene Loyola Formation of the Cuenca Basin, Ecuador, identified as *? Erodona iquitensis* (de Greve) in Bristow & Parodiz (1982: 31) is here reidentified as *Corbicula (Cyanocyclas) cojitamboensis* Palmer, *in* Liddle & Palmer 1941. This is a very common species in the Cuenca Basin Miocene. This species is not dealt with here as it is discussed in detail and a synonymy given by Bristow & Parodiz (1982: 29, figs 6, 7). LL27817 consists of incomplete internal and external moulds of the anterior end of a left valve of *C. cojitamboensis*. Although there is no clear statement on the subject by Bristow & Parodiz, it would appear that this specimen had erroneously been interpreted as the right valve of a specimen of *P. iquitensis*. This reidentification is of some importance as it eliminates the only record of *Pachydon* from the Neogene of the Cuenca Basin.

Genus ***PEBASIA*** nov.

TYPE SPECIES. *Pachydon* (*Anisorhynchus?*) *dispar* Conrad, 1874*a*. Late Caenozoic, Pebasian; Pebas district, Peru. No other assigned species.

NAME. From the locality of Pebas. Feminine.

DIAGNOSIS. Shell very inequivalve, smooth except for growth lines; commissure twisted.

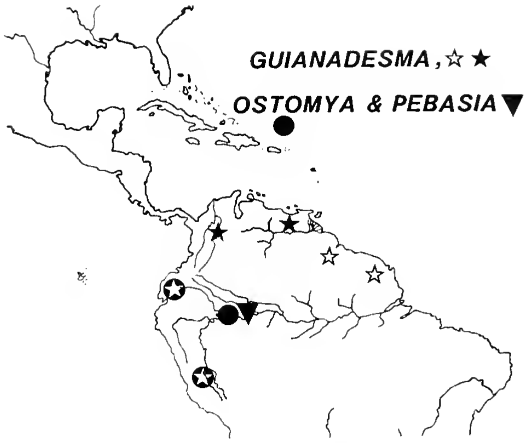


Fig. 431 Neogene and Recent distribution of *Guianadesma* and the extinct genera *Ostomya* and *Pebasia*. ★, Neogene *Guianadesma*; ☆, living *Guianadesma*; ●, Pebasian *Ostomya*; ▼, Pebasian *Pebasia*; ✪, doubtful records of *Ostomya*.

Right valve pholadiform, bilobed, with the two lobes separated by a trough running from umbo to ventral margin; umbo massive, prosogyrous, incurved; right valve hinge similar to that of *Pachydon* with resilium pit lying behind and under massive cardinal tooth and with elongate anterior and posterior lateral teeth lying parallel to commissure.

Left valve twisted, concave, with narrow corselet bounded by angular ridge; triangular area present, resembling that in *Spondylus*; sinus developed in posterior part of area wall to accommodate umbo and possibly also tooth of right valve; socket mounted on inner wall of area, with lanceolate resilifer lying posterior to it as in *Pachydon*.

Muscle scars: posterior adductor scar relatively large; anterior adductor scar lying just ventral to anterior end of area in left valve; in right valve pedal (or byssal) muscle scars situated beside adductors, on side closest to umbo and also just below and in front of umbo; in left valve, scars situated on side of anterior adductor scar closest to umbo and also on middle of area, with a row of pits underneath hinge plate. Pallial sinus shallow.

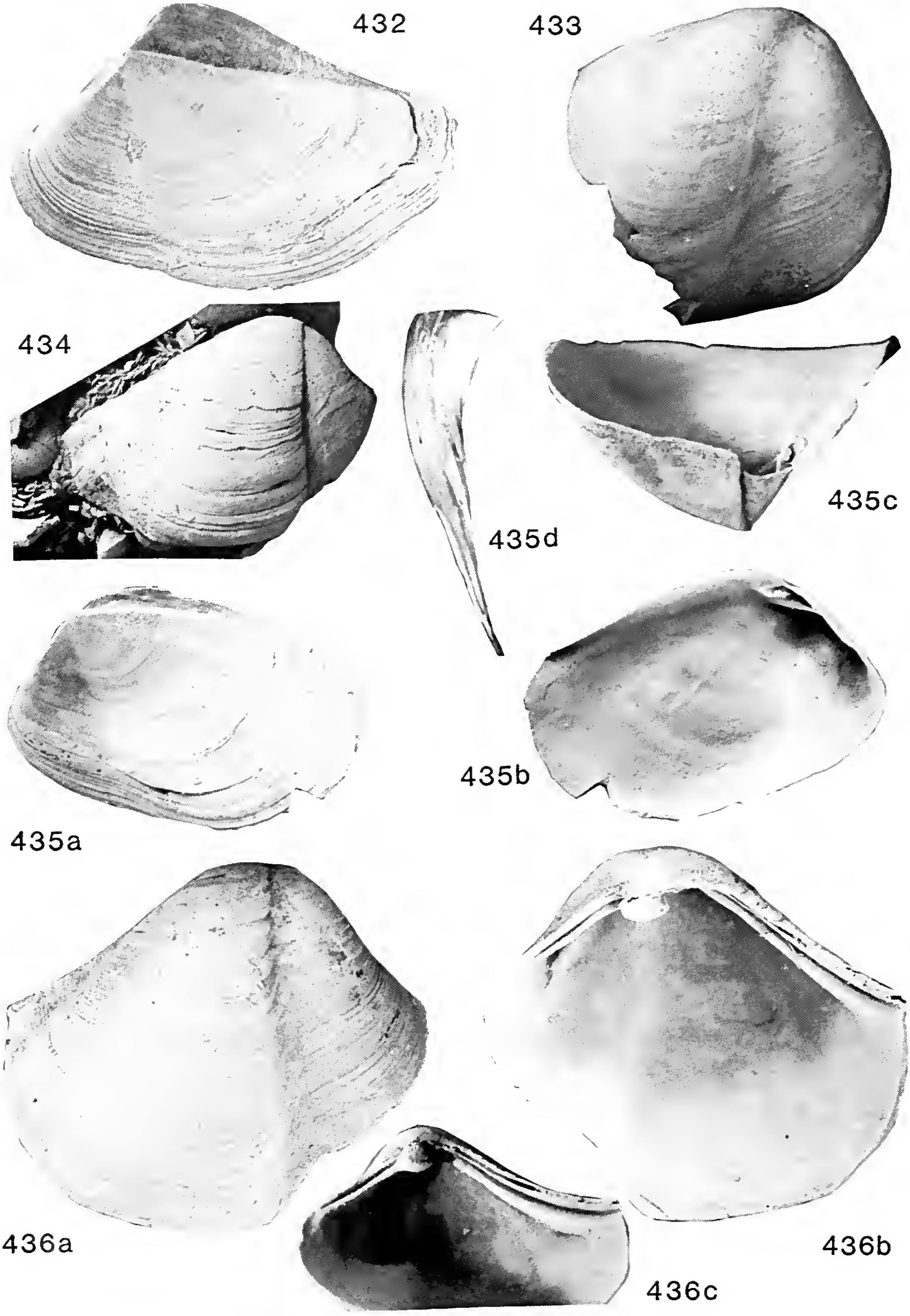
Shell structure: outer layer crossed lamellar; inner layer within pallial line, complex crossed lamellar.

DISTRIBUTION. Late Caenozoic, Pebasian, of Peruvian and Colombian Upper Amazon.

REMARKS. The reasons why the name *Anisorhynchus* is not available for this species have been given already in the discussion on *Pachydon*, p. 292. Pebasia is clearly very similar to *Pachydon* in many respects but is readily distinguished by the *Spondylus*-like area in the left valve. The bilobation of the right valve, though a very obvious feature, seems unlikely to be a fundamental difference. A pedal (or byssal) muscle scar lying under the hinge plate of the right valve is visible in a relatively small specimen of the type species (LL27871); in a larger specimen (LL27953), the scar is invisible because of the greater spiral growth of the valve. No separate pedal (or byssal) scar may be discerned in the region of the posterior left adductor.

Pebasia dispar (Conrad, 1874) Figs 432–436

*v 1874*a* *Pachydon (Anisorhynchus?) dispar* Conrad: 27; pl. 1, fig. 1 (4 figures).



Figs 432–436 *Pebasia dispar* (Conrad). Pebasian; Peru and Colombia. **432**, ANSP 31384, **lectotype** (herein selected) of *Pachydon (Anisorhynchus?) dispar* Conrad, figured by Conrad (1874*a*: pl. 1, fig. 1); either Pebas, Old Pebas or Pichana, Peru; Steere Colln; left valve, × 3. **433**, ANSP 31384, paralectotype, right valve of a different individual, also figured by Conrad (1874*a*: pl. 1, fig. 1), same details as lectotype; × 3. **434**, LL27953; Pichana, Peru; Hauxwell Colln; right valve, × 3. **435**, LL 27910; Pichana, Peru; Hauxwell Colln; left valve; a, external; b, internal; c, rear; d, side view showing concave curvature of outer surface of valve; all × 3. **436**, LL27871; Puerto Nariño, Colombia; Weeda Colln; right valve; a, external, and b, internal views, × 8; c, oblique internal view, × 6.

*. 1938 *Anisorhynchus (?) jeanneti* de Greve: 24; pl. 8, figs 6, 7, 9–17, 20; text-figs 2, 3.

LECTOTYPE (selected herein): ANSP 31384, a left valve. Late Caenozoic, Pebasian; either Pebas, Old Pebas or Pichana (Steere colln). The accompanying right valve of a different individual is a paralectotype.

The type material of *Anisorhynchus (?) jeanneti* de Greve, Late Caenozoic, Pebasian; Iquitos (Peyer colln), in PIMUZ, has not been studied.

FURTHER MATERIAL STUDIED. All Late Caenozoic, Pebasian. BMPD LL27871, a right valve, Puerto Nariño, Colombia (Weeda colln). LL27910, LL27955, two left valves, and LL27953–4, two right valves, Pichana (Hauxwell colln). LL27935, fragments of both valves, Canamá, extracted in 1984 from matrix of C. Barrington Brown colln (1879). Only recorded from Pebasian, as above.

DIAGNOSIS. As for genus; see p. 315.

DESCRIPTION. In the right valve, the growth lines are flexed in the sinus between the anterior and main 'lobe' of the shell. They are also flexed at the boundary between the corselet and flank. This boundary is a well-rounded fold in adult shells, but in the juvenile (LL27954), it is carinate. The cardinal tooth may increase in size relatively faster than the shell. In the three right valves (BMPD), that of the juvenile is disproportionately small and that of the largest adult is particularly massive. In all specimens, the pallial line is difficult to follow but appears to be simple.

DIMENSIONS. In mm.	l	h	br	l/h
Lectotype, l.v., ANSP 31384	24.2	15.2	–	1.59
Paralectotype, r.v., ANSP 31384	–	17.4	*c.* 8.2	–
LL27910, l.v., Pichana	14.1	9.4	*c.* 2.8	1.5
LL27955, l.v., Pichana	7.9	5.4	–	1.46
LL27953, r.v., Pichana	16.7	11.5	*c.* 5.7	1.45
LL27954, r.v., Pichana (damaged juvenile)	*c.* 2.8	*c.* 1.6	–	–
LL27871, r.v., Puerto Nariño (damaged)	8.8+	7.3	*c.* 2.8	–
PIMUZ 855, l.v., Iquitos, de Greve's measurements (1938: 27)	27.7	14.9	–	1.86
Same shell from de Greve's pl. 8, fig. 9	22.1	14.7	–	1.5
PIMUZ 850, r.v., from de Greve's pl. 8, fig. 12	24.7	17.6	–	1.4

REMARKS. Conrad (1874*a*) confused the left and right valves in his description and gave no measurements. He stated that six or seven specimens were before him, including a cast showing both valves in connection. The two shells in sample ANSP 31384 are labelled '? Paratype'. Conrad's illustrations are too poor for either shell to be recognized as being one of those figured. The left valve is here chosen as lectotype because it is the more complete, and the more important characters of the genus are shown by the left valve. De Greve (1938) felt that *P. dispar* was similar but not identical to his new species *Anisorhynchus* (?) *jeanneti*. Examination of material in ANSP and BMPD, in conjunction with de Greve's numerous and informative illustrations, show that the two species are clearly the same. The rather full table of measurements given above suggests that *P. jeanneti* is not relatively more elongate that *P. dispar*.

Although *Pebasia* is somewhat bizarre, it should be measured as a normal dimyarian bivalve, with the length parallel to a line through the adductors: this corresponds with the greatest length. From the orientation of de Greve's figures, he appears to have reached the same conclusion. The species is so inequivalve that the proportions of the two valves are likely to differ: an analogy may be made with the brachial and pedicle valves of brachiopods. Some evidence of this is provided by de Greve: he thought it quite likely that PIMUZ 850 and 855 were right and left valves of the same individual and showed (1938: pl. 8, figs 7, 10 and 17) how well the two fitted together, with the smaller and more elongate left valve fitting into the larger right valve. Checking de Greve's published measurements against his illustrations and scales show, however, that there are some discrepancies. It is clear that the length to height ratio obtained from de Greve's measurements of PIMUZ 855 is too high. The table suggests that this ratio lies between about 1.4 and 1.6 for the species.

All the BMPD shells were recently obtained by breaking down rock matrix with hydrogen peroxide (H_2O_2), and were, therefore, not available for study by Woodward (1871).

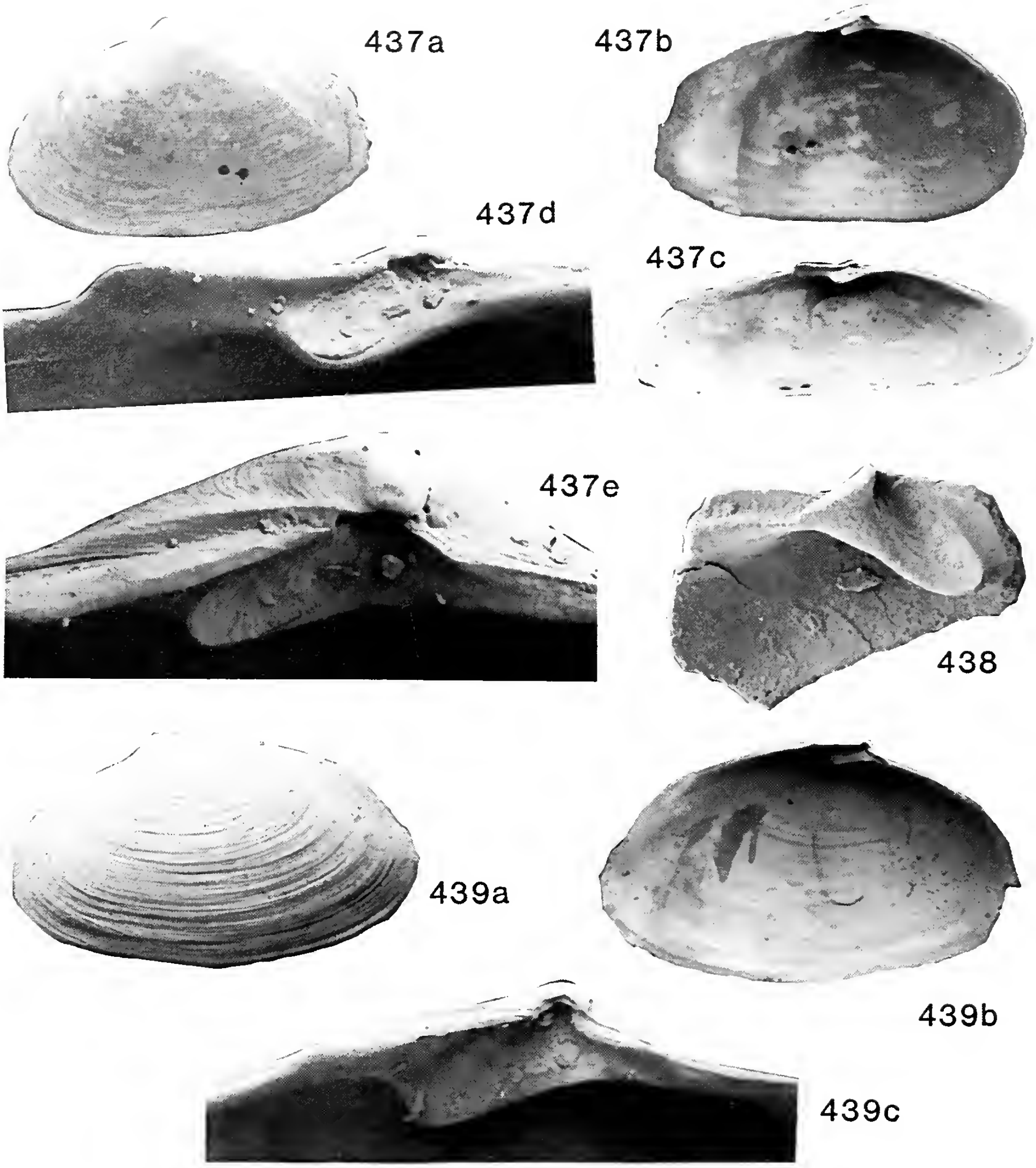
Genus ***OSTOMYA*** Conrad, 1874

TYPE SPECIES. *Ostomya papyria* Conrad, 1874*a*: 30, by monotypy. No other assigned species.

DIAGNOSIS. Small, slender in cross section; outline *Thracia*-like; equivalve or nearly so; thin-shelled, with concentric wrinkles; umbones slightly in front of mid-length, small, pointed, slightly prosogyrous; right valve with angular cardinal tooth of variable strength, apparently with anterior surface not in contact with outside world, sometimes prolonged anteriorly as weak anterior lateral tooth; right valve hinge plate merging posteriorly into thickened platform along dorsal shell margin; resilifers lanceolate, directed posteroventrally at about 45° from hinge line; ligamental nymph of left valve blade-like, perpendicular to commissure; that of right valve lower, considerably thickened; left valve cardinal socket shallow; pallial line obscure, truncated posteriorly, possibly forming shallow sinus; anterior and posterior adductor scars very faint; pedal muscle scars not visible. Shell structure: outer layer crossed lamellar; inner layer, within pallial line, complex crossed lamellar. Nacre absent.

REMARKS. The principal differences between *Ostomya* and *Pachydon* are that the former, at any given length, is less tumid, with a lighter, more blade-like cardinal tooth, a shallower cardinal socket and less strongly impressed muscle scars. A comparison with *Guianadesma* is given under the latter, p. 319.

Conrad had described the genus as 'thin, concentrically plicated; hinge with a spoon-shaped oblique fosset in the left valve and a small tooth near the apex; right valve cartilage fosset very oblique, almost parallel with the hinge line.' The resilifers in the BMPD shells described below are not disposed in widely different directions in left and right valves. Unfortunately, owing to the way in which this material was recovered, no paired valves have been identified, with the possible exception of a right valve fragment thought to match left valve LL27917. The right resilifer sinks below the level of the commissure more than that in the left valve and is more strongly buttressed from below. This is perhaps what Conrad meant.



Figs 437–439 *Ostomya papyria* Conrad. Pebasian; Pichana, Peru; Hauxwell Colln. **437**, LL27916; left valve; a–c, external, internal and oblique internal views, all × 8; d, e, two views of umbonal region showing nymph and resilifer, both × 40. **438**, LL27922; fragment of right valve showing cardinal tooth and resilifer, × 10. **439**, LL27917; left valve; a, external, and b, internal views, both × 8; c, umbonal region, × 40.

Ostomya is known only by its type species: other fossil species previously assigned to it are now removed. *O. colombiana* Pilsbry & Olsson (1935) is transferred to *Guianadesma* and *O. mencheri* Palmer (1945) is placed in synonymy of *G. sinuosum* Morrison (1943), p. 319. Pilsbry (1944) described two poorly preserved species from a single locality in the Red Beds of the Pachitea River, Peru as *O. terminalis* and *O. pachiteana*. Their hinges are unknown. *O. terminalis* might be referable to *Pachydon*, but I am unable to suggest a genus for *O. pachiteana*, though it does not appear to belong to either *Ostomya* or *Guianadesma*.

Ostomya papyria Conrad, 1874 Figs 437–439

. 1874*a* *Ostomya papyria* Conrad: 30; pl. 1, figs 6.
? 1879 *Thracia* sp., Etheridge: 84.
? 1879 *Lutraria* sp., Etheridge: 84.
. 1969 *Ostomya papyria* Conrad; Keen *in* Moore: N847 (*pars*); fig. F24.5

TYPE MATERIAL. Not seen. There is no record of the types in ANSP (Richards 1968).

MATERIAL STUDIED. All Late Caenozoic, Pebasian: BMPD LL27916, complete left valve; LL27917, a complete left valve with the umbo of a right valve, thought to be the same individual; LL27922, fragment of right valve. LL27918–21, ten fragmentary left and right valves; all Pichana, Peru, Hauxwell colln, 1870, extracted 1981. LL27923–5, three left valve fragments; LL27926–9, eight right valve fragments; LL27930, two shell fragments lacking umbones; all Puerto Nariño, Colombia, Weeda colln.

FURTHER RECORDS. Late Caenozoic, Pebasian; either Pebas, Old Pebas or Pichana (Conrad 1874*a*); ? Canamá (Etheridge, 1879). Pebasian only, Upper Amazon Basin of Peru and Colombia.

DIAGNOSIS. As for genus; see p. 317.

DESCRIPTION. The two left valves, LL27916–7, are moderately compressed, the flank and corselet being separated by a weak posterior angulation in one shell but not the other. The ventral commissures of both are slightly twisted. The shell surface is concentrically wrinkled and the growth lines are closely spaced and rugose. No radial sculpture is present. The umbonal regions of the broken right valves show similar concentric sculpture. These wrinkles appear to be frequently obliterated in worn specimens, giving the false impression that spacing between them is a variable feature. Larger shell fragments (LL27930) show irregular, non-commarginal wrinkling at the extremities of the shell. The dorsal margin is raised both anterior to the umbo and also immediately posterior to it over the nymph, producing a slightly auriculate effect. In the left valve, a pit-like socket is gouged into, and sometimes even through, the umbo of the valve, slightly truncating the anterior end of the resilifer. The resilifer is bordered posterodorsally by a weak ridge with a socket above it. The commissure operates as a weak lateral tooth immediately anterior to the umbones. In the right valve also, a pit-like socket invades the umbones. A tooth of variable shape and strength lies anterior to the umbones. It is basically similar to that found in *Pachydon*, but less massive and peg-like. It is frequently prolonged forwards as an anterolateral tooth lying parallel to the dorsal margin, from which it is separated by an elongated socket. The pallial line is obscure but appears to be truncated or weakly sinuate posteriorly. Both the anterior adductor and the posterior adductor, which has a large posterior retractor scar lying above and in front of it, are only just visible.

DIMENSIONS. In mm.	l	h	br	l/h
LL27916, l.v., Pichana.	6.2	3.7	*c.* 1.0	1.68
LL27917, l.v., Pichana.	7.0	4.2	*c.* 1.0	1.67

REMARKS. Although no complete valves have been found at Puerto Nariño, the growth lines indicate that the shells from both this locality and Pichana are very similar. No other small species remotely resembling Conrad's figures have been found in any of our washings. This suggests that these specimens can only belong to Conrad's species, and they are all here assigned to *O. papyria*. It is impossible to make an accurate estimate of valve size from fragmentary material of this type. It is probable that the largest shells from Puerto Nariño were about 20 mm long and 10 mm in height, but it seems unlikely that any of the shells from Pichana would have exceeded 15 mm in length.

It is possible that the records of the marine genera *Thracia* and *Lutraria* from Canamá (Etheridge 1879) are in reality *Ostomya*: they are tentatively added to the synonymy.

Genus *GUIANADESMA* Morrison, 1943

[? = *Anticorbula* Dall, 1898: 839, *nom. nov.* pro *Himella* Adams, 1860: 203 (*non* Dallas, 1852, Insecta), type species *Himella fluviatilis* Adams, 1860: 203 (*nom. dub.*) by monotypy; Recent, ? Marañón River, Peru.]

TYPE SPECIES. *Guianadesma sinuosum* Morrison, 1943; Recent, Guyana.

DIAGNOSIS. Elongate kidney-shaped in outline; umbones well forward, low, prosogyrous; fairly tumid in cross section; slightly inequivalve with left valve dorsal margin resting inside margin of right valve and posteroventral margin of left valve lying within right valve; commissure with strongly twisted ventral margin; periostracum wrinkled; edentulous; resilifers lanceolate, that of left valve lying parallel to plane of commissure on weak hinge plate, that of right valve lying in groove underneath thickened dorsal shell margin and facing ventrally; ligamental attachments lying along dorsal commissure behind umbones, that in left valve directed dorsally, that in right valve directed ventrally; muscle scars irregularly shaped, two pedal/byssal muscle scars lying on line between anterior adductor and umbo; posterior pedal/byssal retractor muscle scar large, joined to anterodorsal side of posterior adductor scar; pallial sinus shallow. 'Byssus present; foot, short, cylindrical; mantle largely fused with foot and byssal opening and opening for the two short separate siphons, with a briefly continued internal septum; inner and outer branchiae subequal, eulamellibranchiate, free below from the abdominal sac and from the mantle' (Morrison 1943). Shell structure: outer layer, crossed lamellar; inner layer, within pallial line, complex crossed lamellar. Nacre absent.

OTHER SPECIES ASSIGNED. *Ostomya colombiana* Pilsbry & Olsson, 1935: 21; Miocene, La Cira Formation; Magdalena Valley, northern Colombia.

GENERIC DISTRIBUTION. Neogene, northern South America. Recent, rivers in the Guyanas, in brackish and possibly fresh water.

REMARKS. In the above diagnosis, the features of the soft parts are largely quoted from Morrison (1943), but characters of the shell are those observed in BMZD specimens and, as pointed out on p. 290, Morrison's reference to the shell being nacreous-porcellanous cannot be supported. *Guianadesma* differs from *Ostomya* in being more irregularly shaped with tumid, ingrown umbones, and with a strong flexure in the ventral commissure of the right valve. Its resilifers are more elongate and lie nearly parallel to the hinge, but at markedly different attitudes in the two valves. Its nymphs and hinge plate are relatively lighter and it is edentulous.

Guianadesma sinuosum Morrison, 1943 Figs 440–442

* 1943 *Guianadesma sinuosum* Morrison: 49; pl. 8, figs 1–6.
. 1944 *Ostomya fluviatilis* (H. Adams) Pilsbry: 147; pl. 11, figs 42–44; text-figs 1a, b.
*. 1945 *Ostomya mencheri* Palmer: 21; pl. 2, figs 1–7.
. 1968 *Anticorbula sinuosa* (Morrison) Altena: 156, 176.
. 1969 *Anticorbula sinuosa* (Morrison); Altena: 26, 28, 29, 43.
v. 1971 *Anticorbula sinuosa* (Morrison); Altena: 82; pl. 10, figs 15, 16 (*cum syn.*).

HOLOTYPE (of *Guianadesma sinuosum* Morrison), USNM 53691, living; rocks midstream of Cuyuni River, opposite Kartabo Point, near junction with Mazaruni River, Essequibo

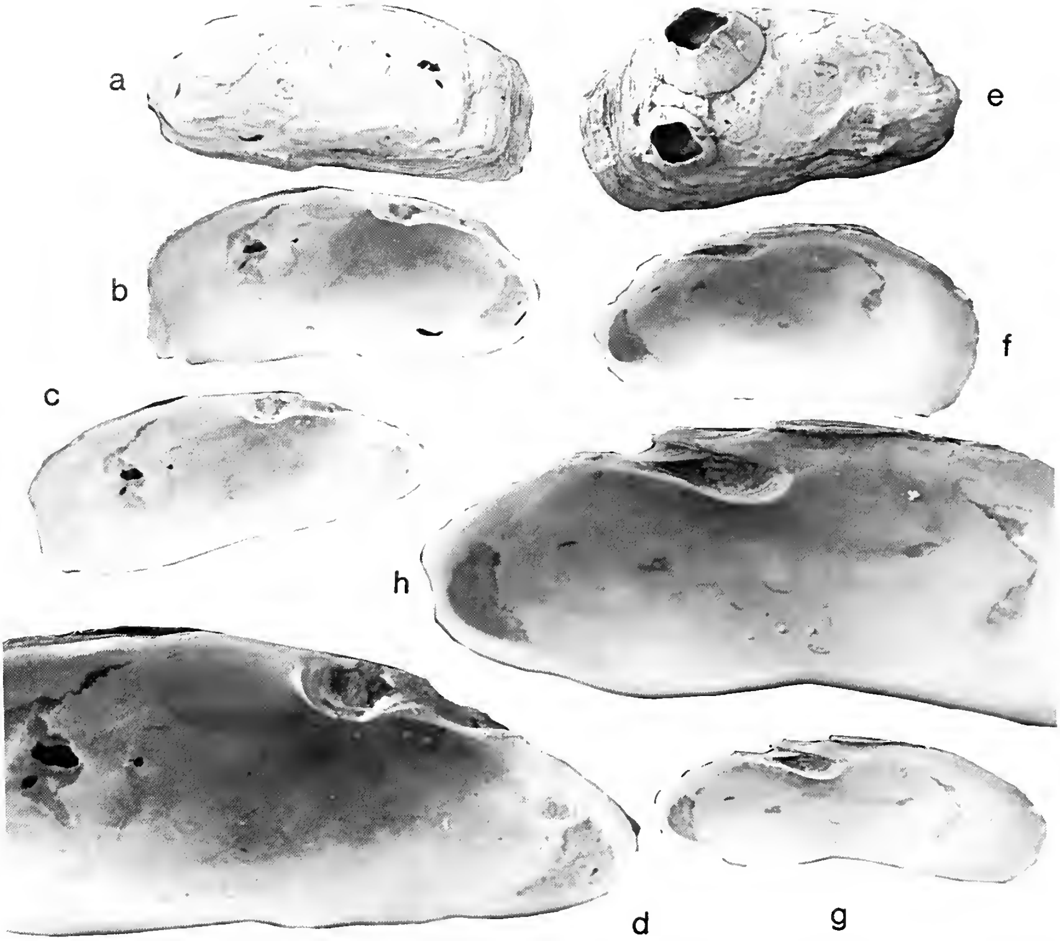


Fig. 440 *Guianadesma sinuosum* Morrison. Recent; Surinam, Maroni (Marowijne) River between Langamankondre and Christiaankondre. BMZD 1984228; pres'd Dr C.O. van Regteren Altena. a–d, all left valve; a, external, × 2.5; b, internal, × 2.5; c, d, internal tilted, × 2.5, × 5. e–h, all right valve; e, external showing barnacles in life position, × 2.5; f, internal, × 2.5; g, h, internal tilted, × 2.5, × 5.

District, Guyana (Morrison colln). Not studied. Paratypes, in USNM and Carnegie Museum, Pittsburgh (Morrison and J. Benkert collns).

MATERIAL STUDIED. Six shells, BMZD 1984228; banks of Marowijne River between Langamankondre and Christiaankondre, Surinam (Altena colln). This would appear to correspond with Locs 95–96 from where Altena (1971: 83 and map, pl. 11) records the species collected live. In his full locality list (1969: 41), however, Christiaankondre is given as Loc. 94 and Langamankondre as Loc. 95.

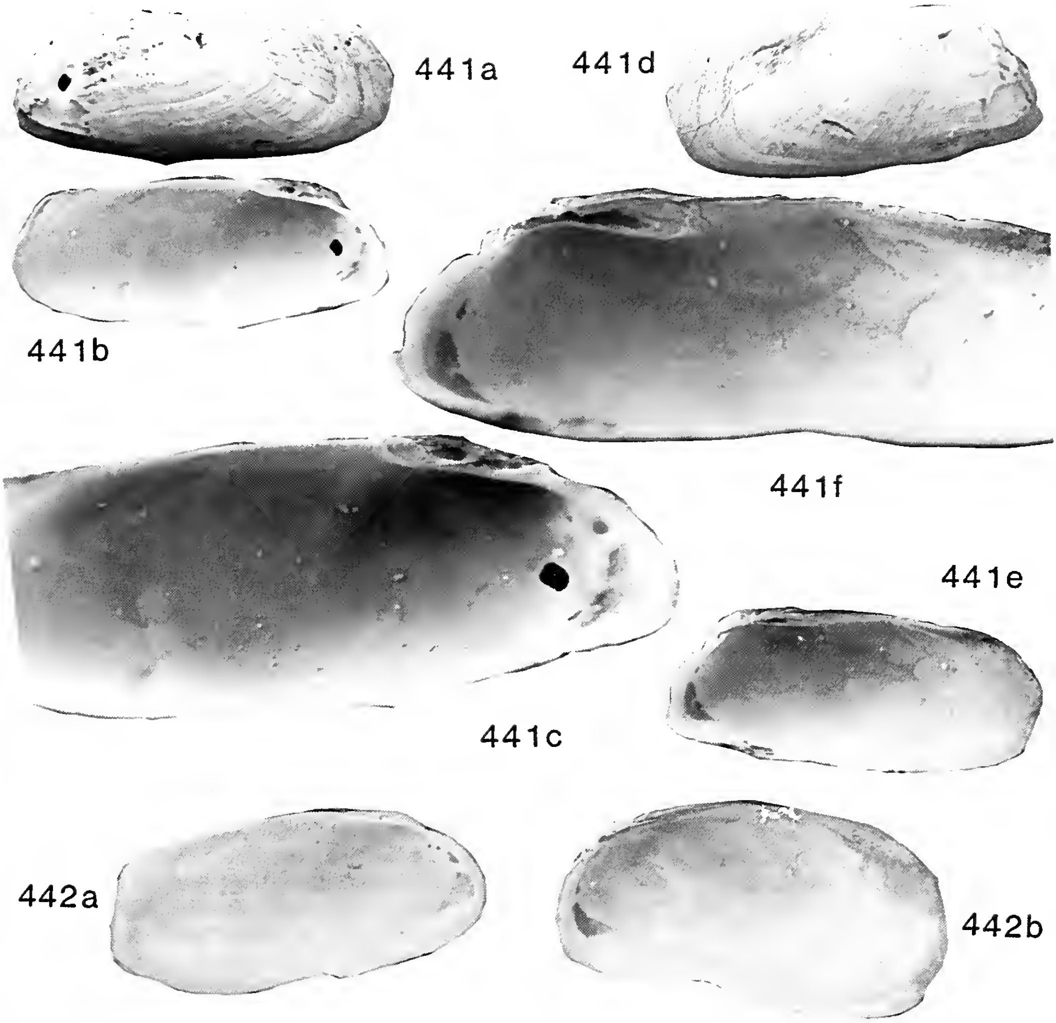
FURTHER DISTRIBUTION. 'Plio-Pleistocene', La Llanera, State of Monogas, Venezuela (Palmer 1945, as *O. mencheri*). Recent, Cuyuni River, Guyana (Morrison 1943); numerous localities, particularly Surinam and Marowijne Rivers, Surinam (Altena 1968, 1969, 1971); washed ashore, Marowijne River, French Guiana (Altena 1971).

DIAGNOSIS. As for genus; see p. 319.

DESCRIPTION. The shape of the shell, including the length to height ratio and the extent to which the posteroventral margin of the right valve overlaps that of the left, is variable. The anterior point of the shell is low down and the anterior adductor is placed almost as far forward as is possible. The outline of the shell is kidney-shaped with a concave ventral

DIMENSIONS. In mm.		l	h	br	l/h
Holotype, USNM 53691. Cuyuni River, Guiana.	l.v.	17.4	9.8	7.0	1.77
	r.v.	17.3	11.1		1.56
Marowijne River, Surinam. Altena 1971: pl. 10, fig. 16	l.v.	24.9	12.3	–	2.02
Marowijne River, Surinam. Altena 1971: pl. 10, fig. 15	l.v.	25.4	12.3	–	2.03
BMZD 1984228, Marowijne River, Surinam (Altena colln).	l.v.	20.8	8.7	8.1	2.39
	r.v.	20.8	9.1		2.28
BMZD 1984228, Marowijne River, Surinam (Altena colln).	l.v.	20.8	9.5	6.8	2.19
	r.v.	21.2	10.9		1.90
'Marañon River', no scale given. Pilsbury 1944: pl. 11, fig. 43	r.v.	–	–	–	1.81
'Marañon River', no scale given. Pilsbury 1944: pl. 11, fig. 43 (different specimen)	l.v.	–	–	–	1.70
Holotype of *Ostomya mencheri* Palmer, 1944, PRI 20084.	l.v.	20	11	8	1.8
Paratype of *O. mencheri* Palmer, 1944, PRI 20087.	r.v.	20	12	8	1.67
Himella fluviatilis, from H. Adams, 1860, 'Rio Marañon'.	–	21.2	12.7	8.5	1.67

Note. Adams' measurements are converted from l, 10 lines; h, 6 lines; br, 4 lines, at 12 lines = 1 inch (1 line = 2.12 mm). Breadths are of both valves together.



Figs 441–442 *Guianadesma sinuosum* Morrison. Recent; Surinam. BMZD 1984228; same locality and collection as Fig. 440. **441**, a–c, all left valve; a, external, × 2.5; b, c, internal, × 2.5, × 5. d–f, all right valve; d, external, × 2.5; e, f, internal, × 2.5, × 5. **442**, a, b, left and right valves, internal views, × 2.5.

margin. The ventral commissure is flexed, more strongly in the right valve than in the left. In all the BMZD specimens the umbones are badly eroded. In some cases other areas have been worn to such an extent that holes have appeared in the shell. The periostracum is concentrically wrinkled, particularly anteriorly, whilst posterior to the flexure it is formed into numerous radiating rib-like thickenings. Concentric and radiating elements form a net-like pattern over much of the shell surface. This is confined to the periostracum: there is no evidence that the patterning extends to the calcareous shell which is unsculptured except for slightly rugose growth lines.

REMARKS. Morrison collected the holotype, USNM 53691, live from rocks in midstream of the Cuyuni River, opposite Kartabo Point, near the junction with the Mazaruni River, Essequibo District, Guyana in July, 1925. He stated (1943: 50) that paratypes were present both in USNM and Carnegie Museum, Pittsburgh. The species was moderately abundant, byssally attached to igneous rocks and gravel in the river current, but absent from rocks surrounded by mud bars (1943: 51).

Altena (1969: 29; 1971: 83) reported finding the species sometimes byssally attached in old borings of teredinids in the Surinam River. The strong flexure of the ventral commissure and the rather modioliform shell outline with a concavity in the ventral margin are entirely in keeping with a byssally attached mode of life, and it is possible that the more elongate, *Lithophaga*-like individuals are those which lived in tubes. The overlap of the two valves is best illustrated by Morrison (1943: pl. 8, fig. 4) – a ventral view – and by Altena (1971: pl. 10, fig. 16) – a view of a left valve with its dorsal margin lying below that of the right valve and showing the larger posteroventral region of the right valve. Because hinge teeth are lacking, the articulation and fit of the two valves depends on the ligament, internal resilium and the way in which the commissures overlap in the region below and just anterior to the umbones. It is difficult to reconstruct the articulation accurately either with the dissociated valves available in BMZD or with fossil material (Palmer 1945: pl. 2, figs 1–7), which is sometimes distorted.

The eroded umbones of even the smallest shell, 6.8 mm long, in BMZD, and the worn appearance of the periostracum seen in all published photographs (Morrison 1943, Palmer 1945, Altena 1971) suggest that at least a fairly high proportion of shell damage occurs during life. This would be consistent with a byssally attached epifaunal existence in river currents. Unfortunately, it has not been possible to examine specimens positively known to have lived in teredinid borings, but the most elongate and least inequivalve specimens in BMZD are the least worn. The illustrations of the shells identified by Pilsbry as *Ostomya fluviatilis* (H. Adams), and also those of *O. mencheri* Palmer, show that they fall within the range of variation of shell-shape exhibited by the well-localized material from the Guianas, and are here placed in synonymy. Palmer had also distinguished her species from *G. sinuosum* because it lacked radial striations. It is now known, however, that this is merely a feature of the periostracum and not the shell.

Ostomya colombiana Pilsbry & Olsson, 1935, was described as being rather like *O. fluviatilis* in shape. The type illustration is a drawing, partly reconstructed, of a left valve 6.7 mm long. No particular features distinguish it from *G. sinuosum* except that the umbo seems to be noticeably more swollen.

Opinions about the salinity tolerance of *G. sinuosum* have changed. Morrison (1943: 51) collected the species from the Cuyuni River with the fresh-water *Doryssa consolidata* (Bruguière). Altena (1969: 24–29) drew attention to the great changes in salinity produced by seasonal variation in rainfall in the Surinam River from which he recorded *G. sinuosum*. It is of interest to note that Morrison's collection was made in July 1925, just after the peak of the wet season and corresponding with the period of lowest salinity. Two of the specimens which Altena presented to BMZD, and which came from the region of his Locs 94–96, between 5 and 15 km from the mouth of the Marowijne River where it is about 5 km wide, are encrusted with barnacles. The positioning of the barnacles, near the posterior of the shells and externally, suggests that they were present while the bivalves were alive. Both the presence of the barnacles and the proximity of open sea show that *G. sinuosum* can live in fairly high salinities. In his series of papers, Altena developed the idea that different groups of species characterized different salinities, though acknowledging that the picture could change with further collecting. He eventually found the downstream limit of *G. sinuosum* (1971: 83) overlapping the upstream limit (1975: 12) of the mainly estuarine *Neritina zebra* (Bruguière). Earlier (1969: 26, 28) he had reported that their ranges did not overlap. This proven co-occurrence of *Guianadesma* and *Neritina* is perhaps analogous to the *Pachydon*+*Neritina* association in rich Pebasian faunas.

REVIEW OF OTHER FOSSIL FAUNAS

Pebas, Peru

Orton Collection 1867, described by Gabb, 1869

Professor James Orton of Vassar College, New York State, spent a few hours on 12 December 1867 collecting at Pebas, which was in those days described as a small village on Rio Ambayacú, one or two miles (1.6–3.2 km) from where it flows into Rio Marañón, some 50 or 60 miles below the mouth of Rio Napo. This was the first collection of fossils to be made from the Pebas Beds, and is of special importance for another reason. Orton collected only from Pebas, and there is therefore no doubt about the locality from which his fossils came. The fossils were described by Gabb and are in ANSP. Gabb (1869: 197) wrote that the locality was a high bluff at Pebas, on the Ambayacú, two miles above its confluence with the Marañón.

The Pebas fauna described by Gabb, 1869:

original determinations	**revised determinations**
Neritina pupa (Linné)	*Neritina ortoni* Conrad
Turbonilla MINUSCULA Gabb v	*Liris minuscula* (Gabb)
Mesalia ORTONI Gabb	*Dyris ortoni* (Gabb)
Tellina AMAZONENSIS Gabb	*Pachydon amazonensis* (Gabb)
PACHYDON OBLIQUA Gabb	*Pachydon obliquus* Gabb
Pachydon TENUA Gabb	*Pachydon tenuis* Gabb

[In this, and in subsequent lists, new taxa are given in capital letters; 'v' indicates that original specimens have been studied by me.]

This collection, though small, shows the unusual character of the 'Pebasian' fauna. It contains no elements of the present-day Amazonian fresh-water fauna. *Neritina* ranges from the intertidal zone into fresh-water streams, but is typically never found far from a shore line. *Pachydon* is an extinct genus allied to *Corbula* and may be regarded as being virtually diagnostic of these 'Pebasian' faunas. Corbulidae are essentially marine, though the related Erodonidae tend more to be found in brackish waters.

Orton's material is of particular importance, not only for historical reasons, but also because it is one of the few early collections with clear-cut locality data. Shortly afterwards Juan Hauxwell, an English traveller who spent about thirty years in Amazonia, made fossil collections predominantly from another locality, Pichana, but mixed with a few fossils from Pebas. Hauxwell's collections were described by both Conrad (1871*a*, *b*) and by Woodward (1871). Steere's collection described by Conrad (1874*a*) was a mixture of fossils from both of these localities and also from a third site, Old Pebas.

Hauxwell Collection, date unknown, described by Boettger, 1878

The fossils described by Boettger (1878) were collected by Hauxwell at some unknown date. Kadolsky (1980: 365) regarded it as probably a third fraction of the collection from Pichana and Pebas described independently by both Conrad and Woodward in 1871. However, he informed me (personal communication) that Boettger's specimens of *Eubora crassilabra* (Conrad) and *E. bella semisculpta* (Boettger) in the Senckenburg Museum, Frankfurt (SMF) are both labelled 'Pebas'. Moreover, Boettger (1878: 486) in his introduction wrote about the Conrad/Woodward collection as though it were entirely separate. He referred to it as coming from two localities near Pebas on the south side of Rio Marañón, i.e. the opposite side (right bank) of the river from Pebas. The mention of two localities is probably due to the fact that Pichana was also referred to as Cochaquinas (in error). Boettger then went on to discuss the relationship between Pebas 'lying on the left (i.e. East) bank of Rio Ambayacú one English mile above its junction with Rio Maranon' and Old Pebas 'lying two English miles below the mouth of Rio Ambayacú'. Finally (1878: 488–9) Boettger discussed the collection which he, himself, was describing. He stated that

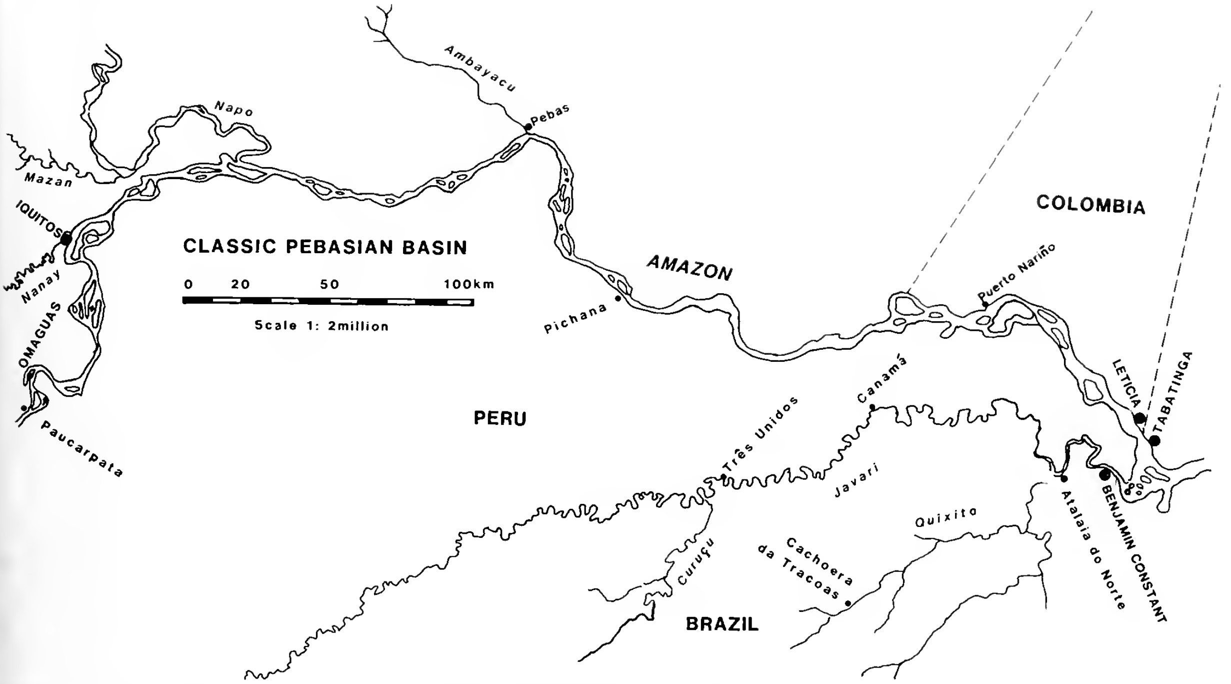


Fig. 443 Classic Pebasian Basin. To show the new locality of Puerto Nariño and the classic localities of the Pebasian Basin of easternmost Peru, and neighbouring areas of Brazil and Colombia.

he owed his material to the kindness of Dr W. Kobelt of Schwannheim, who, in turn, had received it from Herr R. Abendroth of Leipzig in 1877. A letter from the last-named gentleman which accompanied the fossils mentioned that the village of Pebas was ‘forty miles above the Brazilian frontier fort of Tabatinga . . . The fossils came from a blue clay at one place near the town . . . Abendroth's fossils came from Mr Hauxwell, an Englishman, who spent several years in the egion . . .’

Thus, the arguments as to whether or not all Boettger's naterial came from Pebas itself are fairly evenly balanced. He was clearly aware of the presence of the other localities and hence of the possible confusion. On the other hand, part of Abendroth's letter read like a translation into German of he description of Pebas and its relation to Tabatinga given in Hartt (1872). This raises the suspicion that this letter was not based on first-hand observations by the collector Hauxwell. Hauxwell certainly had the time to revisit Pebas. Boettger's auna has much in common with those described by Conrad nd Woodward mainly from Pichana. The true Pebas fauna o far known is very small and the fossils were said (Orton, *in* Conrad 1871*b*) to be more common at Pichana. However, Orton's visit to Pebas was, in any case, so short that he may well not have done that locality justice.

The bulk of the collection is in Senckenburg Museum, rankfurt, and has not been studied herein. The holotype of *Pseudolacuna macroptera* Boettger was refigured by Cossmann (1915) and is now in Université de Paris (Kadolsky, 1980: 72–373), who refigured it. Kadolsky also refigured (1980: fig. 0) the holotype of *Eubora bella semisculpta* (Boettger). everal of Boettger's specimens were refigured by de Greve (1938): details are noted in the Iquitos faunal list given here p. 332). Species not figured by Boettger are indicated by ‘(no g.)’ in the list below.

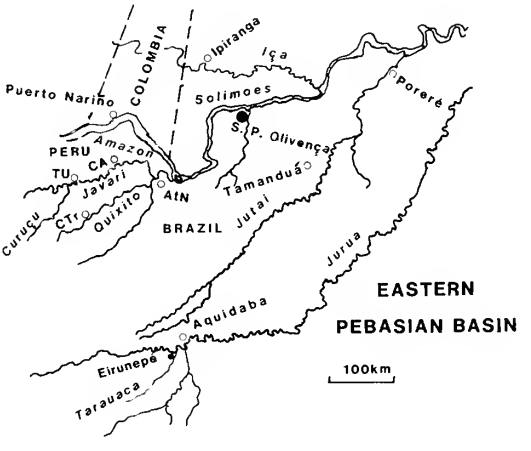


Fig. 444 Eastern Pebasian Basin. Showing the localities of the easternmost part of the Pebasian Basin, lying immediately to the east of the classic area outlined in Fig. 443. Details of most Brazilian localities are based on maps and text in Fernandes *et al.* (1977) and del'Arco *et al.* (1977). All localities shown have yielded Pebasian faunas except for Aquidaba, which has yielded a fauna very like that of the present-day Amazon. Several fossil mammal localities lie adjacent to Rio Jutai. No Pebasian molluscs have been recorded from them. Abbreviations: **AtN**, Atalaia do Norte; **CA**, Canamá; **CTr**, Cachoero de Tracoas; **TU**, Três Unidos. Localities marked as rings, towns as black circles.

original determinations	**revised determinations**
Bulimus linteus Conrad (juveniles only, no fig.)	*Orthalicus linteus* (Conrad)
Neritina ortoni Conrad	*Neritina ortoni* Conrad
Hydrobia (Isaea) ortoni Gabb (no fig.)	*Dyris ortoni* (Gabb)

original determinations	revised determinations
Hydrobia (Isaea) CONFUSA Boettger	*Dyris ortoni* (Gabb)
Hydrobia (Isaea) TRICARINATA Boettger	*Dyris tricarinata* (Boettger)
Hydrobia (Isaea) gracilis (Conrad) (no fig., fragments only)	*Dyris gracilis* Conrad
Lacuna (Ebora) crassilabris (Conrad)	*Eubora crassilabris* (Conrad)
Lacuna (Ebora) bella (Conrad)	*Eubora bella* (Conrad)
Lacuna (Ebora) bella var. *semisculpta* Boettger	*Eubora bella* (Conrad)
PSEUDOLACUNA MACROPTERA Boettger	*Toxosoma eborea* Conrad
Turbonilla minuscula Gabb	*Liris minuscula* (Gabb)
Dreissena FRAGILIS Boettger	*Mytilopsis* sp. (? *scripta* (Conrad) and/or *sallei* (Recluz)
Anodonta batesi (Woodward) (no fig.)	?*Anodontites* sp. (fragments)
Unio sp. (no fig.)	unionid, ?*Diplodon* (fragments)
Anisothyris amazonensis (Gabb)	*Pachydon amazonensis* (Gabb)
Anisothyris tenuis (Gabb)	*Pachydon tenuis* Gabb
Anisothyris cuneata (Conrad)	*Pachydon cuneatus* Conrad
Anisothyris erecta (Conrad)	*Pachydon erectus* Conrad
Anisothyris erecta (Conrad) var. *ELONGATA* Boettger	*Pachydon erectus elongatus* (Boettger)
Anisothyris obliqua (Gabb)	*Pachydon obliquus* Gabb
Anisothyris carinata (Conrad)	*Pachydon carinatus* (Conrad)

Boettger also recorded the following non-molluscan taxa: *Serpula* sp., *Percidarum* sp., *Rajidum* sp.

Boettger listed both (1878: 493) *Hydrobia (Isaea) lintea* Conrad (=*Dyris lintea*) and (1878: 496) *Hemisinus sulcatus* Conrad (=*H. brasiliensis*), specifically mentioning that neither was present in his material.

This fauna of sixteen named molluscan species (if *Mytilopsis* is included), is very similar to that found in the parts of Hauxwell's collection revised herein and described by both Conrad (1871*b*) and Woodward (1871), the bulk of which came from Pichana with only a small proportion from Pebas. On the other hand, Boettger's fauna also includes all six species described by Gabb (1869) from Pebas itself. It is typical of the 'classic' Pebasian, though in common with the Pichana fauna, it lacks the several species of Thiaridae found at Iquitos, Canamá and Três Unidos.

Boettger's paper is reasonably well illustrated. The text, both on the palaeontology and the geological introduction, is of a high standard and it is clear, from the names used by him as well as from his comments, that he had a thorough grasp of previous work on the fauna, though he obviously was not aware of Conrad's two latest papers (1874*a*, *b*).

Pebas collections of Bassler (1925) *and Singewald* (1925)

Marshall (1928*a*) described some fossil naiades from the Pebasian of Pebas and of Paucarpata. Of the three from Pebas itself, two were collected by Singewald and the third by Bassler. Singewald's collection from the Upper Amazon was made in 1925 and sent to the United States Geological Survey in Washington. It came from a number of outcrops on Rio Marañón and Rio Napo (Gardner 1927: 507). Although Gardner's paper suggested that Singewald's collection was rich, the only fossils which appear to have been worked on are these naiades.

Unionacea from Pebas, described by Marshall, 1928*a*:

original determinations	revised determinations
PRODIPLODON BASSLERI Marshall (Bassler colln)	*Diplodon bassleri* (Marshall)
EODIPLODON GARDNERAE Marshall (Singewald colln)	*Diplodon gardnerae* (Marshall)
EODIPLODON PEBASENSIS Marshall (Singewald colln)	*Diplodon gardnerae* (Marshall)

Bassler's collection, made in the same year, 1925, is the only other mentioned in the literature as coming from Pebas. Willard's work (1966) may be regarded as an illustrated catalogue of Bassler's extensive collections from many different localities and horizons in Peru, and it deals with many different phyla. From his illustrations of Pebasian fossils it appears that not all of the determinations are accurate. Furthermore there are discrepancies between the plate descriptions and the various faunal lists. Willard's (1966) pl. 58, fig. 2, is correctly determined as *Pachydon erecta* Conrad from Pebas, but his pl. 58, fig. 3, also said to be of this species, is misidentified and is of a species I cannot name. It is a right valve, resembling that of *P. obliquus* Gabb, but the umbo is not far enough forward. This collection is now in Lehigh University, Bethlehem, Pennsylvania.

Bassler collection from Pebas, listed by Willard, 1966: 68:

original determinations	revised determinations
Corbula sp.	*Pachydon* sp.
Anisothyris obliqua (Gabb)	*Pachydon obliquus* Gabb
Anisothyris tenuis (Gabb)	*Pachydon tenuis* Gabb
Anisothyris erecta (Conrad)	*Pachydon erectus* Conrad
Anisothyris cuneata (Conrad)	*Pachydon cuneatus* Conrad
undetermined pelecypods	
Neritina puncta Etheridge	*Neritina ortoni* Conrad
Turbonilla minuscula Gabb	*Liris minuscula* (Gabb)
Turbonilla sp.	*Liris* sp.
Isaea ortoni Gabb	*Dyris ortoni* (Gabb)
'Anodontia'	indet. naiad
unidentified gastropods	

This list is in keeping with the small fauna originally described from Pebas by Gabb (1869). It contains four of the six original species. The undetermined gastropods and bivalves, together with two of Conrad's species of *Pachydon*, suggest that the Pebas fauna is reasonably rich and is perhaps comparable to the mainly Pichana fauna described in both Conrad's and Woodward's 1871 papers.

Pichana–Pichua–Cochaquinas–Pebas–Old Pebas

*(Conrad 1871*b*, 1874*a*, Woodward 1871)*

As mentioned previously, fossils collected from more than one locality by both Hauxwell and Steere were mixed. Conrad was sent, *via* Professor J. Orton of Vassar College, a collection made by Juan Hauxwell. Conrad (1871*b*: 192), when describing these fossils, quoted Orton as remarking 'a very few of these shells were found where I first discovered the deposit, which was at Pebas, near the mouth of the Ambiyacú; but the rest comprising nearly the whole collection, were obtained nearly 30 miles [50 km] below Pebas, on the South side of the Marañón, at Pichua, just West of Cochaquinas . . . and the shells appear to be more abundant even than at Pebas . . .' Conrad went on to comment (1871*b*: 192–193) on the excellent preservation of the fossils, and that specimens of both *Neritina* and *Pachydon* often retained the epidermis. He concluded that the fauna was not transported far and that it lived in either fresh or brackish water and was certainly not of marine origin.

Fauna of Conrad (1871*b*), mainly from Pichana:

original determinations	revised determinations
Isaea ortoni Gabb v, NYSM 9253	*Dyris ortoni* (Gabb)
Isaea LINTEA Conrad	*Dyris lintea* (Conrad)
LIRIS LAQUEATA Conrad v, NYSM 9259	*Liris minuscula* (Gabb)

original determinations	revised determinations
EBORA CRASSILIBRA Conrad	*Eubora crassilabra* (Conrad) *Eubora woodwardi* Kadolsky
EBORA (NESIS) bella Conrad	*Eubora bella* (Conrad)
Hemisinus SULCATUS Conrad v, NYSM 9226	*Hemisinus brasiliensis* (Moricand)
DYRIS GRACILIS Conrad v, NYSM 9192	*Dyris gracilis* Conrad
Neritina ORTONI Conrad (= *N. pupa* Gabb, *non* Linné)	*Neritina ortoni* Conrad
Bulimus LINTEUS Conrad	*Orthalicus linteus* Conrad
Pachydon tenuis Gabb	*Pachydon tenuis* Gabb
Pachydon CARINATA Conrad	*Pachydon carinatus* Conrad
Pachydon obliquus Gabb	*Pachydon obliquus* Gabb
Pachydon ERECTUM Conrad v, NYSM 8964	*Pachydon erectus* Conrad
Pachydon CUNEATUS Conrad v, NYSM 8963	*Pachydon cuneatus* Conrad
Pachydon OVATUS Conrad v, NYSM 9866	*Pachydon tenuis* Gabb
Pachydon ALTUS Conrad v, NYSM 8961	*Pachydon erectus* Conrad

The figured specimens, at least, are now in New York State Museum (NYSM), see Clarke (1906). Fifteen species are now recognized in the revised list of determinations. NYSM registration numbers are given for those species examined by me.

Woodward (1871) also published on what was probably another part of the same collection made by Hauxwell. This portion was sent in the first instance to a Mr Janson of Museum Street, London (Woodward 1871: 64). Woodward also acknowledged (1871: 64) the publication dated 10 October 1870 by Conrad *in advance of* the American Journal of Conchology. In this, Conrad's names were presumably no more than *nomina nuda*, at best in an abstract or advance programme, which I have not seen, for the scientific meeting at which the shells were to be exhibited. Woodward, however, in the systematic part of his paper gave Conrad's subsequent (1871*b*) plate and figure references. He must therefore have been in contact with Conrad in some way, or had the opportunity of studying either his paper or its prepublication proofs. It was not the report of the meeting (Conrad 1871*a*), which does not list the names.

Woodward's collection is in BMPD. It was not registered until 1922, some specimens in an unknown hand, but the bulk by the late Dr L. R. Cox. The register numbers are L27703–52 (LRC); G25284–99 (LRC); and G25472–87 (unknown hand). The usual entry in the register reads 'Cochaquinas, south side of the Marañón, valley of the Amazons', but the entry on G25472–87 reads 'some purchased from Hauxwell, some through Damon'. Original (or, at least pre-1922) labels with the specimens are rare. Apart from referring to Woodward's illustrations they give no more specific information than 'Tertiary, valley of the Amazons', whilst the rock sample LL27843 is labelled 'shell conglomerate, Tertiary, Valley of the Amazons, 2200 miles above Para, collected by Mr Hauxwell'.

This BMPD collection that Woodward studied contained well over 1000 shells, mainly *Pachydon* but with *Neritina* also common. The rock sample (LL27843) consisted of about 1 kg of rusty brown, indurated mudstone crowded with shells. Some 200 g of this block, and a further 100 g of matrix obtained from the apertures of *Neritina* and the interior of bivalves with both valves together, has been broken down using dilute hydrogen peroxide. Many small shells, representing both small species and also juveniles of large species, have been obtained.

Fauna of Woodward, main collection (listed 1871: 102–107):

original determinations	revised determinations
Ebora crassilabra Conrad **F**	*Eubora woodwardi* Kadolsky (*E. crassilabra* also present)
Ebora (Nesis) bella Conrad **F** (note)	*Eubora bella* (Conrad)
Neritina ortoni Conrad **F**	*Neritina ortoni* Conrad
Odostomia? sp. **F**	*Dyris ortoni* (Gabb)
Anodon BATESI Woodward **F**	*Anodontites batesi* (Woodward)
Anisothyris HAUXWELLI nom. nov. (for *P. tenuis* Gabb) **F** *A. hauxwelli* var. α *distorta* *A. hauxwelli* var. β *crassa*	*Pachydon tenuis* Gabb
Anisothyris (Pachydon) ovata (Conrad)	*Pachydon tenuis* Gabb
Anisothyris carinata (Conrad) **F**	*Pachydon carinatus* Conrad
Anisothyris (Pachydon) obliqua (Gabb) **F**	*Pachydon obliquus* Gabb
Anisothyris erecta (Conrad) **F**	*Pachydon erectus* Conrad
Anisothyris cuneata (Conrad) **F**	*Pachydon cuneatus* Conrad

Note. Although figured and present in the collection, *E. (N.) bella* was stated by Woodward to be absent: possibly it is from Damon's contribution, see below.

In the above list, figured species are marked '**F**'. The revised list of determinations contains eleven species, only one of which, *Anodonites batesi* Woodward, was not present in Conrad's (1871*b*) fauna.

After completing his paper, Woodward received a further collection, from the dealer Robert Damon of Weymouth, Dorset, which had been forwarded to him by Professor Orton. He added a post-script (1871: 108), which mentioned no new forms except:

original determinations	revised determinations
Isaea (Mesalia) ortoni Gabb	*Dyris ortoni* (Gabb)
Isaea tricarinata Conrad (*sic*)	*Dyris tricarinata* (Boettger, 1878)

Woodward commented that two different species had probably been placed together in *I. ortoni*: this is discussed in the systematic section, p. 192. *I. tricarinata* Conrad is a *nomen nudum* (p. 190).

Additional species. During the present study, the following species were found either un-named in the Hauxwell Collection, or extracted from washings of matrix. The first, *Dyris gracilis* Conrad, was present in Conrad's part of the Hauxwell collection. None of the other eleven species were found by either author. All the species attributed to Conrad in the list below were described by him later (1874*a*).

Dyris gracilis Conrad
Dyris HAUXWELLI sp. nov.
Liris ACICULARIS sp. nov.
Toxosoma eborea Conrad
Tropidobora tertiana (Conrad)
Vitrinella (Vitrinellops) HAUXWELLI sp. nov.
Vitrinella (Vitrinellops) sp.
?*Hebetancylus* sp. (? juv.)
Pachydon erectus elongatus (Boettger)
PEBASIA dispar (Conrad)
Ostomya papyria Conrad
Mytilopsis scripta (Conrad)
Mytilopsis sallei (Recluz)

The lists above of revised determinations, when combined, show a total of 28 species present in the Hauxwell collection.

This rich fauna, presumably mainly from Pichana, is most similar to that described by Boettger (1878) and also collected, by Hauxwell, from either Pichana or Pebas (or from both). Differences are minimal. Boettger's fauna lacks *Hemisinus brasiliensis* (Moricand), known from a single specimen. The other seven absentees are all from those easily overlooked, and mostly rare, additional species obtained recently from washings: *Dyris hauxwelli, Liris acicularis, Vitrinella* (*Vitrinellops*) *hauxwelli, V.* (*V.*) sp., *Pebasia dispar, Ostomya papyria* and *?Hebetancylus* sp.

These Hauxwell collection faunas also closely resemble the rich Iquitos fauna (de Greve 1938). Species not known from Iquitos are *Liris acicularis, Vitrinella* (*Vitrinellops*) *hauxwelli, V.* (*V.*) sp., *Hemisinus brasiliensis*, *Dyris gracilis*, *?Hebetancylus* sp., *Ostomya papyria* and *Anodontites batesi*. Species not found in the Conrad/Woodward collections but occurring at Iquitos: *Liris scalarioides* (Etheridge), *Dyris tuberculata* (de Greve), *Vitrinella* (*Vitrinellops*) *degrevei* sp. nov., *Hemisinus kochi* (Bernardi), *Sheppardiconcha tuberculifera* (Conrad), *Sheppardiconcha coronata* (Etheridge), *Longiverena eucosmia* (Pilsbry & Olsson) and *Pachydon iquitensis* (de Greve). This last species is known only by one valve. Both *H. kochi* and *L. eucosmia* are rare, but the remaining species were described by de Greve as being either common or very common at Iquitos. Several of these are gastropods of the fresh-water family Thiaridae, and it may be that the Iquitos deposit represents a slightly less brackish facies. Comparison of the Unionidae is difficult, but the works of de Greve (1938) and Marshall (1928) suggest that the rare specimens of *Diplodon* from Iquitos and Pebas are similar.

Sheppard & Bate (1980) described the ostracod fauna listed below from the residue of matrix of the Hauxwell collection in BMPD.

(3) *Darwinula* sp.
(4) *Cypria AQUALICA* Sheppard & Bate
(5) *Perissocytheridea FORMOSA* Sheppard & Bate
(6) *RHADINOCYTHERURA AMAZONENSIS* Sheppard & Bate
(7) *Ambocythere CAMPANA* Sheppard & Bate
(8) *Cyprideis PURPERI PURPERI* Sheppard & Bate
(9) *Perissocytheridea*? *ELONGATA* Sheppard & Bate
(10) *BOTULOCYPRIDEIS SIMPLEX* Sheppard & Bate
(11) *OTAROCYPRIDEIS ELEGANS* Sheppard & Bate
(12) *Paracypris* sp.
(13) *Pontocypris* sp.

Species (1) and (2) are omitted because they only occur at La Tagua (p. 173). Species (3) and (7) also occur at La Tagua and a different subspecies of (8) also occurs there. Sheppard & Bate considered (4) to be indicative of fresh water, (5) and (8) to (11) of brackish water, whilst (6), (7), (12) and (13) suggested marine conditions. Their palaeogeographic conclusions are discussed later (p. 350).

The next collection from the Pebas/Pichana region was described by Conrad (1874*a*). It was made by Mr J. B. Steere, a graduate of Michigan University, who met Hartt whilst making natural history collections on the lower reaches of the Amazon. Hartt encouraged him to visit Pebas and record the geological section there and to collect fossils. Some details of Steere's findings were given in Conrad (1874*a*: 26) and Boettger (1878: 47–48). The most comprehensive account was reproduced in Hartt (1872: 55–56). Steere first saw fossils in clay beds just above Loreto, but did not have time to examine the exposure properly. Much of the river banks between there and Pebas were low and less than 100 ft (30 m) above river level during the dry season. The fossiliferous clay beds were low in the banks and overlain by 20–30 ft (6–9 m) of red clay comparable to the superficial clays so common on the Lower Amazon. Both Pebas and Pichana are situated on *tierra firme* (land not covered during the annual flood), some hundred feet (30 m) above the river level during the dry season.

Sections measured by Steere at Pebas (Hartt 1872: 56):

(a) In ravine near the road leading up the bank (to Pebas).

V 10 ft (3 m)	Surface deposit: red and white clay and sand, without fossils.
IV 5 ft (1.5 m)	Blue clay, full of fossils.
III 13 ft (3.9 m)	Blue clay; rare fossils, too poorly preserved to be extracted.
II 6 in (15 cm)	Seam of lignite; vegetable remains extend for few inches into clay both above and below seam.
I 15 ft (4.5 m)	Blue clay, with, in the centre, 3 ft (90 cm) band containing shells; base not seen.
Total, 43 ft 6 in. (*c.* 13 m)	

(b) Not far from first section.

V 5–6 ft (1.5–1.8 m)	Red and white clay
IV 5 ft (1.5 m)	Dirty coal
III 3 ft (90 cm)	Blue clay filled with fossils
II 10 ft (3.0 m)	Blue clay
I 2–3 ft (60–90 cm)	Clay full of fossils
Total, 25–27 ft (5.5–6.1 m)	

Steere also measured a third, but unfossiliferous, section nearby: this also draws attention to the fact that the thickness of the different bands varies markedly over short distances. Steere reported a similar succession at Pichana, whilst that at Old Pebas, which is at the mouth of Rio Ambiyacú, is denuded (? eroded or reduced). Steere also stated that bivalves were more numerous in the lower fossiliferous bands and gastropods in the upper (Hartt 1872: 57).

Unfortunately, Steere's fossils also became mixed, as becomes apparent from a letter from Steere to Hilgard, quoted by Conrad (1874*a*: 26). They came from three localities:

(1) Pebas 'one mile from the mouth of the Ambayacú'.
(2) Old Pebas 'two miles below'.
(3) Pichana 'perhaps fifteen miles from the mouth of the Ambayacú'.

Steere sent 'some shells that I know are new and bits of turtle shell, fish-bone, coral, crustaceans etc., which have not been noticed in the bed before.' Conrad, however, stated (1874*a*: 27) that he had found no coral in this or in any other collection of the Amazon fossils.

Steere collection of mixed fossils from Pebas, Old Pebas and Pichana, described by Conrad, 1874*a*:

original determinations (Conrad 1874*a*)	**revised determinations**
Pachydon (Anisorhynchus?) DISPAR Conrad v ANSP 31384	*PEBASIA dispar* (Conrad)
Pachydon altus Conrad, 1871 (lost)	*Pachydon erectus* Conrad, 1871 (see comment below)
Pachydon cuneata Conrad, 1871 (lost)	*Pachydon cuneatus* Conrad
Pachydon (Anisorhynchus) CUNEIFORMIS Conrad (lost)	indet. *Pachydon* sp.

original determinations	**revised determinations**
Dreissena (Mytiloides) SCRIPTA Conrad (lost) (note)	*Mytilopsis scripta* Conrad
Anodonta PEBASANA Conrad (lost)	*Anodontites* cf. *batesi* (Woodward)
Triquetra LONGULA Conrad (lost)	*Diplodon longulus* (Conrad)
OSTOMYA PAPYRIA Conrad (lost)	*Ostomya papyria* Conrad
Nuculana? sp. (lost)	indet. bivalve, possibly *Pachydon*
Planorbis sp. (lost)	probably *Vitrinella* (*Vitrinellops*) sp.
PACHYTOMA TERTIANA Conrad v ANSP 161151	*Tropidobora tertiana* (Conrad)
TOXOSOMA EBOREA Conrad ANSP 161152	*Toxosoma eborea* Conrad
CIRROBASIS VENUSTA Conrad (lost)	probably *Liris* sp.
LIOSOMA CURTA Conrad (lost)	*Toxosoma eborea* Conrad, juv.
CYCLOCHEILA PEBASANA Conrad (lost)	unknown
Hemisinus STEEREI Conrad (lost)	*Hemisinus* sp. indet. (worn)
Ebora crassilabra Conrad, 1871	*Eubora crassilabra* (Conrad)

Note. In the last line of his next paper, Conrad (1874*b*: 83) corrected *Mylitoides* (sic) to *Mytilopsis*. He was clearly referring to *Dreissena (Mytilopsis) scripta*.

Most of Conrad's type specimens are not listed as being present in ANSP in Richard's (1968) type catalogue. The registration numbers of those still known to exist are given above. Conrad's illustrations are poor, and there are also a number of inconsistancies in his text – such as mistaking left for right valves of bivalves. Conrad apparently suffered from poor health, and this may well be to blame.

Conrad (1874*a*: 32) also noted *Myliobates*, determined by Professor Leidy, and an impression in the clay of 'nearly a whole crab'. He mentioned the presence of *P. altus* and illustrated the species (1874*a*: 28; pl. 1, figs 4, 18). Immediately preceding the remarks on this species, he stated that there are no specimens in the collection which would represent *P. erectus*. However, the two are synonymous, and Conrad's figures truly represent this species.

This is an apparently unusual fauna from which several new genera were described by Conrad. In spite of so much of the type material being missing, it has been possible to suggest probable synonyms for several of the new taxa. The revised faunal list is of a typical Pebasian nature and is clearly similar to those described above for the Hauxwell mixed collection.

Canamá

(Brown 1879, Etheridge 1879)

There has been some controversy about the position of this locality, variously referred to as being either Brazilian or Peruvian. On modern maps and in the U.S. Government Gazetteer for Brazil, the only Canamá is marked as being on Rio Curuca, about 125 km upstream of its junction with Rio Javari, at 5° 37′ S, 72° 06′ W. However, Brown (1879: 79) stated that his fossils came from some 200 yards above the settlement of Canamá, which consisted of one or two houses in a clearing on a high bank of the Peruvian (northern) bank of Rio Javari. It lay some 50 miles (80 km) from the mouth of this river, where it joins Rio Marañón opposite Tabatinga. The account in Brown & Lidstone (1878: 483–485 and text illustration) is consistent with this. Canamá was described as the end of their journey up Rio Javari from Tabatinga. It is marked as such on their accompanying map which shows the extent of their travels. It is therefore confidently accepted that Brown's locality is where he described it. It is reasonably close to two other important localities, Três Unidos and Puerto Nariño.

Brown (1879: 78–79) also recorded the presence of similar fossils, without naming them, in 12 feet (*c*. 4 m) of grey clay at a place called Rebeiros (not in Gazetteer) some 20 miles (32 km) below the mouth of Rio Javari on the south bank of Rio Solimões. About 2 m above the fossiliferous Tertiary clay lay some 4 m of red and mottled grey and red clays which Brown considered to be a river deposit. He stated that the red clay contained a great abundance of small univalves. He also stated that fossils like those from Canamá, but usually with a preponderance of bivalves, occurred in grey clays exposed at several places along the banks of Rio Javari below Canamá. As well as molluscan fossils, he noted a band of lignite 2′ 6″ (75 cm) thick at a place called Barreiras Braga (not in Gazetteer). He also found *Unio* and *Anodon* and a gastropod unlike those occurring in the other sections. This suggests the possible presence of a third fossiliferous deposit, matching neither the grey clay of Canamá nor the red clay of the 'river deposit' at Rebeiros.

Section at Canamá (Brown 1879: 79):

River deposit (8′6″; 2.55 m):

3′ (90 cm)	Reddish loam.
5′6″ (1.65 m)	Grey clay, mottled with iron-oxide stains.

Tertiary (37′8″; 11.40 m):

1′ (30 cm)	Dull purplish clay, containing numerous casts of bivalves, chiefly *Anisothyris*.
14′ (4.25 m)	Slightly arenaceous bluish clays, containing great quantities of shells arranged in horizontal lines, chiefly of *Anisothyris* and *Neritina*.
1′ (30 cm)	Nodular concretionary clay-rock, the concretionary centres of which were composed of blue limestone, containing shells of same species as those in the clay.
14′ (4.25 m)	Greenish-blue slightly arenaceous clay, containing shells sparingly scattered through it, of similar genera to those in the beds above, and two thin layers of concretionary calcareous nodules.
1′8″ (50 cm)	Lignite.
6′ (1.80 m)	Light blue clay.

Brown records another section of 30′ 10″ (9.25 m) at the landing stage at Canamá. The top 10′ (3 m) was a yellowish clay and yielded *Melania, Cerithium* and *Anisothyris* as well as 'a very curious little species of *Neritina* marked with black dots' (surely *Neritina puncta* Etheridge, here placed in *N. ortoni* Conrad).

Brown went on to compare his sections with those measured by Steere (*in* Hartt, 1872) at Pebas. However, such detailed comparison of non-marine deposits, including thin bands of lignite, is not really possible. Brown, who was obviously well aware that his fauna was not typical of fresh water, thought that the sea must have reached far inland to perhaps 1,500 miles (2,400 km) west of the present shoreline during the deposition of the Canamá and Pebas deposits.

Like other early workers, Brown's collecting was obviously limited by lack of time and by constraints on carrying capacity. It is also a great pity that much of his collection was lost (see below). The details that he provided of his sections are of real value, as his writings (1879, Brown & Lidstone

1878) give the impression that he was a careful observer. He recorded *Neritina* and *Pachydon* (as *Anisothyris*) occurring together in great profusion. His second record is not so easy to interpret. These two genera were occurring in the same band as *Melania*, which (*sensu* Etheridge) is probably *Dyris* and *Liris*, as well as *Cerithium*, herein interpreted as *Sheppardiconcha coronata* (Etheridge). The genus is extinct but allied to *Hemisinus* and therefore thought to be exclusively fresh-water.

The fauna which Brown collected was described by R. Etheridge, sen. in an appendix to Brown's account (1879) of the geology. Etheridge's paper cannot be compared favourably with the earlier work of Woodward (1871) on the Pichana fauna. Etheridge listed an unjustifiably large number of genera – several of which have never been recorded since from the Pebasian – and named as new several species which were quite clearly the same as those described by previous authors. This was in spite of Hauxwell's collection (Woodward, 1871) being almost certainly available for comparison at that time in the British Museum.

Regrettably, much of Brown's collection was lost a long time ago and was never registered as part of the BMPD collections. Only 29 shells were registered, under 11 numbers, each representing one species, in the old B.M. Geology Department registers. The new gastropod and bivalve registers were not used until 1881: their issue presumably coincided with the reorganization at the time of moving the natural history collections from Bloomsbury to South Kensington. In the following faunal list, the Old Register numbers, together with the number of surviving specimens of each species, are indicated. The only other specimens known to be in existence are those, listed later, which were extracted from matrix in 1982.

The Canamá Fauna:

original determinations	**revised determinations**
Cerithium CORONATUM Etheridge. 97222 (×2)	*Sheppardiconcha coronata* (Etheridge)
Melanopsis BROWNI Etheridge (lost)	*Verena browni* (Etheridge)
Melania TRICARINATA Etheridge, *non* Boettger 1878. 97228 (×1)	*Dyris gracilis* Conrad
Melania BICARINATA Etheridge. 97726 (×3)	*Dyris gracilis* Conrad
Melania SCALARIOIDES Etheridge. 97724 (×2)	*Liris scalarioides* (Etheridge)
Pseudolacuna macroptera Boettger. 97723 (×3)	*Toxosoma eborea* Conrad
Natica? sp. (lost)	possibly *Eubora* sp.
Neritina PUNCTA Etheridge. 97222 (×2)	*Neritina ortoni* Conrad
Neritina ZICZAC Etheridge. 97232 (×3)	*Neritina ortoni* Conrad
Odostomia sp. (lost)	possibly *Dyris* sp.
Hydrobia DUBIA Etheridge. *Assiminea CRASSA* Etheridge. 97225 (×3)	?*Littoridina* (s.l.) *crassa* (Etheridge)
Isaea? ortoni? Conrad (lost)	*Dyris* sp. ?*ortoni* (Conrad)
Dyris? gracilis? Conrad (lost)	*Dyris* sp.
Fenella sp. (lost)	Could be either *Dyris* or *Liris* (see Wenz, 1940: 751, figs 2172–3).
Dreissena ACUTA Etheridge. 97230 (×3)	*Mytilopsis scripta* (Conrad) *Mytilopsis sallei* (Recluz). See below.
Anisothyris carinata (Conrad) (lost)	*Pachydon carinatus* Conrad
Anisothyris tenuis (Gabb) (lost)	*Pachydon tenuis* Gabb
Anisothyris hauxwelli Woodward (lost)	*Pachydon tenuis* Gabb
Anisothyris (Pachydon) TUMIDA Etheridge. 97229 (4 valves)	*Pachydon cuneatus* Conrad
Corbula CANAMAENSIS Etheridge. 97231 (4 valves)	*Pachydon erectus* Conrad
Thracia? sp. (small) (lost)	?*Ostomya* sp.
Lutraria? sp. (small) (lost)	?*Ostomya* sp. (? other valve)

Etheridge (*in* Brown 1879: 84) also discussed the specimens of *Anodon* and *Unio* referred to by Brown (1879: 80) from the cliffs a few miles below Canamá. Both specimens are lost; neither was ever registered.

Additional fauna. Some 50 g of clay became available whilst developing the specimens of *Mytilopsis* in 1982. The following additional species were extracted from this matrix.

Mytilopsis sallei (Recluz) – previously not visible, found under and obscured by *M. acuta.*
Pachydon obliquus Gabb
Pachydon TRIGONALIS sp. nov.
PEBASIA dispar (Conrad) – fragments only
fragments of indeterminate bivalve like *Ostomya*
Dyris lintea (Conrad), juv.
Dyris HAUXWELLI sp. nov.

Several valves of two ostracod species were also obtained, identified by R. H. Bate.

Cyprideis purperi Sheppard & Bate, 1980
Otarocyprideis elegans Sheppard & Bate, 1980

These specimens were not isolated until after the publication of the paper in which these species were described from elsewhere. Both species are indicative of brackish water and were described from the Hauxwell collection which came from the Pebasian, probably of Pichana. Interpretation of the synonymies given in Sheppard & Bate (1980) suggests that they also occur round San Paulo da Olivença (Purper 1977).

The revised determinations show the Canamá fauna to be typical of the Pebasian. It has not been possible to substantiate Etheridge's records of any of the genera which are either atypical or marine. I am unable to suggest any alternative determinations for Etheridge's small *Thracia* and *Lutraria* other than *Ostomya*. All three genera have similar shapes, with rounded anterior and posterior ends and with straight and almost parallel hinge lines and ventral margins. The shell of *Ostomya* is sometimes slightly corrugated. The different arrangement of the myophores in the two valves may have lead Etheridge to think that he was dealing with two different genera. The description he gives of his small ?*Natica*, with a slightly wavy outer lip, could well be of *Eubora*, a genus confined to the Pebasian.

Species of particular correlative value include *Sheppardiconcha coronata* (Etheridge) and *Verena browni* (Etheridge), both of which occur at Três Unidos and Igarapé da Extrema. The former is also known from Iquitos, whilst the latter occurs abundantly at the new locality of Puerto Nariño. A further link with this locality is provided by *Pachydon trigonalis* sp. nov. which is as yet unknown from elsewhere. *Toxosoma eboreum* Conrad, *Neritina ortoni* Conrad and the very rare *Pebasia dispar* (Conrad) are confined to the Pebasian. The suite of several species of *Pachydon* is typical and now includes the type species, *P. obliquus* Gabb. Both

Mytilopsis scripta Conrad and *M. sallei* (Recluz) are now listed in this fauna: the latter is one of the few Pebasian fossils indistinguishable from a still living species. Etheridge's descriptions of *Hydrobia dubia* and *Assiminea crassa* were apparently both based on the same specimens (Kadolsky 1980). This species is tentatively referred to as ?*Littoridina crassa*, but it may belong to an undescribed genus. It is not described here as new, partly because of the paucity of material and partly because of the existing confusion between the living genera *Littoridina* and *Heleobia*. This cannot as yet be resolved, because the type species of the former, *L. guidachaudi* (Souleyet), is so poorly understood. ?*L. crassa* is the only member of the Canamá fauna which is not known from other Pebasian localities.

Brackish elements of the Canamá fauna include *Pachydon* and *Neritina*, recorded by Brown as occurring together in profusion, as well as the much rarer *Mytilopsis* and *Pebasia*. No unequivocally fresh-water bivalves have been recorded from Canamá itself: both the *Unio* (Unionacea) and *Anodon* (Mutelacea) mentioned above came from several miles away. Two gastropods, the living *Verena* and extinct *Sheppardiconcha* (which is thought to be allied to *Hemisinus*) indicate a fresh-water environment. All the remaining gastropods belong to the Hydrobiidae, a family in which both genera and individual species may exhibit a wide salinity tolerance. No terrestrial gastropods are present.

The facies indicated by the Canamá molluscan fauna is fresh to weakly brackish and similar to conditions prevailing at Iquitos rather than in the possibly more strongly brackish Pichana deposit.

Três Unidos and Rio Quixito

(Oliveira & Carvalho 1924, Roxo 1924)

Oliveira & Carvalho (1924: 65–66) described a section and listed fossil molluscs, provisionally identified by J. C. Branner, which they had collected from Três Unidos in 1919. They described this as being a small settlement on the Peruvian (left or north) bank of Rio Javari, inhabited by three Brazilians. It is marked as Profile (perfil) no. 6 on their map. The course of Rio Javari as shown on their map coincides well enough with that seen on modern maps. Their locality thus approximately corresponds with 40° 24′ S, 71° 13′ W, although other sources have suggested that it lies elsewhere (see below). Further confirmation that the position of Três Unidos is as stated here is provided by del'Arco *et al.* (1977: 51 and geological map), who referred to this classic locality as being near their own Locality 4 of Jarina, from where they had collected un-named molluscs in 1975. The correct positioning of Três Unidos now shows that it is about 120 km south-west of the new locality of Puerto Nariño, Colombia and about 80 km south-west by west of Canamá (Brown 1879, Etheridge 1879), which also lies on the Peruvian bank of Rio Javari.

Oliveira & Carvalho during their expedition of 1919 also collected small faunas from Cachoera (rapids or waterfall) de Tracoás (1924: 71, map – perfil no. 14) and Igarapé de Extrema de Manoel Honorato (perfil no. 15). Both of these localities, which are not marked very precisely on their map, lie on Rio Quixito, about 20 km apart in the region of 4° 35′ S, 70° 37′ W. See pp. 330–331.

Oliveira & Carvalho's faunas were dealt with in more detail by Roxo (1924), who figured several species and described two as new. Most of the gastropods have been the subject of competent and well-illustrated partial systematic revisions by Santos & Castro (1967) and by Costa (1981), whilst some were either figured or otherwise mentioned in Parodiz (1969). None of the bivalves have been revised. Roxo (1924) also discussed Pebasian species which were not present in the Três Unidos fauna, but their absence may not always have been appreciated by subsequent authors. Because of this and later changes in determinations, it is not possible to compile a definitive list of this fauna, working from the literature alone.

There have been conflicting views about the positions of these localities. The Três Unidos of Oliveira & Carvalho is not the same as the only entry under that name, of a presumably larger place, listed in U.S. Government Gazetteer for Brazil at 6° 37′ S, 69° 33′ W, nor is it as marked on de Greve's map (1938: pl. 10), much further up Rio Javari at 5° 40′ S, 73° 20′ W, lying almost due south of Iquitos. Roxo (1924) referred to 'Cachoera de Fracos' and 'Fracoas' instead of Tracoás. Del'Arco *et al.* (1977: 51) stated that it was difficult to position 'Cachoera das Fracoas' and Igarapé da Extrema exactly, as they were not shown on their map.

Del'Arco *et al.* also listed some 37 fossiliferous localities, many of which had yielded only un-named bone or plant fragments. Fossil molluscs occurred at several, but were not named except from two (Locs 13 and 28). Loc. 13 at Atalaia del Norte, supposedly Pliocene, has yielded *Aylacostoma* and *Pachydon*: Pebasian fossils have been described from this area (Purper 1977, ostracods; Costa 1980, molluscs). Loc. 28 at Aquidabã, on Rio Jurua (6° 30′ S; 69° 40′ W), supposedly Pleistocene, has yielded a fauna lacking typical Pebasian elements, but with strong resemblances to the living Amazonian fauna. It contains *Ampullaria, Aylacostoma, Hydrobia, ?Doryssa, Helix* and *Stenogyra*, several genera of Unionacea, *Anodontites* (Mutelacea) and *Pisidium* (Corbiculacea), as well as a rich vertebrate fauna. It is covered in greater detail in several works (Roxo 1937, Moura & Wanderley 1938, Oliveira 1940, Oliveira & Leonardos 1943: 636, map – fig. 156, and Palmer 1945). The previously held view that this fauna is of Pebasian age can no longer be supported.

The molluscan localities (2–9 and 13) listed as being Pliocene (i.e. Pebasian on their dating) by del'Arco *et al.* (1977: 51–52) all lay in the Atalaia del Norte–Benjamin Constant region and near the mouth of Rio Javari. None lay on Rio Quixito, so it appears that there has been no follow-up of Oliviera & Carvalho's collecting expedition of 1919. Del'Arco *et al.* (1977: 51) wrote that fossil molluscs of the Pliocene localities were comparable to those of Pebas and Iquitos and that confirmation of this dating was provided by the armadillo *Kraiglievichia*. In support, they quoted (1977: 53) the identification by Dr Bryan Patterson of *K. paranense* from their Loc. 18 on Rio Jutaí. This, however, is one of a series of vertebrate localities lying some 150 km to the south-east of Benjamin Constant and also in the area yielding their Pebasian molluscan faunas. Thus, the brackish-water Pebasian localities and the presumably terrestrial or near-terrestrial vertebrate localities lie rather far apart and represent rather different facies which may or may not be contemporaneous. No faunal elements common to both have so far been described, so there is, as yet, no palaeontological evidence as to their relative ages. Del'Arco *et al.* mapped both their molluscan and their vertebrate localities as Solimões Formation.

The following section of the bank of Rio Javari at Três Unidos was given by Oliveira & Carvalho (1924: 66):

—	Top soil
0.20 m	white clay
0.15 m	lignite
0.20 m	dark clay
1.70 m	dark clay, rich in Tertiary fossils, and with fragments of lignite disseminated throughout
5 m	bluish grey clay with greenish calcareous inclusions
———	river level ———

They listed (1924: 67) the following fauna, identified by J. C. Branner:

Dreissena fragilis Boettger
Anisothyris (Pachydon) tenuis (Gabb)
Anisothyris (Pachydon) carinata (Conrad)
Anisothyris erecta (Conrad) (See below)
Leila (Iridina) sp. nov.
Hydrobia ortoni (Gabb)
Hydrobia scalarioides (Etheridge)
Hydrobia lintea (Conrad)
Hydrobia tricarinata (Boettger)
Pseudolacuna macroptera (Boettger)
Melanopsis browni Etheridge
Cerithium coronatum Etheridge
Neritina zig-zag [no author; presumably *N. zic-zac* Etheridge rather than *zig-zag* Lamk.]

Roxo's fauna (1924) differs slightly. It is not known whether he studied the same specimens as Branner or whether the collection was split between them. The few species figured by Roxo are indicated. Revised names are given in the second column. The generic names are always those used throughout the present work. Species revised in Santos & Castro (1967) are indicated thus *; by Costa (1981) thus †; specific name changes instigated in the present paper, thus +. Roxo's material is in Departamento de Paleontologia do Museu Nacional do Rio de Janeiro (DP, MN).

original determinations		**revised determinations**
Anisothyris hauxwelli Woodward	+	*Pachydon tenuis* Conrad
Anisothyris carinatus (Conrad)		*Pachydon carinatus* Conrad
Anisothyris cuneatus (Conrad)		*Pachydon cuneatus* Conrad
Anisothyris obliqua (Gabb)		*Pachydon obliquus* Gabb
Anisothyris tumida Etheridge	+	*Pachydon cuneatus* Conrad
Tellina amazonensis Gabb		*Pachydon amazonensis* (Gabb)
Dreissena acuta Etheridge (fig. A)	+ +	*Mytilopsis sallei* (Recluz) *Mytilopsis scripta* (Conrad)
Anodonta fragments		?*Anodontites*
Hyria corrugata (Lamarck)		?*Triplodon corrugatus* (Lamarck)
Cerithium coronatum Etheridge	*†	*Sheppardiconcha coronata* (Etheridge)
Melanopsis? browni Etheridge	†	*Verena browni* (Etheridge)
Melania tricarinata Etheridge		*Dyris* sp.
Melania bicarinata Etheridge		*Dyris* sp.
Melania scalarioides Etheridge (see below)	+†	*Liris scalarioides* (Etheridge)
Neritina ortoni Conrad (included *N. pupa* Gabb, *non* Linné)		*Neritina ortoni* Conrad
Neritina puncta Etheridge	+	*Neritina ortoni* Conrad
Neritina ETHERIDGI Roxo, nom. nov. pro *Neritina ziczac* Etheridge, *non* Lamarck	+	*Neritina ortoni* Conrad
(fig. B is un-named *Neritina*)		——
Pseudolacuna macroptera 'Etheridge' (*sic*)	†	*Toxosoma eboreum* Conrad
Ebora crassilabra Conrad		*Eubora* sp.
Hydrobia dubia Etheridge (see below)	+	?*Littoridina crassa* (Etheridge)
Odostomia sp. (of Woodward, 1871)		*Dyris* sp.
Isaea (Mesalia) ortoni Gabb	†	*Dyris ortoni* (Gabb)
Isaea lintea Conrad	†	*Dyris lintea* (Conrad)
Purpura WOODWARDI Roxo, nov. sp. (figs C, D)	+*	*Verena* ?*crenocarina* (Moricand)
Planorbis BOURGUYI Roxo, nov. sp. (fig. E)	+	?*Vitrinella* (s.l.)

Several questions about the Três Unidos fauna must remain unanswered at present and can only be resolved by re-examining the material. First, Branner (*in* Oliveira & Carvalho 1924) identified *Anisothyris* [i.e., *Pachydon*] *erecta* Conrad, but Roxo (1924: 44) stated that *Corbula canamaensis* Etheridge (which is a synonym) was absent. Secondly, there is the rather similar case of *Assiminea crassa* Etheridge which was stated by Roxo (1924: 48) to be absent whilst its synonym *Hydrobia dubia* Etheridge was thought to occur in abundance (1924: 48). *Liris* is recorded variously as *Melania scalarioides* (1924: 46, present at Três Unidos), *Turbonilla minuscula* (1924: 48, unlocalized) and as *Liris laqueata* (1924: 48, absent). The specimen figured by Costa (1981: pl, 1, figs 9, 10) as *L. minuscula* (Gabb) is large for the genus and is provisionally identified as *L. scalarioides* (Etheridge). It must therefore be assumed that these and similar apparent contradictions, such as with *Melania, Dyris, Hydrobia, Odostomia* and *Isaea*, were due to difficulties encountered by Roxo in interpreting the often inadequate descriptions and illustrations provided by earlier authors.

Roxo listed the following species as not occurring in his fauna. *Corbula canamaensis* Etheridge, *Fenella* sp. of Etheridge, *Nesis bella* Conrad, *Dyris gracilis* Conrad, *Liris laqueata* Conrad, *Hemisinus sulcatus* Conrad, *Bulimus linteus* Conrad and *Natica* spp. of both Conrad (1871*b*) and Etheridge (1879).

Purpura woodwardi Roxo was taken by several workers, including Roxo himself, to be evidence of marine conditions. However, it clearly belongs to the fresh-water genus *Verena*.

The status of *Planorbis bourguyi* Roxo is uncertain. Although it is figured (fig. E), there is no description. Roxo stated that two out of the three small shells in his collection had been lost and expressed the hope that a diagnosis could be provided if more specimens were discovered later among the great quantity of material available. It thus appears to be valid. From Roxo's figure, it seems likely to belong to *Vitrinella*, s.l.

Três Unidos has yielded a typical Pebasian fauna with *Pachydon, Eubora, Toxosoma, Dyris* and *Liris*. *Verena browni* Etheridge is known only from three other localities, none of which are far away, Puerto Nariño, Igarapé da Extrema and its type locality, Canamá.

Cachoera de Tracoás

Oliviera & Carvalho (1924: 71) gave no faunal list for this locality (perfil no. 14). The following list has been extracted from Roxo's text (1924): the names are revised to conform with those used in the present paper.

original determinations	**revised determinations**
Anisothyris hauxwelli Woodward	*Pachydon tenuis* Gabb
Anisothyris carinata (Conrad)	*Pachydon carinatus* Conrad
Anisothyris amazonensis Gabb	*Pachydon amazonensis* (Gabb)
Unio sp.	Unionacea/ Mutelacea
Melania tricarinata Etheridge	*Dyris* sp., ? *tricarinata* (Boettger)
Melania bicarinata Etheridge	*Dyris* sp.
Melania scalarioides Etheridge	*Liris scalarioides* (Etheridge)
Odostomia sp.	?*Dyris* sp.

This appears to be a typical, but not very rich, Pebasian fauna.

Igarapé da Extrema de Manoel Honorato

Oliviera & Carvalho (1924: 71) listed some fossils from this locality on Rio Quixito (perfil no. 15). A few fossils from here are also mentioned in Roxo's text (1924) and are indicated thus *.

original determinations		**revised determinations**
Anisothyris (Pachydon) carinata Conrad		*Pachydon carinatus* Conrad
Tellina amazonensis Gabb		*Pachydon amazonensis* (Gabb)
Dreissena acuta Etheridge		*Mytilopsis sallei* (Recluz) *Mytilopsis scripta* (Conrad)
Melania escalarioides Etheridge (*sic*)		*Liris scalarioides* (Etheridge)
Ebora crassilabra Conrad	*	*Eubora sp.*
Pseudolacuna macroptera Boettger	*	*Toxosoma eborea* Conrad
Cerithium coronatum Etheridge	*	*Sheppardiconcha coronatum* (Etheridge)

In addition, Roxo (1924: 46) recorded *Verena browni* (Etheridge) from this locality (as ?*Melanopsis browni*). Thus, the fauna of Igarapé da Extrema is typical of the Pebasian and has particular resemblances to those of the neighbouring localities of Três Unidos, Canamá and Puerto Nariño.

Iquitos

(De Greve 1938)

A large collection of molluscs from Iquitos (3° 42′ S, 73° 42′ W) was made in 1912 by a Swiss expedition under Professor B. Peyer. This was monographed by de Greve (1938), who (1938: 15–18) briefly described the six localities in the vicinity of the town from which the fauna was obtained. The maximum section appears to be of some 6.80 m, mainly of blue clays, but including a 0.5 m lignite band (1938: 16). De Greve's is the most comprehensive and best illustrated work on the palaeontology of any of the Pebasian localities to date. It has probably been used for identifications by all subsequent workers not having easy access to type material. For instance, Wenz (1939) reproduced de Greve's figures to illustrate *Liris* and *Dyris*. Unfortunately, the figure of *Liris* was of a species probably belonging to *Dyris* rather than of its type species, whilst the illustration of *D. gracilis*, the type species of *Dyris*, was misidentified.

The deposits at Iquitos have been dealt with in a few other works. Steere (*in* Hartt, 1872: 56) reported the presence at Iquitos of beds similar to those at Pebas, but could find no fossils. Conrad (1874*b*) described two species, listed below, collected by Orton on a second visit to the region.

Iquitos fossils collected by Orton, described by Conrad (1874*b*).

original determinations	**revised determinations**
HAPLOTHAERUS CAPAX Conrad (lost)	*Anodontites* sp.
Hemisinus TUBERCULIFERUS Conrad	*Sheppardiconcha tuberculifera* (Conrad)

Haplothaerus capax was described from a broken specimen, not listed in Richards (1968). Conrad stated that *Hemisinus tuberculiferus* was very common. The type series is in ANSP: a specimen was figured by Pilsbry (1944), who did not indicate whether it was Conrad's figured syntype.

Ruegg & Rosenzweig (1949), in a paper reviewing current thinking on the Pebasian sediments, gave a map of the town area and also geological sections indicating that underneath a layer of alluvium, there was a thickness of some 35 m of grey, blue and black clays with lignite. The bottom of the clay was not reached. This sequence is much thicker than that indicated by de Greve.

Willard (1966: 65) listed a few fossils from Iquitos, collected by Bassler in 1922. He also figured two further species, not on his faunal list, as coming from Iquitos. Bassler visited several localities in the district which yielded similar small faunas, almost exclusively of the more common species. They add little to our knowledge of the fauna, but are a useful indication of the widespread nature of the Pebasian deposits around Iquitos.

Iquitos fossils collected by Bassler in 1922, recorded in Willard (1966).

original determinations	**revised determinations**
Anisothyris obliqua (Gabb)	*Pachydon obliquus* Gabb
Anisothyris erecta (Conrad)	*Pachydon erectus* Conrad
Anisothyris cf. *erecta* (Conrad)	——
Hydrobia tricarinata Boettger	*Dyris tricarinata* (Boettger)
Hydrobia confusa Boettger	*Dyris ortoni* (Gabb)
Anodontites lacivansis (*sic*) Pilsbry & Olsson (pl. 56, fig. 2)	unidentifiable naiad
Anisothyris cf. *tenuis* (Gabb) (pl. 58, fig. 1)	*Pachydon* cf. *tenuis* Gabb

Bassler's collection is now at Lehigh University, Bethlehem, Pennsylvania.

De Greve (1938) refigured several of Boettger's (1878) type specimens, which come from either Pebas or Pichana. In fact, in the case of some species, all his figured specimens are taken from Boettger's collection and none are of Iquitos shells. Furthermore, in his text, he gave the dimensions of Boettger's shells even though in his faunal list (1938: 125) he indicated that the particular species was very common at Iquitos (i.e. *Hydrobia ortoni, H. confusa* and *H. tricarinata*). On the other hand, there are species such as *Lacuna (Ebora) bella* (Conrad) which de Greve dealt with in his text (1938: 72–73) but neither figured nor placed on his faunal list. This omission of illustrations of Iquitos shells is unfortunate as study of several of these species from different localities seems to show some purely local variation. Kadolsky (1980) recognized three species of his genus *Eubora* in the sample of shells that de Greve had identified as belonging to a single species (see faunal list below). Further revisory work might well reveal similar examples in different genera. Care is therefore necessary in assessing the contents of de Greve's fauna. The species which he actually identified as occurring in Peyer's collection from Iquitos were listed by him (1938: 125) and, in addition, he indicated their registration numbers in the text after their description and measurements.

Iquitos fauna, collected by Peyer Expedition, described by de Greve (1938).

All the species listed below, with very few exceptions, were illustrated by de Greve. Key: Figured specimens from Iquitos only, *; from either Pebas or Pichana (*ex* Boettger, 1878), B; from both collections *B; not figured O. R, rare; C, common; VC, very common (after de Greve, p. 125). v, examined herein. The collection is in PIMUZ.

original determinations	**revised determinations**
Neritina ortoni Conrad *C	*Neritina ortoni* Conrad
Neritina AMAZONENSIS de Greve v*R	*Neritina ortoni* Conrad
Neritina ROXOI de Greve v*R	*Neritina ortoni* Conrad
Neritina etheridgei Roxo v*R	*Neritina ortoni* Conrad
Helicina (?) tertiana (Conrad) *R	*Tropidobora tertiana* (Conrad)
Lacuna (Ebora) crassilabris (Conrad) *C	*Eubora woodwardi* Kadolsky *Eubora grevei* Kadolsky *Eubora pygmaea* Kadolsky
Pseudolacuna macroptera Boettger *VC	*Toxosoma eborea* Conrad
Ampullaria sp., fragments C	——
Hydrobia (Conradia) ortoni (Gabb) vB, VC	*Dyris ortoni* (Gabb)
Hydrobia (Conradia) confusa Boettger B, VC	*Dyris ortoni* (Gabb)
Hydrobia (Conradia) tricarinata Boettger B, VC	*Dyris tricarinata* (Boettger)
Hydrobia (Conradia) lintea (Conrad) *VC	*Dyris lintea* (Conrad)
Dyris gracilis Conrad *C	*Dyris HAUXWELLI* sp. nov.
Liris laqueata Conrad *B, VC	*Liris minuscula* (Gabb)
Liris minuscula (Gabb) *VC	*Liris scalarioides* (Etheridge)
Liris TUBERCULATA de Greve v*VC	*Dyris tuberculata* (de Greve)
Semisinus sulcatus (Conrad) v*R	*Hemisinus kochi* (Bernardi)
Semisinus tuberculiferus (Conrad) v*C	*Sheppardiconcha tuberculifera* (Conrad)
Semisinus PEYERI de Greve v*R	*Longiverena eucosmia* (Pilsbry & Olsson)
Cerithium(?) coronatum Etheridge *C	*Sheppardiconcha coronata* (Etheridge)
Planorbis sp. v*R	*Vitrinella* (*Vitrinellops*) *DEGREVEI* sp. nov.
Anodontites sp. (p. 125, ?= 'Nayad shell' of p. 19, text-fig. I) C	*Anodontites* sp.
Hyria sp. *R	*Diplodon ?longulus* (Conrad)
Anisorhynchus JEANNETI de Greve *R	*PEBASIA dispar* (Conrad)
Anisothyris amazonensis (Gabb) *B, R	*Pachydon amazonensis* (Gabb)
Anisothyris tenuis (Gabb) *VC	*Pachydon tenuis* Gabb
Anisothyris cuneata (Conrad) R	*Pachydon cuneatus* Conrad
Anisothyris ovata (Conrad) O, R	*Pachydon tenuis* Gabb
Anisothyris erecta (Conrad) B, VC	*Pachydon erectus* Conrad
Anisothyris erecta (Conrad) var. *elongata* Boettger B, C	*Pachydon erectus elongatus* (Boettger)
Anisothyris obliqua (Gabb) *VC	*Pachydon obliquus* Gabb
Anisothyris IQUITENSIS de Greve *R	*Pachydon iquitensis* (de Greve)
Anisothyris carinata (Conrad) *C	*Pachydon carinatus* Conrad
Congeria fragilis Boettger B (Boettger collection only, does not occur at Iquitos)	
Congeria cf. *fragilis* Boettger *R *Congeria* n. sp. aff. *fragilis* Boettger *C (and nov. vars I to IV) *Congeria* cf. *acuta* (Etheridge) O, R *Congeria scripta* (Conrad) *R	*Mytilopsis sallei* (Recluz) and *Mytilopsis scripta* (Conrad)

In addition, de Greve described, under 'Problematicum', a possible member of the Porifera, *IQUITOSIA BLUNTSCHLII* (1938: 110, text-figs 24, 25) and (as 'Vermes') a small adherent polychaete (1938: 108; pl. 3, figs 29, 30). This polychaete has also been extracted (1982) from the Hauxwell collection matrix, probably from Pichana.

The Iquitos molluscan fauna (Conrad 1874*b*), de Greve 1938) is one of the richest Pebasian fauna so far known. It comprises 31 named species. The only specifically unnamed taxa are the *Ampullaria* sp. and *Anodontites* sp. of de Greve and the unidentifiable naiad of Willard: both of the latter might be the same as *Haplothaerus capax* Conrad. The main absentee is *Verena browni* (Etheridge), described from Canamá, and very common at both Três Unidos and Puerto Nariño. Other species not present are rare, and with the exception of naiades such as *Anodontites batesi* (Woodward) are also small and therefore easily overlooked: these include *Ostomya*, the smaller species of *Vitrinella* (*Vitrinellops*) and *Dyris gracilis* Conrad.

Two living species are present. This is the only known fossil occurrence of *Hemisinus kochi* (Bernardi). The earliest known occurrence of *Mytilopsis sallei* (Recluz), however, is in the late Oligocene of Panama. Only a few taxa present also occur in non-Pebasian deposits. *Pachydon cuneatus* Conrad was recorded by Rutsch (1952) from the Neogene of Venezuela. A specimen of *Neritina*, very similar to *N. ortoni*, was recorded from the marine Miocene (now thought to be N.8) of the Paraguana Peninsula, Venezuela by Jung (1965) as *N.* aff. *woodwardi* Guppy, a very different species. Specimens identified as *Dyris tricarinata* (Boettger) are identified herein as occurring in the Neogene San Cayetano Formation of the Loja Basin, Ecuador (Bristow & Parodiz 1982), but this appears to be a very variable species upon which too much stratigraphical reliance should not be placed. *Mytilopsis scripta* (Conrad), according to the synonymy constructed herein, also occurs in the La Cira fossil horizon of the Middle Magdalena Valley (Pilsbry & Olsson 1935) and at La Tagua, Colombia as well as in probable late Oligocene strata of western Peru (Olsson 1931). A further link with strata of the Middle Magdalena Valley is provided by the reidentification of *Semisinus peyeri* de Greve as *Longiverena eucosmia* (Pilsbry & Olsson 1935). This species now has several synonyms and is believed to occur not only in the type horizon, the Mugrosa fossil band, but also in the La Cira fossil band, and is recorded from the Miocene of the Cuenca Basin as *H. peyeri dickersoni* by Palmer (*in* Liddle & Palmer 1941). *L. colombiana* sp. nov. from La Tagua is a very similar species.

The age of the Magdalena Basin faunas is still in dispute and is discussed further in the next section (p. 333), where it is concluded that the Mugrosa and La Cira horizons are not of very different ages and that the older of the two, the Mugrosa, is not likely to be older than latest Oligocene and might even be early Miocene. The combined occurrence in the Iquitos fauna of a few species from the Magdalena Basin faunas (one of which also occurs in the Miocene of the Cuenca Basin) with two living species suggests that the

Iquitos is no older than Miocene, and is likely to be later than Lower Miocene.

It is difficult to put an upper limit on the age of the Iquitos fauna. It is, like others from the Pebasian, very different from that of the present day Amazon Valley, except for the presence of the living *Hemisinus kochi* (Bernardi). The only other living species is *Mytilopsis sallei* (Recluz) from no nearer than the Caribbean. This rather marked lack of Recent elements, even at generic level, is evidence of a considerable change in conditions between the time of deposition of the Iquitos sediments and the present day. This, in itself, cannot be construed as proof that this deposit is particularly old. Considerable changes have occurred in many parts of the world during the Pleistocene. The differences apparent in the Amazon region, though striking, are of a comparable order of magnitude. The distribution, discussed above, of the comparatively few fossil species known from other faunas points to a Miocene rather than a later age. It is therefore concluded that the Iquitos fauna is more likely to be Middle to Upper Miocene in age than either earlier or later.

This Iquitos collection is both rich and with reliable locality data, and is thus the best example of the Pebasian fauna available for ecological assessment. De Greve (1938: 17, table 1) showed the distribution of genera at his six Iquitos localities. Genera here considered to be indicative of either brackish or fresh water occur with other genera typical of truly fresh water. There is no apparent indication that any particular locality is either more or less saline than any other. *Pachydon* occurs at all six, whilst *Mytilopsis* and *Liris* occur together at four localities (I, II, V and VI). The taxa with the widest salinity tolerance are *Neritina* and *Pachydon*, both of which are very common, along with the moderately common *Mytilopsis*. None of the Hydrobiidae (Littoridininae, Lithoglyphinae and Cochliopinae) can be regarded as definitely indicative of either brackish or fresh-water. All the Thiaridae (*Hemisinus, Longiverena*, and presumably also the related but extinct *Sheppardiconcha*) are fresh-water genera. *Hemisinus*, however, occurs both in South America and on Caribbean islands, so it must have exhibited tolerance to salt water at some stage in its life history unless all its occurrences on islands are human introductions. Some of these appear from de Greve's (1938: 125) assessment to be moderately common, but they are by no means a dominant part of the fauna.

As is the case with other Pebasian faunas, the exclusively fresh-water naiades (Unionacea and Mutelacea) are comparatively rare. Bivalves of the fresh-water Superfamily Corbiculacea are not known from Iquitos, nor are aqatic or terrestrial pulmonate gastropods. The amphibious (fresh-water and terrestrial) prosobranch *Ampularia* is known only from fragments, apparently obtained from a lignite band, and does not occur with the rest of the molluscan fauna.

The preservation of the shells figured by de Greve (1938) is excellent, except for the apertures of gastropods which are often broken. It is concluded that the clays of the Iquitos deposit were laid down in an area, such as a lagoon or series of lagoons, in which saline and fresh water could mingle. This probably bordered a low-lying, densely forested region which provided the material for the lignite bands.

Magdalena Valley, Colombia

The non-marine Tertiary outcrops over large areas of the Magdalena Valley, and from this region came the only previously-described molluscan faunas from Colombia of relevance to the present study. Anderson (1928) described as Eocene a small fauna from near San Juan de Rio Seco in the Upper Magdalena valley. He also published on the stratigraphy of the region (1927). Below, it is suggested that this fauna came from the Santa Teresa Formation and is probably Miocene in age.

Pilsbry & Olsson (1935) described three faunas from the Middle Magdalena Valley: the last section of their paper was contributed by Wheeler and was on the stratigraphy. Their conclusions were that the Los Corros faunas was Eocene, the Mugrosa was Middle Oligocene, and the youngest, the La Cira, was Upper Oligocene to Lower Miocene. Here it is suggested that there is no molluscan palaeontological evidence for the age of the Los Corros fauna more precise than 'probably Palaeogene'. It also appears that the Mugrosa, which has species in common with the La Cira, is not much older than the latter. The former is unlikely to be earlier than Late Oligocene and may be younger, while the latter is almost certainly Miocene. The La Cira is tentatively correlated both with Anderson's (1928) fauna and with the new La Tagua faunas.

Wheeler's (1935: 33–34) account of the stratigraphy of the Middle Magdalena Valley indicated that the La Cira fossil horizon consisted of several distinct fossiliferous bands in some 350 ft (105 m) of sediments lying at the top of the Colorado series, which varies in thickness between 2600 and 6900 ft (780–2070 m). Below this lay the Mugrosa Formation, which varied in thickness between 1200 and 4500 ft (360–1350 m). Its topmost bed, the Mugrosa fossil horizon, was between a few inches and 25 ft (up to 7.5 m) thick, and could be traced for some 75 miles (120 km). The Mugrosa was underlain immediately by the Los Corros fossil horizon, some 30–50 ft (9–15 m) thick, forming the topmost part of the Esmeraldas Formation of the Chorro Series.

Molluscan faunas similar to those discussed above have been reported, but never illustrated, by Butler (1939, 1942) and de Porta (1966, 1974), the last reference being to his *Lexique Stratigraphique* volume on the Tertiary of Colombia.

Palynological dating

At this point, it seems appropriate to discuss briefly the work on palynological dating, as applied to these Tertiary non-marine deposits of Colombia. In later works (Hopping 1967, Germeraad *et al.* 1968), it is apparent that palynologists have successfully matched their zones with those erected on planktonic foraminifera. In earlier works (van der Hammen 1957, 1961), neither spore nor foraminiferal zones were named. A difficulty with all these papers is that it has been virtually impossible to equate actual molluscan localities with the material, much of which came from boreholes, worked on by palynologists.

LA CIRA FORMATION. Van der Hammen (1957: 67) placed this in the Upper Oligocene. In discussing the age, he mentioned both the molluscan fauna from the Middle Magdalena Valley described by Pilsbry & Olsson (1935) and the vertebrates from near La Dorada, from much higher in the Magdalena Valley (Stirton 1953). Stirton's material comes from nowhere near the molluscan fauna localities. Although no indication of the localities yielding the spore flora was given, it is clear from his later work (van der Hammen 1961: 102) that his interpretation of the La Cira was the same as that of Wheeler (1935: 34): he considered it the top of the Colorado Series (or Formation). In the same work, however, (1961: 106) he wrote that the La Cira of the Upper Magdalena Valley corresponded to the Colorado Formation (i.e. as a whole, rather than the uppermost part). The Colorado was also dated as Upper Oligocene. Van der Hammen (1957: 90) had explained that his usage of the term Upper Oligocene followed that of Stainforth (1948) rather than of Eames (1953). Thus, his dating of the La Cira and Colorado Formations places them both within the Lower Miocene, in present-day terminology.

Hopping (1967: 38–42, figs 10, 11) discussed in great detail the distribution of the stratigraphically important *Crassoretrilites vanraadshooveni* (*nom. nud.*, validated Germeraad, Hopping & Müller 1968: 287; pl. 1, fig. 3). In the Magdalena Valley its first occurrence is in the lower part of the Real Formation, just above the top of the La Cira Formation which lay entirely within the Zone of *Verrutricolporites rotundiporis*. Hopping (1967: 46, fig. 13) showed the base of this zone coinciding more or less with the top of the zone of *Globigerina ciperoensis ciperoensis* (now Zone P22, whose top is about 22.5 m.y. old, and is just below the Oligo-Miocene boundary). The base of the *C. vanraadshooveni* Zone was shown in the lower part of the zone of *Globorotalia fohsi fohsi* (now N10, Middle Miocene, about 13 m.y. old). These figures give the rather wide age band of 9.5 million years in which the La Cira Formation could have been deposited. Hopping wrote (1967: 42) of the La Cira Formation that in the Middle Magdalena Valley area the interval of rocks concerned is developed in a fresh-water facies containing no other fossils. This statement ignores the macrofossil fauna entirely.

MUGROSA FORMATION. Van der Hammen (1961: 106), in common with Pilsbry & Olsson's (1935) work on the molluscs, dated this formation as Middle Oligocene (approximately Late Oligocene by modern terminology). Hopping (1967: fig. 10) sheds no direct light on the problem. He showed the La Cira Formation underlain by the 'A–B Sands' about which he gave no further information. These are presumably the 'A' zone of the Colorado Series, which is separated from the 'B' zone of the Mugrosa formation by the Mugrosa fossil horizon (Wheeler 1935: 32–33). These two bands are not separated in Hopping's diagram, but it seems likely that the Mugrosa fossil band would lie somewhere below the base of the zone of *V. rotundiporis* (i.e. below the top of the zone of *G. ciperoensis ciperoensis*, Zone P22). This would place the Mugrosa fossil horizon within the Oligocene.

Although de Porta (1974: 426) gave the age of the Mugrosa Formation as Upper Eocene to Oligocene, it appears that this conclusion was still based partly on Pilsbry & Olsson's molluscan evidence as well as newer palynological work. He suggested that van der Hammen (actually published 1961, but quoted by de Porta as 1958, appearing in 1960) had shown that the lower part of the Mugrosa Formation was the equivalent of the upper part of the San Fernando Formation, which had been placed in the zone of *Verrucatosporites usmensis* (Germeraad *et al.* 1968: fig. 18). This zone is thought to coincide with the Upper Eocene and may include small amounts of both Middle Eocene and Lower Oligocene (Germeraad *et al.* 1968: 244; fig. 15). Part of the Esmeraldas Formation, whose topmost bed is the Los Corros fossil horizon, is also said to lie within this zone. Although van der Hammen (1961: 97) deals with the San Fernando Formation, he does not refer to any correlation between it and the Mugrosa Formation. In addition, de Porta (1974: 496–500) discussed four different usages of the term San Fernando Formation, with ages ranging between ? Upper Eocene and ? Pliocene. In any case, the Mugrosa fossil horizon is at the top of the Mugrosa Formation, and therefore, even if the correlation between these two formations were correct, is likely to be distinctly younger than the zone of *V. usmensis*. In view of all these somewhat convoluted correlations, it must be concluded that the above work provided no satisfactory age determination for the Mugrosa molluscan fossil band.

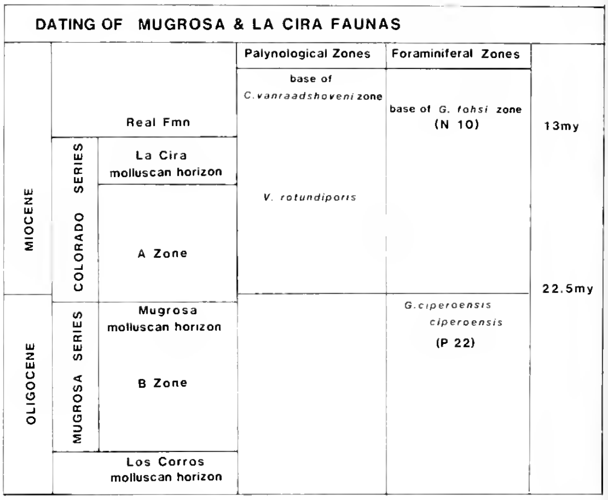


Fig. 445 Dating of Mugrosa and La Cira molluscan faunas. Correlation chart showing inferred relationship between molluscan-bearing strata and palynological zones, and hence with planktonic foraminiferal zones. The La Cira molluscan horizon lies somewhere within the Zone of *Verrutricolporites rotundiporis*, which in turn lies between N1 and N9. The base of the Zone of *Crassoretrilites vanraadshoveni* is thought to be rather younger than the La Cira fauna. The palynological evidence for dating the Mugrosa fauna is less satisfactory and gives an older age than is suggested by the molluscan evidence (see Fig. 3, p. 171).

LOS CORROS FAUNA, TOP ESMERALDAS FORMATION. The bulk of the Esmeraldas Formation lies within the zone of *Retitricolporites guianensis* and the overlying zone of *Verrutricolpites usmensis*, according to Germeraad *et al.* (1968: fig. 17, section 2, Rio Lebrija). The top of the Formation, which yielded the Los Corros molluscan fauna, is not shown and is therefore presumably younger than the *V. usmensis* Zone which, as shown above, is mainly Upper Eocene but probably also including small amounts of both the Middle Eocene and early Oligocene (Germeraad *et al.* 1968: 244; fig. 15).

The Los Corros molluscan fauna is therefore, on palynological evidence, more likely to be of some unspecified Oligocene age than to be late Eocene.

San Juan de Rio Seco fauna (Anderson 1928)

There is some question about the horizon and position of this locality. Anderson (1927, 1928) thought it was in the coal-bearing Guaduas Series, and gave no precise locality. Butler (1939) suggested that it was not part of the Guaduas Series and proposed the name '*Corbula hettneri* Horizon' for these strata. He placed Anderson's locality at km 106 on the Bogotá to Cambao highway (K 106), but without providing supporting evidence. He repeated this conclusion (1942), which was later accepted by de Porta (1965: 37; 1966: 168, 173) who assigned the *Corbula hettneri* horizon to his new Santa Teresa Formation (1965). In neither of his papers did

Butler produce any adequate explanation of how he came to decide that Anderson's locality lay near K 106. Butler commented (1939: 99) that he had not observed Guaduas coal nearby. His section showed the *Corbula hettneri* horizon outcropping near the core of a syncline, presumably that now known as the Guaduas–Jurusalen syncline. His map (1942: 173) showed K 106 some 7 km NE by N of San Juan de Rio Seco.

DATING OF LOS CORROS FAUNA

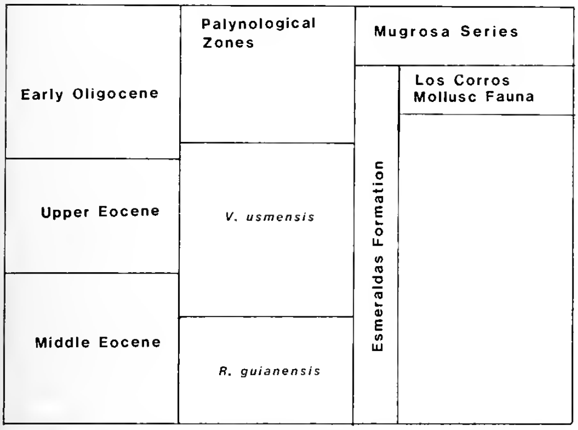


Fig. 446 Dating of Los Corros molluscan fauna. Correlation chart showing this fauna as being probably of some unspecified age later than the palynological Zone of *Verrutricolporites usmensis*, with the Zone of *Retitricolporites guianensis* as being distinctly older.

Anderson (1927: 599) regarded his fauna, collected by Downs McCloskey and Thomas Wark, as coming from the Guaduas Series. These he described as coal-bearing and carbonaceous beds, developed extensively in the Upper Magdalena Valley. He stated (1927: 604) that beds on Rio Sogamosa and upper tributaries of Rio Colorado (Middle Valley), and at San Juan de Rio Seco (Upper Valley), had yielded a fauna including *Ampullaria guaduasensis*, *Melanella magdalensis*, *Cyrena karsteni*, *Corbula hettneri* and numerous plant remains. This now appears to be a mixture of faunas from the two regions (see below). He also mentioned that similar beds and faunas were to be found a little to the east of Girardot. He argued (1927: 603) that the Guaduas series was Eocene, chiefly because of its stratigraphical position above the Guadalupe (of known Cretaceous age) and beneath presumably Miocene strata. He regarded (1927: 603, 1928: 13) the occurrence in Venezuela of similar coal-bearing beds which contained Eocene foraminifera as supporting his Eocene date for the Guaduas Series. Anderson had no palaeontological evidence for correlating his fossil locality of San Juan de Rio Seco with the true Guaduas Series.

The fauna from some 300 km further north in the Rio Sogamosa region of the Middle Valley of Rio Magdalena which Anderson referred to is likely to be from one of the horizons yielding the faunas later described in Pilsbry & Olsson (1935). The names in Anderson's list (1927: 604) quoted above are *nomina nuda*, and some were never to be formally described by him. He listed the following fauna as occurring in the Middle Valley (1928: 12): *Melania, Ampullaria, Corbula* and *Cyrena*. Later on the same page he listed the fauna from the Upper Valley at San Juan de Rio Seco (*Melanella karsteni* etc., see below). His reference to *Melania* is here interpreted as *Hemisinus*, whilst his *Cyrena* might well have been a reference to *Sogamosa cyrenoides* Pilsbry & Olsson. Both of these genera belong to families which are present in the Middle Valley faunas but not known from San Juan de Rio Seco.

Anderson also described in the same paper (1928) a large number of Colombian marine molluscs which were indisputably of Palaeogene age. He presented no evidence connecting the strata, from which these marine taxa were obtained, with the non-marine beds.

Anderson's type specimens are in CAS. These, and also a large sample (CAS 31695) have been re-examined. The latter yielded several hundred specimens of *Pachydon hettneri* (Anderson) and, in a separate container from possibly a different rock band, a few dozen examples of *Pachydon cebada* (Anderson). In this sample only three additional gastropods were found: unfortunately all were small and too poorly preserved even for superfamilial determination.

All the labels with the collection read 'from near San Juan de Rio Seco, East border of the Upper Valley of the Magdalena River, Colombia, from the lower part of the Guaduas Beds, not far from the horizon of the coal veins'. No additional information about Butler's (1939) views on this locality is present with the collection. It seems very unlikely that Butler ever saw this material.

Fig. 447 *Melanella karsteni* Anderson (1928). CAS 2722; holotype. Probably from the Miocene Santa Teresa Formation, at km 106 on the Cambao to Bogotá Highway; originally described as being from the Eocene Guaduas Beds near San Juan de Rio Seco; × 4.

Fauna from San Juan de Rio Seco, described by Anderson (1928).

original determinations	revised determinations
Melanella KARSTENI Anderson v (Fig. 447)	Family indeterminate, possibly Littoridininae
Ampullaria GUADUASENSIS Anderson v	*Verena guaduasensis* (Anderson)
Corbula HETTNERI Anderson v	*Pachydon hettneri* (Anderson)
Corbula CEBADA Anderson v	*Pachydon cebada* (Anderson)
Corbula scheibei Anderson v	partly *P. cebada*, partly indeterminate *Pachydon*.

Pachydon is characteristic of the Pebasian and associated faunas. *Pachydon hettneri* also occurs in the La Tagua fauna, which has several species in common with the Pebasian. *Pachydon cebada* (Anderson), see p. 311, is a senior synonym of *Corbula abundans* Pilsbry & Olsson (1935), which is common in the La Cira fauna of the Middle Magdalena Valley. The holotype and only specimen of *Verena guaduasensis* (p. 256) is decorticated and lacks sculpture. Its shape and size is reminiscent of the living Brazilian type species, *V. crenocarina* (Moricand), which is represented by extinct subspecies in the La Cira fauna.

On this new interpretation of the molluscan palaeontological evidence, it is clear that there is a reasonably strong correlation between the San Juan de Rio Seco, La Cira and La Tagua faunas. It seems probable that all three are more likely to be early Miocene than late Oligocene.

Los Corros fauna, Middle Magdalena Valley (Pilsbry & Olsson 1935)

This is the oldest of the three thin but persistent fossil horizons with non-marine molluscan faunas described in Pilsbry & Olsson (1935) from the east side of the Middle Magdalena Valley. It contains no species common to the faunas dealt with herein. However, some consideration of it is appropriate because of its stratigraphical position below the Mugrosa and La Cira Formations. Current usage (de Porta 1974: 228, 380) still follows the views of Pilsbry & Olsson in regarding the Los Corros fossil horizon as the uppermost part of the Esmeraldas Formation and as being Middle to Upper Eocene in age. De Porta's dating was based not only on the molluscan evidence, but also on the palynological evidence discussed above.

Pilsbry & Olsson's type specimens are in ANSP and some of them have been re-examined. From their text, it is clear that at least some material remained in private collections, including that of Olsson.

original determinations	**revised determinations**
Hemisinus (Basistoma) CORROSENSIS Pilsbry & Olsson v	*Hemisinus* (s.str.) *corrosensis* Pilsbry & Olsson
Potamides MCGILLI Pilsbry & Olsson	*Potamides* (s.lat.) *macgilli* Pilsbry & Olsson
DIPLOCYMA WHEELERI Pilsbry & Olsson v	no change
Diplocyma SUCIONIS Pilsbry & Olsson	no change
SOGAMOSA CYRENOIDES Pilsbry & Olsson	no change

The Los Corros fauna thus consisted of five new species. *Diplocyma* was assigned to the Potamidinae and *Sogamosa* to the Corbiculidae. This small assemblage would have lived in water of low salinity, or fresh. Potamidinae tolerate brackish conditions, but the Thiaridae (of which *Hemisinus* is a member) are virtually restricted to fresh water. The Corbiculidae also live mainly in fresh water but are sometimes estuarine, and larger shells may be washed out to sea (Keen 1971: 111).

Pilsbry & Olsson's dating of the Los Corros fauna as Eocene was based on very weak evidence. They (1935: 7) thought that *Tympanotonus lagunitensis* (Woods) from the Saman Eocene of western Peru belonged to their new genus *Diplocyma*. However, the type series of this species (Sedgwick Museum, Cambridge), originally described as *Potamides lagunitensis* by Woods (1922: 90; pl. 11, figs 10–12) from the Eocene Lobitos Formation of the Pacific coastal region of Peru, appears to lack the strong opisthocyrt collabral folding of the early whorls of *Diplocyma*. The adult sculpture is rather simple and consists of two spiral rows of tubercles spaced at about twelve to the whorl: this in no way resembles the sculpture of either of the Los Corros species assigned to *Diplocyma*. The apertural features, in common with those of *Diplocyma*, are unclear.

Pilsbry & Olsson compared none of their other new taxa with species occurring elsewhere. Their argument that the Los Corros was Eocene also appears to have rested on the fact that marine Upper Eocene rocks were very widespread in the coastal region of northern Colombia. They therefore advanced the proposition (1935: 7) that it was reasonable to believe that the non-marine equivalents of these rocks should occur in the Tertiary embayments so well exemplified by the deposits of the Magdalena Valley. Clearly this argument cannot be taken seriously, either as evidence for the correlation they suggest, unsupported by any species in common, or, for that matter, of a physical connection at that time between the basins in which these different sediments were laid down.

There appears to be virtually no palaeontological evidence for dating this small fauna. None of the taxa present have been found elsewhere. In addition, none show any particular resemblance to those occurring either in the overlying Mugrosa and La Cira or at San Juan de Rio Seco (Anderson 1928). At present, *Potamides* is a very loosely defined, and hence long-ranging, genus with a living type species. The identification of *Hemisinus* seems reasonably sound. The first occurrence of the genus cannot be pinpointed with any accuracy, however, as arguments as to the ages of most records tend to be circular. Its type species is Recent, and at the present day the genus occurs both in the Caribbean region and in South America; *H. corrosensis* is not dissimilar from several of these living species. The inference from this is that the Los Corros fauna might well be younger than originally supposed. The palynological evidence can be interpreted as suggesting that the age is probably early Oligocene rather than Eocene. What little is known of the molluscs would not be in disagreement with such a conclusion.

Mugrosa Fauna, Middle Magdalena Valley (Pilsbry & Olsson 1935)

original determinations	**revised determinations**
Hemisinus (Hemisinus) SIGMACHILUS Pilsbry & Olsson (Rio Llano, Block 10S–11E) v	*Hemisinus sigmachilus* (Pilsbry & Olsson)
Hemisinus (LONGIVERENA) HOPKINSI Pilsbry & Olsson (near El Centro)	*Longiverena eucosmia* (Pilsbry & Olsson)
Hemisinus (LONGIVERENA) EUCOSMIA Pilsbry & Olsson (well 660, depth 1803–1815) v	*Longiverena eucosmia* (Pilsbry & Olsson)
Hemisinus (LONGIVERENA) LAPAZANA Pilsbry & Olsson (near El Centro, 16S–8E)	*Longiverena eucosmia* (Pilsbry & Olsson)
Hemisinus (LONGIVERENA) MUGROSANA Pilsbry & Olsson (Rio Llano) v	*Longiverena eucosmia mugrosana* (Pilsbry & Olsson)

The Mugrosa fauna is thus reduced to two genera, both with living type species, of the fresh-water Thiaridae, each represented by a single species, one with a distinct subspecies. Three synonyms of *Longiverena eucosmia* are recognized above. In the overlying La Cira fauna two further synonyms of this species are thought to occur, *L. lacirana* (Pilsbry & Olsson), and more doubtfully the poorly preserved *L. waringi* (Pilsbry & Olsson). Most of these synonyms are known only from their (mainly different) type localities. Both *L. hopkinsi* and *L. lapazana* were collected from near El Centro by Wheeler and may well have been found together, and their type illustrations certainly show them to be very similar. It is suggested here that the variation that occurs in these *Longiverena* is almost certainly only of local significance. *L. eucosmia* is also recognized as occurring in the Pebasian of Iquitos

(*Semisinus peyeri* de Greve, 1938) and in the Loyola Formation of the Cuenca Basin (*Hemisinus peyeri dickersoni* Palmer, *in* Liddle & Palmer 1941). In addition, the very similar *L. colombiana* sp. nov. (p. 249) is described from the La Tagua fauna. *Hemisinus sigmachilus* is a smooth species, based on a broken specimen; it is similar to a *Hemisinus* occurring in the Mangán Formation of the Cuenca Basin, but the lack of distinctive characters makes positive recognition unwise. Similar species are found living.

Pilsbry & Olsson (1935: 8, 13) suggested that some of the Mugrosa Formation *Hemisinus*, such as *H. mugrosana*, were closely related to the group of species in this genus described by Brown & Pilsbry (1914) and by Cooke (1919) from the Antiguan and Cuban Oligocene. *H. antiguensis, H. latus* and *H. siliceus* were described from Antigua by Brown & Pilsbry (1914). Their illustrations of the first-named (1914: pl. 9, figs 1, 3, 5, 6) are of blocks of rock crowded with shells not showing any generic characteristics. The sculpture appears to be of numerous, close-set, opisthocyrt collabral ribs, whilst (1914: 210) two or three spiral cords are said to be present above the lower suture. This sculpture is not similar to that occurring either in *L. mugrosana* or in any of the other Magdalena Valley *Longiverena* discussed herein. *H. siliceus* is a typical, smooth *Hemisinus*. *H. latus* also appears to be smooth, but its type illustration (1914: pl. 9, fig. 4) does not show the aperture clearly so its generic determination cannot be confirmed.

Cooke (1919: 117–120; pl. 3) described several Cuban and Antiguan species which he assigned to *Hemisinus*. They belong to a mixture of genera. His illustration of *H. siliceus* (1919: pl. 3, fig. 3) is definitely of a smooth *Hemisinus*. His figures of *H. antiguensis* are not necessarily correctly identified and may not all be of one species: none resembles the Colombian specimens. None of the other species belongs to either *Hemisinus* or *Longiverena*. Two of his species, *H. costatus* and *H. bituminifer*, which Pilsbry & Olsson (1935: 13) compare with *L. mugrosana*, are misidentified at superfamilial level: both belong to the Epitoniidae, a fully marine family.

Hence this correlation with the Antiguan and Cuban Oligocene, which has never been challenged before, and is quoted by de Porta (1974: 425), must now be considered worthless. The molluscan evidence for the age of the Mugrosa Formation now rests on the two species recognized above. Their occurrences elsewhere are all in rocks now thought to be no older than Miocene. The recognition of *L. eucosmia* in the La Cira Formation suggests that the Mugrosa is not much older.

La Cira fauna, Middle Magdalena Valley (Pilsbry & Olsson 1935)

Fourteen molluscan species were all described as new by Pilsbry & Olsson from the La Cira formation of the Middle Magdalena Valley. Wheeler (1935: 34) gave no details of the several fossil beds he encountered. From the rather sparse locality data, coupled with information on the different collectors (Pilsbry & Olsson 1935), it would seem that at least five minor, and apparently almost mutually exclusive, faunal associations are present (see below). The degree of overlap is not known. To give one example, the type locality of *Potamopyrgus laciranus* was quoted (1935: 9) as near Zopffs, La Cira district. They wrote that it occurred at many other localities in the La Cira district, being quite abundant in the La Cira haematitic sandstones with *Corbula abundans* and *C. magdalensis*. Whether any of these three species occur with any others is not entirely clear from the remainder of their paper.

All species listed below were described as new by Pilsbry & Olsson (1935). Authors' names are therefore omitted from the first column. Omission of authors' names from the second column implies no change in nomenclature, either at generic or specific level.

original determinations	**revised determinations**
Hemisinus (LONGIVERENA) WARINGI	*Longiverena* cf. *eucosmia* (Pilsbry & Olsson)
Hemisinus (LONGIVERENA) LACIRANA	*Longiverena eucosmia* (Pilsbry & Olsson)
Hemisinus (Verena) AVUS v	*Verena crenocarina ava* (Pilsbry & Olsson)
Hemisinus (Verena) LAEVICARINA v	*Verena crenocarina ava* (Pilsbry & Olsson)
Hemisinus? GRACILLIMUS	family uncertain
Potamopyrgus LACIRANA v	*Dyris lacirana* (Pilsbry & Olsson)
Triplodon LATOURI	*Diplodon (Ecuadorea) latouri* (Pilsbry & Olsson)
Diplodon (Rhipidodonta) OPONCITONIS	*D. (R.) oponcitonis*
Monocondylaea? MARSHALLIANA	*M.? marshalliana*
Anodontites LACIRANA	*A. lacirana*
Mytilopsis CIRA	*Mytilopsis scripta* (Conrad)
Corbula (Corbula) ABUNDANS v	*Pachydon cebada* (Anderson)
Corbula (Erodona) MAGDALENSIS v	*Pachydon cebada* (Anderson)
Ostomya colombiana	*Guianadesma colombiana* (Pilsbry & Olsson)

Comparatively few of the above species have been studied herein. The naiades, for instance, have been omitted because they are not comparable to species found in either the La Tagua or the Pebasian faunas. From references to the La Cira fossil band (Wheeler 1935, Butler 1939, 1942, de Porta 1966), many of these species would seem to be both abundant and widespread. These authors comment on the poor state of preservation of most fossils seen in the field. This explains the paucity of material in institutional collections. The following associations are recognized herein:

(1a). Near Zopffs, La Cira district (Waring Colln). *Dyris lacirana*, *L. eucosmia* (as *H. (L.) waringi*), *V. crenocarina ava* (as *avus*).
(1b). 7700N–4600W, Station West of Zopffs (Waring Colln). *Hemisinus? gracillimus*.
(2a). Haematitic sandstone near La Cira (? Waring Colln). *Dyris lacirana, Pachydon cebada* (as both *C. abundans* and *C. magdalensis*).
(2b) Near La Cira, square mile 1N–9E (Wheeler Colln). *L. eucosmia* (as *H. (L.) laciranus*).
(3) Rio Oponcito, near Guanabanas (Ollson & La Tour Colln). *V. crenocarina ava* (as *laevicarina*), *T. latouri*, *D. (R.) oponcitonis*, *M. marshalliana*, *A. lacirana*, *M. cira*, *G. colombiana*.

These different associations, collected by different people from different places, immediately raise the possibility that the concept of the La Cira fossil band, occurring at the top of what is nowadays referred to as the Colorado Formation, is a gross over-simplification of the situation. The presence of *L.*

waringi in (1a) suggests that *L. eucosmia* does indeed occur at an horizon other than in the Mugrosa Formation. In (2b), this species occurs by itself: as it does usually in the Mugrosa Formation. Association (3) contains all the fresh-water naiades reported from the formation. *Verena* is also thought to be exclusively fresh-water. However, both *Mytilopsis* and *Guianadesma* tolerate brackish conditions. Both (1a) and (2a) also contain a mixture of fresh and brackish water species. The only species at (2b) is the fresh-water *L. eucosmia*. The true generic, or even familial, position of *Hemisinus? gracillimus* is unknown, so nothing can be deduced about the facies of (1b), beyond the unlikelyhood of it being marine.

Pilsbry & Olsson (1935: 8) suggested that the La Cira Fauna was either Upper Oligocene or Lower Miocene. They argued that if the Mugrosa was Middle Oligocene, then the La Cira could not be older than Upper Oligocene, but there seems to be no good reason why the two have to be separated in age in this way. They apparently raised the possibility of a Lower Miocene age for the La Cira on the grounds that all the genera were still living. However, both *Hemisinus* and *Longiverena*, the only two genera occurring in the Mugrosa Formation, are also living.

There is comparatively little molluscan evidence as to the age of the La Cira associations. *Pachydon cebada* (Anderson) occurs in the San Juan de Rio Seco fauna of Anderson (1928), which also contains *P. hettneri* (Anderson) now recorded from La Tagua. A rather more tenuous link between Anderson's locality and the La Cira fauna is provided by the occurrence in both of not very well preserved specimens of *Verena* which bear some resemblance to the living type species *V. crenocarina*. If these two faunas are the same age as the La Tagua fauna, then they are most probably Neogene. Such an age is also suggested by the presence of *L. eucosmia*, which is here shown to occur in the Pebasian of the Amazon Basin and in the presumed Miocene of the Cuenca Basin, Ecuador. It should be stressed, however, that these correlations are based on a very few species in common, occurring, for the most part, in rather small faunas, which have a greater number of species not common to other faunas. The situation in the true Pebasian Basin is very different. There, the faunas are usually richer, and comparatively large suites of fossils may be found occurring at several localities which are not, admittedly, normally separated by such great distances.

Fauna of La Dorada district, Magdalena Valley (Butler 1942)

Butler's fauna (1942: 803), which he correlated with the La Cira, came from a short distance west of the junction of the Puerto Liévano and Puerto Salgar spurs of the Cundinamarca Railroad, perhaps 6 km NE of La Dorada. He stated that it was rich in bivalves and tentatively identified *Corbula*, 'possibly some *Hemisinus* forms, *Ostomya* sp.(?), and fish teeth'. He described the aspect of the fauna as being strikingly similar to that of his *Corbula hettneri* Horizon. However, Thiaridae, such as *Hemisinus* and *Longiverena*, have yet to be reported from that Horizon. Butler also felt that the general faunal aspect, lithological character and stratigraphical position of his locality were similar to that of the La Cira Formation in the Middle Valley. He stated that several fossil beds, rich in *Hemisinus*, occurred in creeks to the south of the railroad. Whatever doubts there may be about Butler's identifications, he must almost certainly have been dealing with a fauna containing both the brackish-water *Pachydon* and members of the fresh-water Thiaridae.

This fauna came from strata assigned by Butler (1942) to the Colorado Series. The immediately overlying beds in this area, which Butler regarded as part of the Honda Series, have since been named the La Dorada Formation (Wellman 1970: 2356–2357).

Fauna of Quebrada el Tabaco, Santa Teresa Formation (de Porta 1966)

De Porta listed a small fauna from this locality in the San Juan de Rio Seco district, although he was unable to establish the field relationship between it and Anderson's (1928) fauna. He (1966: 172) identified *Anodontites laciranus, Diplodon (Rhipidonta) oponcitonis* and *Hemisinus (Longiverena) waringi*, all of which were described by Pilsbry & Olsson (1935) from the La Cira Formation of the Middle Magdalena Valley.

These records show that non-marine faunas similar to those of the Middle Valley occur in the Upper Valley of the Magdalena. They also serve to confirm the molluscan palaeontological evidence that Anderson's fauna, which possesses species in common with both the La Cira and La Tagua faunas, is much younger than at first thought.

Inter-Andean basins, Ecuador

Reference should be made to the annotated bibliography of Ecuadorian geology (Bristow 1981), which postdates the Lexique (Bristow & Hoffstetter 1977).

Tertiary rocks outcrop over vast areas of the Oriente in Ecuador and there are reports of un-named non-marine molluscs occurring in them (Tschopp 1953). In contrast, the geology and palaeontology – particularly of molluscs – of the inter-Andean basins are comparatively well documented and have recently been reviewed in some depth (Bristow & Parodiz 1982). As is discussed below, the faunas are predominantly fresh-water, and the evidence of brackish conditions, though definite, is less than in most of the other faunas considered in the present work. Of particular importance is their report of a radiometric dating (1982: 8) of 19–20 million years for an andesite immediately underlying the Loyola Formation which has yielded by far the richest molluscan fauna. Their paper is divided into two parts. The first, by Bristow, describes the geology of all the Ecuadorean inter-Andean basins and reviews other non-marine deposits of neighbouring regions. The second part, by Parodiz, describes the molluscan faunas, which include many species known from earlier works. The large collections which Parodiz studied were made by Bristow and were split between the Carnegie Museum, Pittsburgh and BMPD. Other material in BMPD are some duplicates of *Sheppardiconcha bibliana* Marshall & Bowles, 1932, collected by Sheppard himself, who wrote on the geology (1934). The main part of Sheppard's collection, including type material, is in USNM. There are also in BMPD a few samples collected in 1926 by Professor C. Carrion, including some slabs of well-bedded marl with moulds of *Dyris* aff. *tricarinata* (Boettger) recorded by Bristow & Parodiz (1982: 16) as *D.* cf. *gracilis*, 'form' *carinata*. Palmer (*in* Liddle & Palmer 1941) described a large collection of fossils from the Cuenca Basin made by Liddle. These are now in PRI. There are thus fairly large collections of fossils from these basins in several institutions.

In the BMPD collections, a few taxa such as *Sheppardiconcha* *bibliana* Marshall & Bowles, *Diplodon (Ecuadorea) bibliana* Marshall & Bowles and *Neocorbicula cojitamboensis* (Palmer) are very common from several localities. In addition, at some horizons, there are bedding planes crowded with small hydrobiids. The three above-named species are indubitably of fresh water origin, though the hydrobiids could be from brackish water. However, of the thirty species recognized by Bristow & Parodiz (1982), most appear to be rare. Moreover, the vast majority of specimens are so poorly preserved that confident identification is seldom possible. These are not easy faunas with which to work.

No attempt is made here to revise the faunas described in Bristow & Parodiz fully. Species dealt with are those which are thought to occur in other faunas under consideration, or which appear to be closely related to relevant taxa. The result of this partial revision is that, with one exception, all the species from the Cuenca Basin said to occur in other faunas are now thought not to do so, having been misidentified in Bristow & Parodiz. The exception is *Aylacostoma peyeri dickersoni* (Palmer), now placed in the synonymy of *Longiverena eucosmia* (Pilsbry & Olsson), which occurs in both the Mugrosa and La Cira faunas of the Middle Magdalena Valley, Colombia as well as in the Pebasian of Iquitos.

In both the Mangán and Biblián Formations clays and shales alternate with arenaceous beds. Shales predominate in the Loyola succession. The fossil samples from the San Cayetano Formation are of moulds, mainly external, of small species on bedding planes in a creamy marl. The Tumbatú Formation samples are flat slabs of a monospecific shell limestone. The arenaceous beds of these inter-Andean basins are often crowded with fossils, usually belonging to only one of the few commonly occurring species. Such lithologies may well represent periods of extremely rapid deposition and have no exact parallel in any of the samples encountered from the Pebasian and La Taguan collections studied here.

Below, the faunas described in Bristow & Parodiz (1982) are reviewed in order.

Chota Basin, Tumbatú Formation

Bristow & Parodiz recorded (1982: 5, 40) only one molluscan species from the entire basin, which they identified both as *Liris minuscula* and *L.* aff. *minuscula* (Gabb). *L. minuscula* was originally described from Pebas, and the genus *Liris* has otherwise never been recorded from outside the Pebasian Basin. This material, BMPD GG19807–8, is regarded here as belonging to a rather variable, un-named, species provisionally assigned to *Liris* and dealt with in the systematic section herein (p. 208). Bristow & Parodiz also (1982: 40) referred to it as occurring in the San Cayetano Formation, but did not mention it in the appropriate stratigraphical section of their paper (1982: 16). No specimens to support this second record are present in BMPD.

Bristow & Parodiz did not formally suggest a date for the Tumbatú Formation, except that they thought the Pebas deposits were probably Upper Miocene to Lower Pliocene. Any implied correlation is obviously much weakened by the rejection of their specific determination. These authors also appeared to accept comments by Hall (*in* Bristow & Hoffstetter, 1977: 268) that similarities existed between bentonitic shales of the Tumbatú and Mangán Formations of the Cuenca Basin and also that similar lithologies occurred in the Arajuno, Curaray and Upper Pastaza Formations of the Ecuadorian Oriente. All these formations, including the Mangán, they assumed to be Upper Miocene. However, as is pointed out herein, there is no good palaeontological evidence yet available for dating these strata of the Oriente. Furthermore, correlation based on similar lithologies cannot be considered definite. The Tumbatú Formation is almost certainly Neogene, but evidence is lacking for any more precise age determination. *Liris* could be either from brackish or fresh water.

Cuenca Basin, Mangán Formation (dated as Upper Miocene by Bristow & Parodiz, 1982)

They (1982: 14) listed a fauna of two bivalve and five gastropod species from this formation. Species which they also report from the Loyola Formation are indicated thus *.

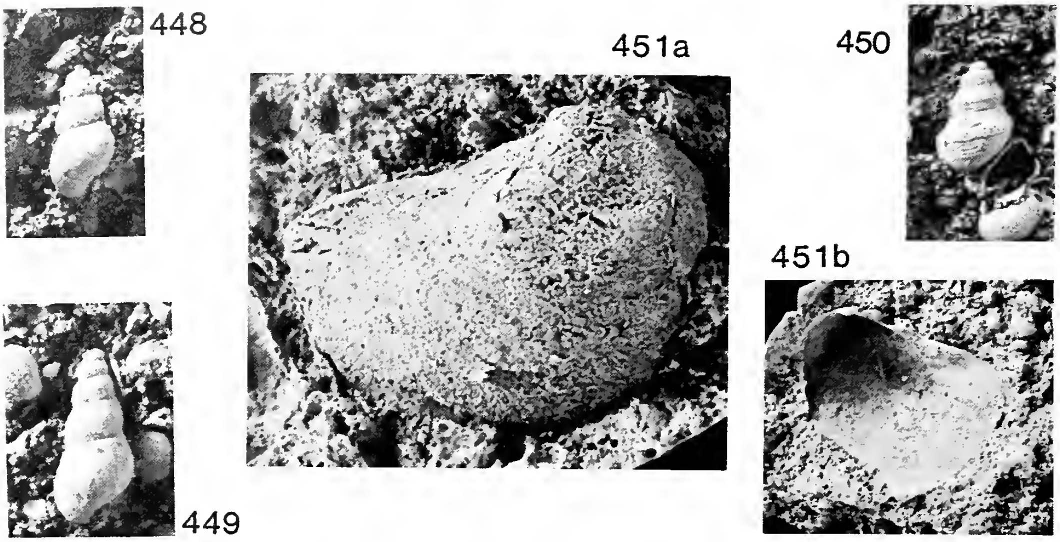
original determinations	**revised determinations**
Fossula cf. *derbyi* (von Ihering)	not revised
Neocorbicula cojitamboensis (Palmer) *	*Corbicula cojitamboensis* Palmer
Doryssa bibliana (Marshall & Bowles) *	*Sheppardiconcha bibliana* Marshall & Bowles
Aylacostoma browni (Etheridge)	*Aylacostoma* sp.
Aylacostoma sulcata (Conrad)	*Hemisinus* sp.
Neritina pacchiana Palmer *	accepted
Palaeoanculosa KENNERLYI sp. nov.	accepted

The ostracod *Vetustocytheridea bristowi* van den Bold (1976) was described from the Cuenca Basin, occurring in both the Mangán and Loyola Formations. Van den Bold did not clearly state the known range of the genus, but indicated that other species occurred in the early Miocene of the Gulf and Caribbean areas.

Although not in their faunal list (1982: 14), Bristow & Parodiz described and figured (1982: 41, fig. 16) a specimen which they identified as *Toxosoma eborea* Conrad, the only described species of the genus, which is known only from the Pebasian. Their figured specimen is not well preserved, but it shows clear signs of collabral folding, whilst *T. eborea* is smooth, and is almost certainly misidentified at generic as well as specific level. The specimen, BMPD GG19816, comes from the Loyola Formation (Loc. CRB 36) and not the Mangán Formation (CRB 26b) as they stated. It is presumably the source of their reference (1982: 18, table 2) to this species.

Both *Verena browni* (Etheridge) and *Hemisinus sulcatus* Conrad, which is herein assigned to the living species *H. brasiliensis* (Moricand) (see p. 244), occur in the Pebasian, but BMPD specimens from Mangán locality CRB 42, upon which Bristow & Parodiz' determinations were based, are now shown in the systematic section not to belong to these species. Their specimen of '*Aylacostoma browni*' from the Loyola Formation (GG19869) belongs to a different species, *Sheppardiconcha bibliana*. The Mangán fauna now appears to be endemic to the Cuenca Basin, with the possible exception of *F.* cf. *derbyi*, which they compared with specimens of unknown age from Rio Grande do Sul, Brazil (Bristow & Parodiz 1982: 14).

Bristow & Parodiz dated the Mangán Formation as Upper Miocene because it was separated by about 1800 m of sediments from the underlying Loyola Formation, which has several species in common and which they thought was Middle Miocene. In spite of the changes in identifications, it would appear that the Mangán Formation, yielding the



Figs 448–451 Miocene fossils from the Cuenca Basin, Ecuador; Bristow Colln. **448–450**, from well-bedded mudstone at Loc. CRB 11, Loyola Formation; all × 10. **448**, **449**, GG19814/1, 2; *?Dyris* sp., probably the species listed as *Lyrodes* sp. in Bristow & Parodiz (1982: 7). **450**, GG19814/3; indeterminate Hydrobiidae, *?Dyris* sp., probably the species identified as *Hydrobia ortoni* in Bristow & Parodiz (1982: 7). **451**, LL27817; *Corbicula (Cyanocyclas) cojitamboensis* Palmer. The specimen identified as *Erodona iquitensis* in Bristow & Parodiz (1982: 10, 31, but *not* that illustrated in their fig. 8); Loc. CRB 7, Basal Loyola Formation. Latex casts; a, external view of left valve, × 4 (interpreted as right valve in Bristow & Parodiz); b, internal view of left valve, × 2. See p. 315.

common *C. cojitamboensis* and *S. bibliana*, is likely to be fairly similar in age to the richer Loyola Formation. In an area of predominantly coarse sedimentation, the strata intervening between these two formations may well have been deposited fairly rapidly, so there is no real reason to postulate that the Mangán Formation is much younger than the Loyola.

Neritina can occur in fresh water, but is the only genus in this fauna which also has brackish and marine species. The remaining taxa are of exclusively fresh-water families.

Cuenca Basin, Azogues and Guapán Formations (dated as Middle Miocene by Bristow & Parodiz, 1982)

They (1982: 7, 11–12) recorded only three molluscan species from these formations. Both *Corbicula cojitamboensis* and *Aylacostoma* cf. *dickersoni* (=*Longiverena* cf. *eucosmia* herein) are known from other formations in the Cuenca Basin, whilst *Diplodon* sp. belongs to a genus common in the basin. All three indicate a fresh-water environment.

Cuenca Basin, Loyola Formation (dated as upper part of Lower Miocene by Bristow & Parodiz, 1982)

Of particular importance is the radiometric dating by Snelling (1974, unpublished report of Brit. Geol. Surv.; see Bristow & Parodiz, 1982: 8) of the Descanso andesite, which immediately underlies the Loyola Formation, at 19–20 million years. This is equivalent to Lower Miocene, late Aquitanian, Zone N5, and may be regarded as the maximum possible age for the formation.

The Loyola molluscan fauna is by far the richest from the Cuenca Basin. The biota includes plants (leaves, pollen and the almost ubiquitous *Chara*). Fish remains and the endemic ostracod *Vetustocythiridea bristowi*, which also occurs in the Mangán Formation, are also present. Bristow & Parodiz (1982: 11) argued that perhaps the best independent date for the Loyola Formation was the identification of the crab, *Necronectes proavitus* (Rathbun, 1919), originally described from the Gatun Formation of Panama which they stated was Middle Miocene. This age determination, however, must be revised in the light of new work. J. E. P. Whittaker (BMPD, unpublished report) has dated as probably N17 (Upper Miocene) the planktonic foraminifera obtained from Gatun clay, mainly extracted from mollusc shells provided by myself and the late W. P. Woodring (USGS). As the ages of many other formations in the same general area are frequently fixed by reference to the Gatun, they also may be due for revision. The potential age range for the Loyola Formation is thus widened to include the Upper Miocene. The presence of this crab, if correctly determined even at only generic level, occurring so far from its normal area of distribution, may be taken as evidence for some connection between the Cuenca Basin and the Panamic-Pacific marine province during the Neogene. (The crab was also recorded from other supposed Middle Miocene strata of the Caribbean area (Collins & Morris 1976: 125, *cum syn.*), but new information on the age of these latter occurrences is not available.)

Twenty-six molluscan taxa were listed from the Loyola Formation by Bristow & Parodiz (1982: 10).

original determinations	**revised determinations**
Diplodon (Ecuadorea) guaranianus biblianus (Marshall & Bowles)	*Diplodon (Ecuadorea) biblianus* (Marshall & Bowles)
Diplodon (Ecuadorea) BRISTOWI sp. nov.	accepted
Diplodon (Ecuadorea) liddlei (Palmer)	not checked
Monocondylaea azoguensis (Palmer)	not checked
Monocondylaea pacchiana (Palmer)	not checked
Monocondylaea sp.	not checked

original determinations	**revised determinations**
Anodontites olssoni (Palmer)	not checked
Pisidium sp.	not checked
Neocorbicula cojitamboensis (Palmer)	*Corbicula cojitamboensis* Palmer
Erodona iquitensis (de Greve)	*Corbicula cojitamboensis* Palmer
Ostomya cf. *fluviatilis* (H. Adams)	indet. ?bivalve
?Calliostoma sp.	not checked, determination extremely unlikely even at superfamilial level
Neritina LOYALAENSIS sp. nov.	accepted
Neritina pacchiana Palmer	accepted
Neritina sp.	not checked
Puperita aff. *sphaerica* (Olsson & Harbison)	probably indet. *Neritina*
Poteria (Pseudoaperostoma) bibliana (Marshall & Bowles)	not checked
Pomacea (Limnopomus) manco Pilsbry	not checked
Hydrobia ortoni (Gabb)	indet. ? Hydrobiidae
Lyrodes sp.	possibly *Dyris*
Potamolithoides biblianus Marshall & Bowles (*not* Conrad as stated)	accepted
Aylacostoma browni (Etheridge)	GG19869 from CRB 18 is possibly *Sheppardiconcha bibliana*. Note that Mangán specimens are *Verena*
Aylacostoma dickersoni (Palmer)	*Longiverena* cf. *eucosmia* (Pilsbry & Olsson)
Doryssa bibliana (Marshall & Bowles)	*Sheppardiconcha bibliana* Marshall & Bowles
Gyraulus sp.	not checked
Succinea sp.	not checked

The ostracod *Vetustocytheridea bristowi* van den Bold is also present. It is discussed briefly under the Mangán Formation, in which it also occurs (p. 339).

Specimen BMPD LL27817, from CRB 7, was identified in Bristow & Parodiz (1982) as *Erodona iquitensis* and is treated fully in the systematic section under *Pachydon iquitensis*, p. 315. It is here reidentified as *Corbicula cojitamboensis* Palmer, a common species in the Loyola Formation. Had its original identification been correct, this would have been the only record of Pachydontinae in the Cuenca Basin. LL27812, from CRB 26, identified as *Ostomya* cf. *fluviatilis* is also misidentified. It is not certain that it is a bivalve. *Puperita sphaerica* was described by Olsson & Harbison (1953) from the Pliocene of Florida. The greatly enlarged illustration (Bristow & Parodiz 1982: fig. 13) is barely recognizable as a neritinid, and certainly should not be taken as evidence for the presence of this particular species. Small Hydrobiidae occur quite commonly on bedding planes on blocks of gray shale (CRB 7, 11) along with small, uncommon, specimens of a corbiculid, which could be *Pisidium* sp. (s.lat.). The Hydrobiidae might be referrable to *Dyris* or *Lyrodes*, or both, but no specimens suggestive of the Pebasian *Dyris ortoni* (Gabb) have been seen (Bristow & Parodiz 1982: 39).

It thus becomes apparent that the molluscan fauna of the Loyola Formation is nearly all endemic. Possible exceptions are *Pomacea manco*, originally described from poorly preserved material from the Pachitea River Red Beds (Pilsbry 1944) and *Longiverena eucosmia* (Pilsbry & Olsson, 1935) known from the Mugrosa and La Cira fossil horizons of the Middle Magdalena Valley of Colombia and from the Pebasian of Iquitos. Three genera in the Loyola fauna, *Diplodon (Ecuadorea), Monocondylaea* and *Neritina* are each represented by three species: the quality of the material is such that it is difficult to be sure that these are all distinct.

This reassessment of the Loyola fauna shows that there is little direct palaeontological evidence as to its age. The radiometric age determination places a lower limit of Lower Miocene, whilst the presence of *Necronectes proavitus*, *Longiverena eucosmia*, and perhaps *Vetustocytheridea bristowi*, suggest that a post-Miocene age is highly unlikely.

As in the case of the Mangán Formation, the only family with some brackish and marine members is the Neritidae, though some species of *Neritina* are from fresh water. *Succinea* is a land pulmonate gastropod. All the other molluscs belong to exclusively fresh-water families.

Cuenca Basin, Biblián Formation (dated as lower part of Lower Miocene by Bristow & Parodiz, 1982)

The Biblián Formation has yielded (1982: 8) two species of molluscs, *Diplodon (Ecuadorea) bibliana* and *Sheppardiconcha bibliana*, both of which occur in the overlying Loyola Formation. Both species are indicative of fresh water. Its stratigraphical position below the Loyola, coupled with the occurrence of these two species, suggests that Bristow & Parodiz' age determination is likely to have been correct.

Loja Basin, San Cayetano Formation

This is the only other formation from which Bristow & Parodiz recorded fossil molluscs (1982: 16, 41). The specimens they cited as *Dyris gracilis* Conrad and 'form' *tricarinata* (Boettger) are dealt with here in the systematic section, under *Dyris tricarinata* (Boettger), p. 191. *Dyris gracilis* is very different from these San Cayetano specimens, which are preserved as external moulds on bedding planes of marl. The preservation is such that this determination must be slightly indefinite. Nevertheless, this is one of the least controversial records of Pebasian species from the Inter-Andean Basins of Ecuador. The age indicated by this gastropod cannot be determined closer than Neogene. *Dyris*, which is extinct, could be indicative of either fresh or brackish water.

In both the Loja and Malacatos Basins, there is said to be (Bristow & Parodiz 1982: 16) a conformable upward passage from the Trigal Formation to the San Cayetano Formation. The molluscs are recorded from the Loja Basin, but from the Malacatos Basin there is one Trigal sample said to contain the ostracod *Cyprideis stephensoni* Sandberg, 1964. On this occurrence, Bristow & Parodiz dated the Trigal Formation as Miocene. The species is recorded by van den Bold (1976: 6) as occurring in probably the uppermost Middle Miocene of Louisiana and the Culebra Formation of Panama. This identification, if correct, must be taken as indicating a likely Miocene age for the conformable San Cayetano Formation, and is also additional evidence for some connection between the Cuenca Basin and the Caribbean.

Oriente of Ecuador

Bristow (1981) should be consulted for further references.

Tschopp (1953: 2345) suggested that a Tertiary succession of up to 5000 m of rock laid down in fresh to brackish waters disconformably overlies a slightly eroded series of Cretaceous marine rocks in the Oriente of Ecuador. He dealt (1953: 2338, and stratigraphical sections in text-figs 4–6) with three formations which he regarded as Miocene, and from which, among other biota, he reported the presence at several levels of unnamed non-marine molluscs. Few details were given, but the clays of the Upper Arajuna (and possibly also the Upper Pastaza Formation – the wording is ambiguous) in the Vuano area were thought to have been laid down under conditions which allowed abundant plant life in rivers and swamps populated by turtles and fresh-water molluscs.

The overlying Curaray Formation of almost horizontal clays and sandstones exposed east of 76° 30′ W, between Rio Napo in the north and Rio Conambo in the south, contains lignitic seams and coaly black clays. It has yielded a fauna with crustacean and fish remains, turtles, crocodiles represented by both bones and teeth, as well as the remains of other unspecified vertebrates. Molluscs were an important element of the fauna and both arenaceous foraminifera and ostracods were also present. Of possible significance is the record of an ostracod similar to *Vetustocyprideis bristowi* van den Bold (1976) from this formation (Bristow 1973: 34; Bristow & Hoffstetter 1977: 108): the type strata of the species (*sensu stricto*) is the basal Loyola of the Cuenca Basin.

In his section on correlation, Tschopp (1953: 2339) briefly mentioned the similarities which he thought existed between these formations and those of other regions, but without giving detailed reasons. He suggested that both the Arajuno and Upper Pastaza Formations were comparable to the Honda of the Magdalena Valley of Colombia, whilst the Curaray showed affinities with the Colombian Miocene. It is difficult to assess his views as he did not suggest which of the numerous formations from widely different areas he had in mind when referring to the Colombian Miocene. Furthermore, the Honda Formation of the Upper Magdalena Valley is accepted as being of Miocene age by most authors: it is considered to be later than both the La Cira fossil band of the Middle Magdalena Valley and also its possible equivalent the *Corbula hettneri* Horizon of the Upper Valley (Butler 1942). Tschopp also suggested that part of the Contamana Group of Peru (Kummel 1948: 1254 *et seqq.*) might be the equivalent of all three of these formations of the Ecuadorean Oriente.

The age determinations that Tschopp gave for both older and younger Tertiary formations in the same region are all based on similar arguments. No palaeontological evidence was advanced as confirmation of the suggested ages. Some ostracods and arenaceous foraminifera were named, but were not used for correlation with strata whose ages had been established. The only definite limits on ages of the Tertiary sequence in the Oriente are set by the marine Cretaceous below and the present day above. It follows that without examining fossils from these formations, little can be deduced as to their age from Tschopp's account. The whereabouts of Tschopp's collection of fossils is unknown and he did not indicate whether anybody else had examined them. It seems reasonable to accept, however, that fresh to brackish sedimentation occurred in the Oriente of Ecuador during the Tertiary, probably whilst other formations considered herein were being deposited. Somewhat surprisingly, Tschopp made no reference to the Tertiary of the Cuenca and other inter-Andean basins of Ecuador.

Bristow & Hoffstetter (1977: 17 (fig. 3), 35, 107, 229) placed all three of the formations discussed here into the Upper Miocene, but the only new palaeontological evidence that they presented appears to be the reference to the ostracod *V.* aff. *bristowi* mentioned above. Campbell (1970: 20–22) also briefly reviewed Tschopp's work. He, too, concluded that there was no firm palaeontological evidence available with which these Tertiary deposits of the Oriente might be dated. His most significant observation was that they predated the late Andean orogeny: this argument is taken up below (p. 352) in discussing the palaeogeography.

Venezuela

No large faunas of Tertiary non-marine molluscs have been described from Venezuela, but there are several records, mainly of isolated species, which suggest a definite link between the present Caribbean coast and the Amazon Basin during the Neogene.

Late Cainozoic of Monogas

Palmer (1945) described nine species from east of La Llanera in the State of Monogas. Her discussion (1945: 7–8) showed that, in Norman Weisbord's opinion, her locality might be the equivalent of the Quiriquire Formation, whose type area appeared to be some 50 km distant from La Llanera. On these grounds they both concluded that the fauna was likely to be Pliocene, or less probably Pleistocene. Petzall *et al.* (1978: 529–530) date this formation as Lower Miocene. More importantly, although they mention the presence of non-marine molluscs, they do not refer to Palmer's fauna. It seems likely, therefore, that the latter is no longer regarded as being from this formation. Most of Palmer's species have not been revised herein as they have little bearing on the present work.

original determinations	**revised determinations**
Hyria trinitaria Maury (1925*b*)	not revised
Hyria WEISBORDI sp. nov.	not revised
Prodiplodon TIPSWORDI sp. nov.	*Diplodon tipswordi* (Palmer)
Castalioides laddi Marshall, 1934.	*Diplodon (Ecuadorea) bibliana* (Marshall)
Corbicula (Cyanocyclas) DESOLAI sp. nov.	not revised
Corbicula (Cyanocyclas) MONAGASENSIS sp. nov.	not revised
Ostomya MENCHERI sp. nov.	*Guianadesma sinuosum* (Morrison)
Asolene QUATALENSIS sp. nov.	not revised
'Planorbis' LLANERENSIS sp. nov.	not revised

The type occurrence of *Hyria trinitaria* is from Trinidad, said to be Pliocene (Maury 1925*b*: 235 (83); pl. 24 (13), fig. 2). *Castalioides laddi* Marshall (1934) was described from the Venezuelan Neogene as a new species and genus. *Castalioides* certainly appears to be a synonym of one of Marshall's numerous other naiad genera, *Ecuadorea*, which is now placed as a subgenus of *Diplodon*. *D. (E.) laddi* cannot be confused with the living *D. (E.) pazi* (Hidalgo). Parodiz (1969: 66) placed the former in the synonymy of *Ecuadorea bibliana* from the Miocene of the Cuenca Basin of Ecuador, with which I agree, even though the Cuenca Basin material is seldom well enough preserved to show all the details of shell sculpture.

Guianadesma sinuosum is dealt with in the systematic section, p. 319. It is living in the rivers of Guiana and Surinam and can tolerate slightly brackish conditions. Palmer (1945: 21–22) said her species was more similar to this living form and to those from the Pebas beds than to the older fossil species. Although true *Ostomya* was described from the

Pebasian, it has no close resemblance to *Guianadesma*. *Ostomya colombiana* Pilsbry & Olsson (1935) from the La Cira beds of the Middle Magdalena Valley of Colombia is here (p. 319) placed in *Guianadesma*, but it is too small and characterless to be usefully compared with the Venezuelan specimens.

It is not possible to give a precise age determination for this small fauna as only three out of the nine species present occur elsewhere. Although clearly Neogene, the further records, as discussed above, of those three species provide conflicting evidence as to the age.

Rutsch (1952), in a short paper, drew attention to the first occurrence of *Pachydon* of which he was aware from outside the Upper Amazon Basin. He had been shown by Leuzinger material in the collection of the Mene Grande Oil Company in Venezuela, and, on his return to Switzerland, had examined the collection from Iquitos in PIMUZ described by de Greve (1938). He concluded that well-preserved *Pachydon carinatus* Conrad definitely occurred in the 'La Puerta' Formation of Zulia and Miranda and that perhaps *P. cuneatus* Conrad occurred in the Yucales formation of the Santa Ines Group of Monogas and Guarico, as well as in Aragua. Petzall *et al.* (1978: 344) referred the La Puerta Formation to the Upper Miocene, whilst the Yucales Formation was regarded as invalid. Salvador (1964: 194) argued that the name, which had first been used by Leuzinger in Mene Grande Oil Company reports, might apply to various strata ranging in age from Oligocene or Lower Miocene up to Pliocene. No further references to the record of *P. carinatus* have been found, and although the records of *?P. cuneatus* are referred to by both Padrón (1956: 677–678) and by Tello (1975: 356), neither author added any new information. As well as the rather unsatisfactory nature of the original information, on both localities and stratigraphy, there is one further difficulty. Rutsch's paper, unfortunately, was unillustrated, so these most interesting records cannot be checked.

Jung (1965) described a marine fauna of 146 species from the Cantaure Formation of the Paraguana Peninsula, which is now dated as Miocene N8, approximately uppermost Lower Miocene (Peter Jung, personal communication). Jung identified a single shell as *Neritina* aff. *woodwardi* Guppy. This specimen, which is dealt with in the systematic section (p. 183), is tentatively reidentified as belonging to the Pebasian *Neritina ortoni* Conrad because of similarities in the form of the lower part of the columellar callus and inner lip region. These areas are very unusual in *N. ortoni* and serve to distinguish it from all other known western hemisphere species of *Neritina*. The much smaller marine genus *Smaragdia* is the only living genus in the family which is similar in this respect.

Macsotay (1968) described a few non-marine gastropod fossils from different formations in the State of Miranda. These were identified as *Amnicola ernesti* von Martens, *Hydrobia amnicoloides* Pilsbry, *Pachychilus laevissimus* (Sowerby) and *Strophocheilus ovatus iguapensis* Maury, none of which appear relevant to the present enquiry. In addition Macsotay described as new two species. *Hemisinus (Sheppardiconcha) picardi*, from the Siquire Formation, is not very well preserved, but appears to have some resemblance to *Sheppardiconcha lataguensis* sp. nov. (p. 237) from La Tagua. His *Hemisinus (?Hemisinus) barloventoensis* also occurs in the Siquire Formation, though its type locality is in the Cumaca Formation. It, too, is described from incomplete specimens and is here assigned to *Verena*: it has a striking resemblance to, but nevertheless appears to be specifically distinct from, *V. lataguensis* sp. nov. (p. 258), also from La Tagua. Both the Cumaca and Siquire Formations were considered to be either Middle or Upper Miocene in age (Petzall *et al.* 1978: 194, 587).

Argentina

Rich marine Tertiary molluscan faunas have been described from Argentina. In contrast, the non-marine faunas appear rather unimportant: many are summarized in Parodiz (1969). Von Ihering (1907: 461–468) commented on Late Cainozoic occurrences of a few, mainly living, species of *Strophocheilus, Chilina, Ampullaria, Diplodon* and *Corbicula*. He also referred to the living *Erodona mactroides* Bosc (as *Corbula*) occurring in marine beds of the Oligocene (nowadays considered to be almost certainly Neogene) but later restricted to brackish horizons. Comacho (1966) recorded *Succinea, Ancylus, Planorbis, Ampullaria, Lymnaea, Strophocheilus* and *Bulimulus* from the Quaternary of Buenos Aires Province. He also dealt with fossil occurrences of mainly living species including several (1966: 122–124) *Littoridina* (now probably all referrable to *Heleobia*) and to both *Erodona mactroides* and *Diplodon charruanus lujanensis* von Ihering (1907: 80), an extinct subspecies of a living species.

Aceñoloza & Toselli (1981: 186) referred to the presence of *Corbicula stelzneri, Diplodon* and *Ampullaria* in the San Lucas Formation in northwestern (sub-Andean) Argentina. It is in this region that any connection with the Amazon Basin would be most likely during the Neogene. Previously Windhausen (1931: 405) had referred to the occurrence of *Cyrena, Corbicula* and *Hydrobia* in the Estratos Calchequeños of the same region and quite probably in the same or equivalent strata. Parodiz (1969: 93; pl. 11, figs 2, 3) validated *Neocorbicula stelzneri*, previously a *nomen nudum*, from the Estratos Calchequeños, which he considered to be Middle Miocene. He gave no detailed synonymy, remarking that there was no guarantee that the numerous records of *Corbicula stelzneri* referred to the same species. These non-marine faunas contain Corbiculacea, not present in the Pebasian, and lack all the typical Pebasian genera. No previous author has, in fact, tried to compare them with the Pebasian, though Windhausen (1931: 403) drew attention to the bivalve occurrences in the 'Taterenda Formation' of the Rio Sapuru region of Bolivia (Mather 1922), which is discussed on p. 344.

The living Argentinian non-marine faunas are well known. Pilsbry (1911) described numerous species of his genus *Potamolithus*, which appears to be common in the eastern regions of the country and in neighbouring Uruguay. It has been assigned (Davis & Pons da Silva 1984) to the Lithoglyphinae of the Hydrobiidae, and is the only South American genus hitherto placed in the subfamily, which is known also living in North America. *Lithoglyphus* itself is living in Europe, where its fossil history is short, ranging back no further than the Pliocene. The endemic Pebasian genera *Eubora, Tropidobora*, and, with much less confidence, *Toxosoma* are herein regarded for the first time as probably belonging to the Lithoglyphinae (p. 214). This is the only possible connection between the Pebasian and Argentinian – either Tertiary or Recent – faunas that has come to light. So far, both the Pebasian and Argentinian records of Lithoglyphinae are equally difficult to explain, particularly as the group appears to have a very sparse fossil record world-wide.

So far, no other molluscan evidence has been found suggesting connection between the La Plata region and the Pebasian and related fossil provinces of Colombia and Ecuador. The fossil and living occurrences in Argentina of genera such as *Diplodon, Heleobia* and *Ancylus* cannot be considered significant in this context because they are so widespread. This lack of evidence for such a connection is accepted in view of the quality and quantity of work on the Argentinian Tertiary and Recent faunas. Workers such as von Ihering and Parodiz, to name but two, were well aware of the Pebas fauna, and it seems inconceivable that they would have failed to recognize the more obvious Pebasian elements, such as *Pachydon*. The Lithoglyphinae, discussed above, are comparatively small and have always presented a problem that few authors have been prepared to face. The hinge of *Erodona* shows that it is not closely related to *Pachydon*.

Bolivia

There are records from Bolivia of Tertiary beds crowded with poorly preserved *?Tellina*. *Tellina*, a marine genus, and *Pachydon* have certain similarities. The ventral commissure in both is frequently twisted and *Tellina*, like *Pachydon*, is usually smooth-shelled. In addition, it would be most unusual for *Tellina* to be found crowded together in the manner described by Mather (1922). The genus is a common constituent of inshore sands, and is comparatively rare as a fossil, because in these unstable environments most of the shells are fragmented and dispersed soon after death. When fossilized, *Tellina* usually occurs as one of the less common members of a diverse marine fauna. *Pachydon*, in contrast, is often found crowded together in a manner typical of non-marine deposits which are frequently rich in numbers of individuals but poor in numbers of species. It is just possible, therefore, that the two genera have been confused and that the occurrences detailed below represent some southward extension of the Pebasian deposits. Non-marine deposits of the north-west of Argentina, however, appear to contain a fauna which is completely unlike that of the Pebasian.

Mather described (1922: 729) the Taterenda Formation of probable Tertiary age and consisting of 3000 to 4000 ft (900–1200 m) of soft sandstones, shales, unconsolidated sands and clays occupying lowland areas. In a channel of Rio Sapuru on the west side of Sierra de Charagua (19° 27′ S, 63° 15′ W) (1922: 747 and text-fig. 17) he found a band crowded with bivalves and ostracods. The ostracods were identified as a single species of the long-ranging *Bythrocypris*. The bivalves were thought to be *Tellina* (1922: 750), but were too poor for positive identification, according to E. O. Ulrich (U.S. eological Survey, Washington). Mather also reported the presence of identical bivalves in similar strata north of Rio Grande, 3 miles (5 km) NW of Abapó (18° 45′ S, 63° 22′ W). Ahlfeld & Branisa (1960: 143) rename the Tatarenda Formation as Grupo estratos del Chaco (1960: 82); they also refer to the Estratos de Abapó and a distinct lithological horizon as Las Capas de Pelecypodos.

El Molino fauna, ? Palaeocene

Pilsbry (1939) described a small fauna, allegedly of Palaeocene age, from El Molino, NW of Potosi. It consisted of the following species:

Doryssa(?) ANDICOLA (pl. 9, figs 1a, b).
Planorbis MOLINO (pl. 9, fig. 3).
Planorbis sp. indet. (unfigured).
Corbicula DORMITATOR (pl. 9, fig. 2).
Pisidium sp. indet. (unfigured).

From the illustrations it appears that these fossils are not well preserved, but they are not similar to any of the species from the strata discussed herein, from countries further north. This material has not been reexamined by me. Parodiz (1969) dealt with the three specifically named taxa: he, too, did not attempt to revise Pilsbry's work.

CONCLUSIONS

Summary of systematic zoological and palaeontological results

This study is partly limited in extent by its original aim of describing the new fossil faunas from La Tagua and comparing them with the well-known faunas of supposed Pliocene age in the Pebasian Basin. The work has continued in these directions, even though it has, perforce, expanded to consider other fossil faunas including those of the Cuenca Basin, Ecuador and those previously thought to be of Palaeogene age from the Magdalena Basin of Colombia. In consequence, although efforts were made to borrow type material from other institutions, loans were restricted to species which, at the time, appeared to be strictly relevant to the original aims of the study. The result is that not all species occurring in the non-marine Tertiary of the northwestern quadrant of South America are dealt with as fully as those in the Pebasian and La Taguan faunas. The Corbiculacea, which are unknown in these faunas, are omitted entirely, whilst the Unionacea and Mutelacea, which are comparatively rare in these same faunas, are not covered in great detail.

The generic and suprageneric classification of the fossils seemed to be of vital importance to any revisory work. Considerable efforts have therefore been made to understand the classification and distribution of the living non-marine molluscan fauna of both South and Central America, efforts justified by the consequent increased knowledge of the relationship between the fossil faunas and those of the present day, both at the taxonomic level and as a basis for considering the palaeogeography and related topics such as migration routes. As part of the taxonomic work, dates and authorship of suprageneric taxa have been thoroughly revised. Those given here are often different from those quoted in the *Treatise on Invertebrate Paleontology* (**N**, Bivalvia; Cox *in* Moore 1969), whilst the major part of the volume on Gastropoda (**I**) has yet (1989) to appear.

Neritacea

The several nominal species of *Neritina* (*sensu lato*) described from the Pebasian are here united in *N. ortoni* Conrad, 1871*b*. A single specimen, figured under another name by Jung (1965) from the marine Miocene of northern Venezuela, is tentatively referred to it. *N. ortoni* does not closely resemble any other known fossil or Recent species from either South America or the Caribbean, and there must be some doubt about its generic or subgeneric determination. Certain features of its ventral surface resemble those of the marine genera *Velates* (Eocene) and the living *Smaragdia*. A single operculum, extracted from washings of matrix from Pichana, a Pebasian locality rich in *N. ortoni*, appears to lack the peg characteristic of both *Neritina* and *Smaragdia*. The operculum of *Velates* is unknown.

Rissoacea

Three subfamilies, Littoridininae, Lithoglyphinae (probably; see p. 214) and Cochliopinae, all belonging to the Hydrobiidae, are present in the Pebasian. The Littoridininae are by far the most important, occurring in all the other fossil faunas under consideration and with a widespread distribution throughout South and Central America at the present day (Taylor 1966).

LITTORIDININAE. Two extinct genera of Littoridininae are of importance, and were described by Conrad (1871*b*) from the Pebasian of Pichana. *Dyris* is distinguished from living *Heleobia* by spiral ribbing, sometimes confined to its early post-nuclear whorls, whilst *Liris* has axial folding. Taylor's (1966) assignment of both to the North American genus *Tryonia* is not followed here. Parodiz (1969) reduced the number of Pebasian species of *Dyris* from five to two, recognizing only *D. ortoni* (Conrad) for large, rather smooth, shells and *D. gracilis* Conrad (the type species) for those with strong, persistent, spiral ribbing. The examination both of type material and of comparatively large samples from several localities, some new, suggests that more rather than fewer species should be recognized at our present state of knowledge.

However, the ideas of both Parodiz and Taylor should be borne in mind when examining an unresolved taxonomic problem, which has not previously been reported. In a few of the specimens studied herein, either the spiral or axial sculptural elements are reduced, producing shells with morphology intermediate between *Dyris* and *Liris*. For the time being, both genera are retained as they are useful for groups of fossil species clearly distinct from any Recent species. The view is taken that an attempt to merge the two would only be justified as part of a complete revision of the subfamily. Any such revision would have to redefine many of the Recent genera with respect to their type species, and, in view of the misunderstandings which had arisen with both *Dyris* and *Liris*, should preferably involve re-examination of their type specimens too. A probably unnecessarily large number of generic names is available, and much of the variation in form may be owing to radiation in isolated basins. A possible example of this is afforded by the several genera described from Lake Titicaca (Haas 1955), the majority, or even all, of which could have been derived from a rather 'normal' *Heleobia*-like ancestor. This situation is somewhat analogous to the diversity shown by Thiaridae (*sensu* Wenz, 1939) in Lake Tanganyika. With these reservations in mind, it may be suggested that the living *Heleobia*, *Lyrodes* and *Pyrgophorus* may share the same common ancestry as *Dyris*. The type species of the living *Potamopyrgus* is from New Zealand: use of the name for South American species seems inappropriate.

Both *Liris* and North American *Tryonia* exhibit rather similar axial folding, and it is felt that this resemblance could also well be owing to convergence. There are no South American genera particularly resembling *Liris*: it, too, may well share common ancestry with *Dyris*. *Liris laqueata* Conrad, 1871*b*, the type species, proves to be a junior synonym of *Turbonilla minuscula* Gabb, 1869. An attempt is made to rectify the confusion caused by the two being regarded by all subsequent authors as very different species.

A species based on three specimens from the Pebasian of Canamá and described by Etheridge (1879) as *Assiminea crassa* is, following Kadolsky (1980), tentatively assigned to *Littoridina*, though its generic position is not fully understood.

Potamopyrgus laciranus (Pilsbry & Olsson, 1935) from the La Cira formation of the Magdalena Valley, Colombia, is placed in *Dyris*. Bristow & Parodiz (1982) recognized *Liris minuscula* (Gabb) in the Tumbatú Formation of the Loja Basin, Ecuador. Their identification of *Liris* is provisionally accepted, but their specific determination is not. The species, which remains formally undescribed, is the only probably true record of *Liris* from outside the Pebasian Basin.

The following species are described as new: *Dyris hauxwelli*, Pebasian, Pichana, Peru; *Dyris semituberculata*, La Tagua Beds, La Tagua, Colombia; *Liris acicularis*, Pebasian, Pichana, Peru.

LITHOGLYPHINAE. Davis & Pons da Silva (1984) assigned the living Argentinian fresh-water genus *Potamolithus* to the Lithoglyphinae: previously it had been classified rather unconvincingly in several unsuitable positions in the Rissoacea, mainly within the Littoridininae. The endemic Pebasian genera *Eubora, Tropidobora* and *Toxosoma* are herein also provisionally placed in this subfamily. The first two have obvious resemblances to *Potamolithus*, but have a strong siphonal notch lacking in both *Potamolithus* and *Mexithauma*. *Toxosoma* has always presented a problem because, unlike other known Hydrobiidae with the exception of *Hemistomia*, it possesses a columellar plait. However, there is no other family to which it seems more likely to belong. It has a strong resemblance to some species of *Drymaeus*, a South American tree snail of the Bulimulacea, but the much smaller *Toxosoma* has a shell whose structure and texture is quite clearly prosobranch and not pulmonate. The similarity between the two appears to be a remarkable example of homoeomorphy between two genera living in very different habitats.

Records of *Toxosoma* from the intermontane basins of Ecuador (Bristow & Parodiz 1982) are unfounded. It is suggested below (p. 353) that the presence of Lithoglyphinae in the Pebasian Basin is evidence that it had some fresh-water link with the La Plata region. It is felt, however, that too little is known about either the true geographical distribution or the geological history of this group for such evidence to be relied on to any great extent. *Lithoglyphus* itself is living in Europe, and other genera assigned to the family live in North America. From neither region is there evidence of it having an extensive geological record before the Pleistocene.

COCHLIOPINAE. The subfamily is distributed mainly in the Caribbean, Central America and the southern United States (Texas etc.). The present fossil record is the first from South America and may well be the first from anywhere of *Nanivitrea*, described living in Jamaica and Cuba. The only other South American record of the genus is of *Valvata kugleri* Forcart, 1948, described from Venezuela Recent and assigned herein to *Nanivitrea*. *Nanivitrea colombiana* from the La Tagua Beds of La Tagua, Colombia is described as new.

VITRINELLIDAE. At least two species of Vitrinellidae, both best assigned to *Vitrinella (Vitrinellops)*, are present in the Pebasian. This is, as far as is known, the first record of this marine family in non-marine strata. The embryonic shell appears to be of only half a whorl and is suggestive of lecithotrophic development. In contrast, all the embryonic shells of marine vitrinellids which have been examined suggest that a free-swimming veliger stage is normal in the family.

Cerithiacea

Following the views of Morrison (1954), the Thiaridae (*sensu* Wenz, 1939) are divided into dioecious Pleuroceridae, which includes the genus *Doryssa*, and the parthenogenetic Thiaridae, to which are assigned the Hemisininae. Parodiz (1969), following Morrison's apparently mistaken views on the shell features distinguishing the two families, placed numerous fossil species in *Doryssa*. All of those species with which the present study is concerned are now regarded as Hemisininae, which may be distinguished from Pleuroceridae by the presence of a basal apertural notch. *Doryssa* is no longer recognized as occurring fossil in north-western South America. For comparative purposes, the genus is discussed and illustrated (p. 230), with particular emphasis on its living type species, *Bulimus ater* Bruguière, from French Guiana.

HEMISININAE. The type species of the living genera *Basistoma, Hemisinus, Verena, Longiverena* and *Aylacostoma* and also the fossil *Sheppardiconcha* are described, and fairly extensive synonymies are suggested. *Sheppardiconcha* is considered to be particularly close to *Basistoma*. Shells of Hemisininae are almost invariably decollated, so that their early whorls cannot be studied using adult specimens. Embryonic shells, syringed from dead shells in the dry collection of BMZD, of all the living genera except *Aylacostoma* are illustrated. In all of these, the initial shell is hemispherical and develops into a loosely coiled planorbiform phase of little more than one whorl. After this, the shells of the various genera fairly rapidly develop their own characteristics, which in some cases, but not all, is very like that of the adult shell.

Most of the Recent genera and species of Hemisininae dealt with herein come from the southern and eastern parts of Brazil, whilst the fossil localities are all in the Upper Amazon Basin and from even further west in the Magdalena and Cuenca Basins and from La Tagua on Rio Caqueta. *Hemisinus* also occurs living in the Caribbean as well as eastern South America, and is known fossil from the Miocene of the Dominican Republic. The differences between the fossil and Recent distributions of the majority of these genera raise the possibility that they developed in the more westerly basins and spread to the eastern parts of the Continent following the breakdown of the drainage divide in the middle to lower Amazon which existed in the late Tertiary, according to the hypothesis of Kätzer (1903). These ideas, however, cannot be properly tested, as both the details of Recent distribution and the taxonomy (as witness the locality data and synonymies given herein) of the various taxa involved are not properly understood. Furthermore, our knowledge of their distribution is very much controlled by the fact that all the fossil deposits lie to the west, whilst their most suitable habitats at the present day occur in the east, where they are also possibly more accessible to the average collector, as opposed to the professional oil and survey geologists and geographers responsible for much of the fossil collecting.

In addition to the synonymizing of many nominal living species, the following taxonomic changes are suggested. *Hemisinus tuberculiferus* Conrad, from the Pebasian of Iquitos, Peru, is assigned to *Sheppardiconcha. Hemisinus sulcatus* Conrad, from the Pebasian of Pichana, Peru is assigned to the living *H. brasiliensis* (Moricand). *Hemisinus sulcatus* de Greve, *non* Conrad, from the Pebasian of Iquitos, is assigned to the living *H. kochi* (Bernardi). The majority of the species described by Pilsbry & Olsson (1935) from the Mugrosa and La Cira Formations of the Middle Magdalena Valley, Colombia, are placed in their species *Longiverena eucosmia*: *Semisinus peyeri* de Greve, from the Pebasian of Iquitos, and *Hemisinus peyeri dickersoni* Palmer, from the Cuenca Basin, Ecuador, are also placed in the synonymy of this species. *Purpura woodwardi* Roxo from the Pebasian of Três Unidos, Peru is assigned to the living *Verena crenocarina* (Moricand). Both *Hemisinus (Verena) avus* and *H. (V.) laevicarina* Pilsbry & Olsson, from the La Cira formation of the Middle Magdalena Valley, Colombia, are placed in *Verena crenocarina ava. Ampullaria guaduasensis* Anderson, from what is now thought to be the Santa Theresa Formation of the Upper Magdalena Valley, Colombia, is placed in *Verena. ?Melanopsis browni* Etheridge, described from the Pebasian of Canamá, Peru, is also assigned to *Verena*.

The following new species are all described from the La Tagua Beds of La Tagua, Colombia: *Sheppardiconcha lataguensis, Longiverena colombiana* and *Verena lataguensis*.

Pulmonata

Only two species of pulmonate gastropod have been discovered in any of the fossil deposits dealt with herein. Both are from the Pebasian of Pichana, Peru.

ORTHALICACEA. Bulimus linteus Conrad, which was also recorded as occurring at Pebas by Boettger (1878), is now assigned to *Orthalicus*. The superfamilial name Orthalicacea is here used rather than Bulimulacea.

LYMNAEACEA. A single, minute, limpet-like shell, adhering to a broken fragment of a bivalve, was extracted from matrix from Pichana. It is provisionally assigned to *Hebetancylus*. This is thought to be the first fossil record of the genus.

Order Unionida ('Naiades': Unionacea and Mutelacea)

Following Parodiz & Bonetto (1963), the Unionacea, with glochidia larvae, and the Mutelacea, with lasidia – a distinction first noted by Ihering (1893) – are treated as separate superfamilies. The thicker and coarser outer prismatic layer of the shell observed in all Mutelacea examined herein is advanced as an additional distinction between the two. A table (p. 265) is provided giving references to members of these superfamilies described as occurring in the Tertiary of north-western South America. Neither superfamily is of importance either in the Pebasian or in the La Tagua Beds, though shell fragments are a noticeable feature at a few localities. This is in contrast to the present-day Amazon fresh-water fauna, in which they, along with the Corbiculacea, are the most important bivalve groups, as in virtually all normal fresh-water faunas of the Tertiary and present day. Naiades form a significant part of the fauna both at some horizons in the Magdalena Basin Tertiaries and in the Cuenca Basin, where some beds are covered in *Diplodon (Ecuadorea) bibliana* (Marshall & Bowles, 1932). All naiades are truly fresh-water and there relative abundance is clearly of importance when assessing facies considerations.

*UNIONACEA.*The genus *Diplodon*, its living type species, *Diplodon ellypticus* Spix, 1827, and its various subgenera, in particular *Ecuadorea*, are discussed in some detail. Although a few species have been described from the Pebasian, only very juvenile shells have been extracted from BMPD collections from Pichana, Peru. A single specimen from La Tagua is identified as *Diplodon (Ecuadorea)* aff. *bristowi* Parodiz, a Cuenca Basin species known only by its holotype. This determination is too uncertain for stratigraphical conclusions to be drawn from it.

MUTELACEA. The genus *Anodontites* and the Pebasian species *Anodon batesi* Woodward, 1871, from Pichana, which is here placed in it, are both redescribed.

Dreissenacea

A reappraisal of the apparently largely ignored work of Andrussov (1897) shows the geographical and stratigraphical distribution of *Mytilopsis* to be very different from that suggested in modern works, including the *Treatise* (Keen, *in* Moore 1969). The genus is recognized as occurring in the European Eocene, but its present-day distribution in Europe is interpreted as the result of reintroduction by man. Its distribution in the western hemisphere from the late Oligocene onwards is of some importance when considering the palaeogeography of north-western South America, see pp. 279 and 352. Two species are recognized in the faunas under consideration, *M. scripta* (Conrad), originally described from the Pebasian, and the living Caribbean *M. sallei* (Recluz), for which an extensive synonymy is constructed (p. 280).

Mytilopsis has a very wide salinity tolerance, enabling it to withstand hypersaline conditions and apparently to migrate across seas: nevertheless, it is normally found in fresh to brackish water.

Corbiculacea

The superfamily is not dealt with herein, as it is absent from the Pebasian and the La Tagua Beds. Accounts of its occurrences elsewhere are given by Bristow & Parodiz (1982; Cuenca Basin, Ecuador), Pilsbry & Olsson (1935; Middle Magdalena Valley, Colombia) and Palmer (1945; Neogene of State of Monogas, Venezuela). Corbiculacea and *Pachydon* of the Corbulidae seem to be of inversely proportionate importance in the fossil faunas under consideration herein.

The superfamily is predominantly fresh-water. The Pisidiidae are apparently entirely fresh-water, but, as Keen (1971: 111) has pointed out, the Corbiculidae are also sometimes found in brackish water and shells of more robust species may even be washed out to sea and mingled with those of marine faunas.

Myacea (Corbulidae, Subfamily Pachydontinae)

Pachydon Gabb, 1869, of the Corbulidae, normally a marine family, is by far the most important genus of bivalve, both in numbers of species and of individuals, in the Pebasian. Its type species, *P. obliquus* Gabb, is highly inequivalve and with a strongly twisted commissure. At several localities, however, it occurs with other clearly congeneric species of less unusual appearance, which are almost equivalve. Such species, when occurring in other strata, have invariably been assigned to *Corbula*. In the present work, *Pachydon* is recognized as abundant in the La Tagua Beds, and at several levels (including the *Corbula hettneri* Horizon, of the Santa Teresa Formation) in the Upper Magdalena Valley, Colombia. It is absent from the Cuenca Basin: a single specimen from the Loyola Formation, identified by Bristow & Parodiz (1982) as *Erodona iquitensis* (de Greve) has proved on re-examination to belong to the rather common species *Corbicula cojitamboensis* Palmer. Fuller details of the distribution of *Pachydon*, possibly including Venezuela (Rutsch 1952) and the more remote parts of the Upper Amazon Basin (Willard 1966), are given on pp. 292 and 353.

Over a dozen species of *Pachydon* are now recognized. At some Pebasian localities, five or six morphologically distinct forms, with no individuals showing intermediate characters, may occur together: in consequence, their treatment as separate species seems fully justified. *Corbula abundans* and *C. magdalensis*, both of Pilsbry & Olsson, 1935, from the La Cira formation of the Middle Magdalena Valley, are placed in *Pachydon [Corbula] cebada* Anderson, 1928, from what is now thought to be the Santa Teresa Formation of the Upper Magdalena Valley. *Pachydon [Corbula] hettneri* Anderson, 1928, from the same locality occurs in the newly described La Tagua fauna.

Three other genera of Corbulidae, *Ostomya* Conrad, 1874*a*, *Guianadesma* Morrison, 1943, and *Pebasia* gen. nov. (p. 315) also occur, but much more rarely, in the Tertiary of north-western South America, and are dealt with below. All four of these genera are here placed in the Pachydontinae of Vokes, 1945. Their shell structure is consistent with membership of the Corbulidae.

Pebasia is described to accommodate a single species, *Pachydon (Anisorhynchus?) dispar* Conrad, 1874*a*, from the Pebasian. In Conrad's original description of this species, the left and right valves were confused. It is highly inequivalve with a pholadiform right valve and *Spondylus*-like left valve. It probably shares common ancestry with *Pachydon*.

Ostomya was described by Conrad, who confused its left and right valves, to accommodate a single, small, species, *O. papyria* Conrad, 1874*a*. The type specimens are lost, but the taxon is now redescribed from newly extracted specimens from matrix from Pichana, Peru (one of the localities from which Conrad's collection came). *Ostomya*, which has often been assigned to the Lyonsiidae, is here transferred to the Corbulidae: its shell lacks the nacreous layer characteristic of Lyonsiidae. The only two other species assigned by earlier workers to *Ostomya* are here transferred to *Guianadesma*. *O. mencheri* Palmer, 1945, from the Neogene of Venezuela, is regarded as a synonym of the living type species, *G. sinuosa* Morrison, 1943, from the Guianas. *O. colombiana* Pilsbry & Olsson, 1935, is also transferred to this genus.

Guianadesma Morrison, 1943, is here used both for *Himella* H. Adams, 1860, and for its replacement name, *Antecorbula* Dall, 1898. These are here treated as *nomina dubia*, being based on an unfigured type species whose type material is lost. *Guianadesma* and *Ostomya* may share common ancestry.

New taxa of Corbulidae described herein are the genus *Pebasia* (see above) and two species, *Pachydon ovalis*, La Tagua Beds, La Tagua, Colombia, and *Pachydon trigonalis*, Pebasian, Puerto Nariño (type locality) and Canamá.

Summary of stratigraphical results

This section is concerned mainly with two aspects of the findings detailed in the sections devoted to systematic palaeontology and to descriptions of localities and their faunas: the correlation between the faunas under consideration, and evidence from any source, molluscan or otherwise, on the age of these faunas.

The faunas of several Pebasian localities have been generally recognized as being basically similar to each other. However, hitherto there have been no very serious attempts to correlate the faunas of various regions of north-western South America with each other. One exception to this is the

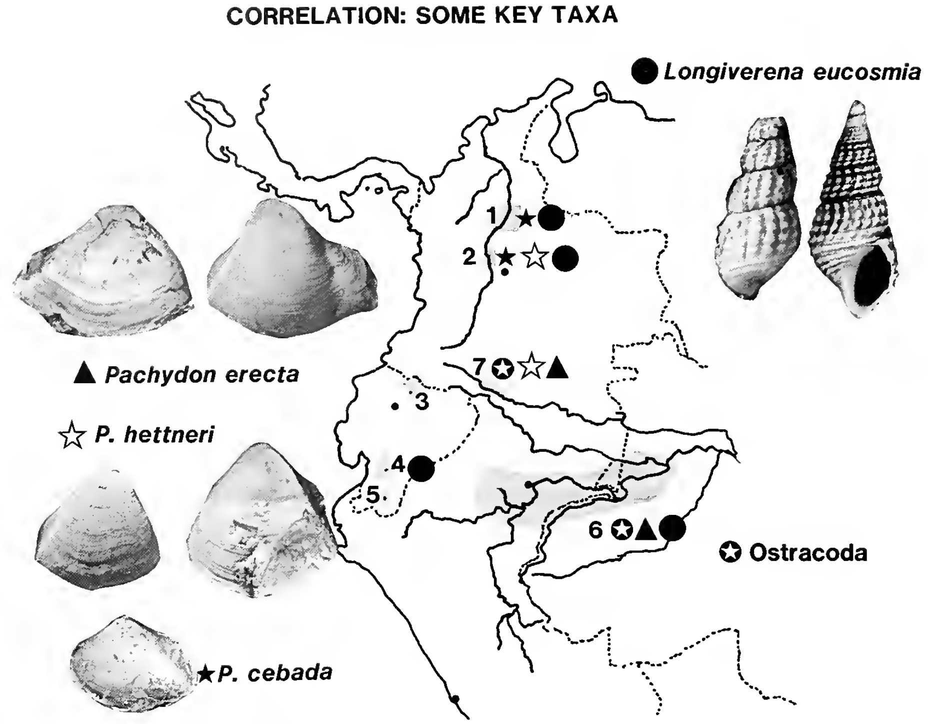


Fig. 452 Correlation: some key taxa. Diagram showing some of the more important links between molluscan species from the Mugrosa and La Cira faunas of the Middle Magdalena Valley (1), the Santa Teresa fauna of the Upper Magdalena Valley (2), both of Colombia; the Cuenca Basin of Ecuador (4); the classic Pebasian area of Peru and Brazil (6); and the La Tagua area (7). In addition identical ostracod species are known from both (6) and (7). (3) and (5) mark the Chota and Loja Basins respectively.

Pachydon erecta Conrad, left specimen from La Tagua, right from Canamá (Pebasian); *P. hettneri* (Anderson), left specimen from La Tagua, right from near San Juan de Rio Seco (2); *P. cebada* (Anderson), also from (2); *Longiverena eucosmia* (Pilsbry & Olsson), left shell from Mugrosa Formation (1), right from Iquitos (Pebasian) (6).

study of the faunas of the intermontane basins of Ecuador (Bristow & Parodiz 1982), some of whose findings are critically analysed herein. It is concluded that there is some evidence for correlation between these deposits and the Pebasian, but it is now based on sounder grounds, and ones almost entirely different from those they suggested.

The advances made in the present study have depended on the recognition that in the Magdalena Valley there are strong faunal links between the Santa Teresa Formation (Anderson 1928, San Juan de Rio Seco), originally dated as Eocene, and the La Cira Formation (Pilsbry & Olsson 1935) originally dated as Upper Oligocene or Lower Miocene. The fauna of the latter is shown to include the most common of the two species occurring in the underlying Mugrosa Formation, originally dated as Middle Oligocene. The first two are now thought to be Miocene, and the Mugrosa Formation cannot be separated from them on palaeontological grounds. The only argument in favour of the Mugrosa being pre-Miocene is that it lies between 780 and 2070 m below the La Cira fossil horizon, but this is far from conclusive. The newly-described La Tagua molluscan fauna has provided an important link between these Magdalena Valley faunas and those of the Pebasian. In addition, the La Taguan and Pebasian ostracod fauna (Sheppard & Bate 1980) has yielded confirmatory evidence that the two are of broadly similar ages.

Below are listed the rather limited number of taxa whose known distribution in the fauna of more than one region is considered to be of correlative value.

Taxa of value in correlation between regions

Pachydon. Described from the Pebasian, where it is the dominant faunal element. Now recognized in La Cira and Santa Teresa Formations of Magdalena Valley and abundant at La Tagua.

Pachydon cebada (Anderson). Common to La Cira and Santa Teresa Formations.

Pachydon hettneri (Anderson). Common to Santa Teresa and La Tagua faunas.

Pachydon erectus Conrad. Described from Pebasian, and present at La Tagua.

Mytilopsis. Found in La Cira, La Tagua and Pebasian faunas.

Mytilopsis scripta (Conrad). As above.

Liris. Described from Pebasian, otherwise known only from Tumbatú Formation of Chota Basin, Ecuador, by an unnamed species not occurring in the Pebasian.

Dyris tricarinata (Boettger). Described from and common in Pebasian. Also occurs at La Tagua and in San Cayetano of Loja Basin, Ecuador.

Longiverena eucosmia (Pilsbry & Olsson). Described, with several synonyms, from Mugrosa Formation and now also recognized in La Cira Formation, both of Magdalena Valley. Also from the basal Azogues and Loyola Formations of the Cuenca Basin, Ecuador and the Pebasian of Iquitos, Peru.

Sheppardiconcha lataguensis sp. nov. Very similar to *S. eucosmia*. Known only from La Tagua.

The age determination of non-marine strata is always a problem unless they either contain fossils, such as spores, which may also be found in the marine succession, or can be dated radiometrically. Palynological work in Ecuador has been discussed briefly by Bristow & Parodiz (1982), who found its conclusions too controversial to be satisfactory. Similar work in Colombia is reviewed on p. 333 (Magdalena Valley faunas), and seems, in contrast, to be basically sound, though in need of reinterpretation because of later changes in the position of the Oligo-Miocene boundary. Some doubt about the use of the palynological evidence must remain for two reasons. First, insufficient details about the geographical and stratigraphical location of the spore samples are available for their relationship with the molluscan localities to be understood. Secondly, it is suspected that some of the palynological samples were dated by reference to ages originally applied to the vertebrate and non-marine molluscan faunas rather than by reference to planktonic foraminiferal zones.

The palaeontological evidence for dating the deposits dealt with herein are listed below.

Age-diagnostic taxa

Mytilopsis scripta (Conrad). In addition to its distribution as given above, this species is now recognized in late Oligocene strata in the Pacific coastal strip of western Peru. It was originally described from there as *M. trigalensis* by Olsson (1931).

Mytilopsis sallei (Recluz). A widespread living Caribbean species, now recognized in the Pebasian and also in the late Oligocene of western Panama, as *M. dalli* (Clerc *in* Joukowsky, 1906).

Neritina ortoni Conrad. Confined to the Pebasian but also probably occurring in the Miocene (N8) Cantaure Formation of Venezuela, represented by a single specimen identified by Jung (1965) as *N.* aff. *woodwardi* Guppy.

Hemisinus brasiliensis (Moricand). *Hemisinus sulcatus* Conrad, described from the Pebasian, is assigned to this species now living in the Atlantic drainage of South America.

Hemisinus kochi (Bernardi). *Hemisinus sulcatus* de Greve, *non* Conrad, from the Pebasian of Iquitos appears identical to this living species, with a distribution similar to that of *H. brasiliensis*.

Verena crenocarina (Moricand). *Purpura woodwardi* Roxo from the Pebasian of Três Unidos is definitely a *Verena*, and appears to belong to this species, with a similar present-day distribution to the two species of *Hemisinus* above.

Necronectes proavitus (Rathbun). This crab was originally described from the Gatun Formation (probably mainly Upper Miocene) of Panama, and has been identified from the Loyola Formation of the Cuenca Basin, Ecuador (Collins & Morris 1976, Bristow & Parodiz 1982).

Pelocypris zilchi (Triebel). This ostracod, recorded by Sheppard & Bate (1980) from La Tagua, was the only member of the fauna they described known from outside the Upper Amazon Basin. It was described from strata in San Salvador of supposed Plio-Pleistocene age.

Vetustocytheridea bristowi (van den Bold). This ostracod species is described from the Loyola and Mangán Formations of the Cuenca Basin. Bristow & Parodiz (1982) regarded it as probably diagnostic of the Miocene. The genus is known only from the Miocene of the Caribbean and southern United States (van den Bold 1976).

Other evidence of age

The andesite underlying the Loyola Formation of the Cuenca Basin, Ecuador and radiometrically dated as 19–20 million years (Late Aquitanian, N5) (Snelling, unpublished report *in* Bristow & Parodiz, 1982: 8), effectively provides a maximum possible age for the Cuenca Basin deposits.

The similarities between the La Cira and Santa Teresa faunas of the Magdalena Valley and those of La Tagua means that they must have been deposited before the mountain building period in which the Cordillera Oriental of Colombia was sufficiently raised to block any connection between the Magdalena Valley and the Upper Amazon Basin. This event was dated by Campbell & Bürgl (1965) as occurring at the end of the Miocene. In this work they outline (1965: 583–585) the history of the eastern Cordillera. The same sedimentary cycles during the late Tertiary may be traced across it from the Magdalena Valley on its western flank to the Llanos to the east of it, leading them to conclude that it was not subjected to strong diastrophism or uplift until the end of the Miocene, though there were some preliminary movements prior to the deposition of the Upper Miocene (Honda Series). Overlying deposits assigned to the Pliocene were virtually unfolded. Elsewhere in this summary they referred to a new sedimentary cycle starting in the Middle Miocene before the deposition of the Colorado Series, which is thought (Butler 1942) to be the equivalent of the La Cira Formation of the Middle Valley. Campbell & Bürgl do not explain their evidence for dating these various events, except for a footnote (1965: 583) referring to the difficulty in identifying the Oligo-Miocene contact in the Colombian non-marine province because of the reassignment of the Aquitanian to the Miocene. On the basis of this currently accepted interpretation of the base of the Miocene, Hopping's work on the palynology (1967), summarized on pp. 333–334 (Magdalena Valley), placed the La Cira Formation (*sensu lato*) somewhere between the Oligo-Miocene boundary and Zone N10 of the Middle Miocene. Thus, Campbell & Bürgl and Hopping are more or less in agreement on a revised age for the La Cira Formation. In his later study (1970) on the Oriente of Ecuador, Campbell was still of the opinion that the link between that region and the Magdalena Valley, through a portal in the Mocoa region, was not closed until the late Miocene.

All the evidence so far presented points to the bulk of these faunas from both Colombia and Ecuador being of approximately the same age, probably Miocene. They clearly predate the late Tertiary Andean orogeny, and the main proviso must be about the accuracy with which this is dated in reference to the marine succession.

The Mugrosa Fauna from the Magdalena Valley, on stratigraphical but not on palaeontological grounds, might be distinctly older than the overlying La Cira Formation and therefore possibly pre-Miocene.

The Los Corros Fauna of the Esmeraldas Formation is, as discussed in the section on the Magdalena Valley faunas (p. 336), definitely older, being Oligocene or even possibly late Eocene.

The Pebasian faunas of the Upper Amazon Basin have in recent years been generally accepted as Pliocene, but on no firm palaeontological evidence. In fact, virtually all the evidence presented in this paper is entirely new. Living species are recognized in the Pebasian for the first time. These are *Mytilopsis sallei* (Recluz), *Hemisinus brasiliensis* (Moricand), *H. kochi* (Bernardi) and *Verena crenocarina* (Moricand). In contrast, no living species have been found in any of the other faunas discussed above, which are now regarded as Miocene. Again for the first time, fossil species occurring in other faunas are recognized in the Pebasian. *Pachydon erectus* Conrad and *Dyris tricarinata* (Boettger) are found both in the Pebasian and at La Tagua. The latter also occurs in the intermontane basins of Ecuador. *Longiverena eucosmia* (Pilsbry & Olsson) is common to the Mugrosa, La Cira, Loyola and basal Azogues Formations and also the Pebasian of Iquitos. The ostracod fauna described by Sheppard & Bate (1980) is discussed in the sections on the Pichana (Pebasian), p. 326, and the La Tagua, p. 173, faunas. The large proportion of species in common, particularly in view of the fact that they are thought to have lived in rather different salinities, suggests that these two deposits are of quite similar ages.

The Pebasian molluscan fauna differs very markedly from the living fauna, both in the presence of many extinct genera, and in that it contains taxa which, like those of the other faunas under consideration, indicate conditions of deposition very unlike those of the present day. Such changes, however, do not necessarily indicate the passage of a great deal of time, as witness the varied sequence of faunas during the Pleistocene in different parts of the world. If we accept Kätzer's (1903) hypothesis that an inland basin of deposition, roughly coinciding with the present-day Upper Amazon Basin, existed during the Tertiary until the drainage divide between it and the eastern end of the present Amazon was breached, then the Pebasian fauna, along with the Colombian and Ecuadorian faunas, lived before the breakdown of the drainage divide. This event would have radically altered conditions in that basin and allowed the entry of the present-day eastern Amazonian fauna.

The balance of the evidence suggests that a Pliocene age for the Pebasian cannot be entirely ruled out. However, a Miocene age, broadly similar to that of the other faunas, seems much more probable. The few living species present in the Pebasian but absent in the other faunas might indicate that the Pebasian was possibly the youngest of this group.

It is clear from Simpson (1961) and from examination of faunal lists that there are several other faunas, from localities lying to the south of the true Pebasian outcrop and situated mainly in the Rio Jurua area, which are distinct from those of the Pebasian. The molluscs listed from these localities appear to be approximately the same as those in the present-day Amazonian fauna, and therefore have virtually nothing in common with that of the Pebasian. Certainly, none of the living species now recognized in the Pebasian has been recorded in any of these faunas: they also lack all the extinct genera characteristic of the Pebasian. The molluscan evidence is that these faunas are indisputably younger than the Pebasian. Their age cannot be deduced from the data available, but their similarity to the living fauna suggests that they might be Pleistocene or even Holocene. There seems to be no reason to suppose that the mammal faunas of these localities are Pebasian.

Palaeogeography

At a very early stage in this study, the question arose as to the origin of the brackish to marine elements – mainly *Neritina*, *Mytilopsis* of the Dreissenacea and various genera, in particular *Pachydon*, of the Corbulidae – in the Pebasian and La Taguan molluscan faunas. Even before consulting any literature (Weeks 1948) on palaeogeography, it seemed apparent from consideration of the physical geography of the Continent that there were basically four possible connections between the upper Amazon region and the sea: northwards to the Caribbean; eastwards along the course of the present-day Amazon, between the Guyana and Brazilian shields; southwards towards the estuary of Rio La Plata; or westwards to the Pacific.

At first sight, the Caribbean connection appeared to be the most attractive option, bearing in mind that the Pebasian faunas were generally considered to be Pliocene, by which time the Andes would have reached some considerable height and effectively blocked a westward connection to the Pacific. Growing familiarity with both the literature and additional relevant fossil faunas, which were clearly pre-Pliocene, suggested that the westward connection was also a distinct possibility. However, none of the evidence for either of these two alternative routes seems to exclude the other. On the other hand, with respect to the remaining alternatives, no good evidence has been found suggesting that migration took place of either marine or brackish taxa up the present Amazon Valley from the Atlantic, or northwards from La Plata. Nevertheless, similarities between the fossil freshwater faunas, in particularly those genera of Hydrobiidae now placed in the Lithoglyphinae, of the Upper Amazon Basin and the Recent Amazonian and La Plata faunas suggest that possible fresh-water links between these regions are worthy of consideration. Gardner (1927) suggested such a link, based on her assumption that *Azara (= Erodona)* and *Anisothyris (=Pachydon)* were closely related: this, however, is not the case as the two have very different hinges (Fig. 355, p. 289).

Sheppard & Bate (1980: 121), on the basis of their study of the ostracod faunas of La Tagua and Pichana, which they considered to be contemporaneous and Plio-Pleistocene, suggested that the sea lay to the east and that a marine transgression had entered along the line of the present Amazon Basin (? or valley). Their palaeogeographic map (1980: 120, text-fig. 5) was constructed to explain the salinity gradient between Loc. 54, La Tagua (where the only ostracod was a fresh-water species), the nearby Loc. 33/480–560, La Tagua, with a mixture of fresh-water, brackish and marine ostracod species, and Pichana, some 500 km further south, with a greater proportion of brackish and marine ostracods and only two fresh-water species. Their map, showing an east–west coastline lying to the south of Pichana, could equally well be interpreted as suggesting a connection with the Pacific: a possibility they had dismissed because of the Andes mountain chain. Furthermore, other explanations may be put forward to explain this salinity gradient. Thus, rotation of their map so that the coastline lay slightly to the east of Pichana in a north–south direction would lead to the inference that there was a channel in open sea, parallel to the coastline, running towards the Caribbean and La Plata. Other alternatives present themselves as the hypothetical coastline is rotated. For example, if it lay in a SE–NW line somewhere to the south-west of Pichana, the same salinity gradient could be drawn into the map, and a connection with the Marañón Portal again becomes a possibility. The salinity gradient can also be explained in the context of Late Cainozoic geography not being static, and the various deposits not being precisely contemporaneous. The two La Tagua ostracod faunas indicate different facies, and samples from the others, including different fossiliferous layers at Loc. 33, were not studied. It may therefore be suggested that though valuable ideas are presented about the facies and the relative ages of these deposits, the palaeogeographic evidence in favour of an eastward connection down the Amazon Valley is far from conclusive.

The Pebasian Basin, eventually isolated from the sea, and with internal drainage, is in some respects analogous with the Sarmatian Basin of the eastern European Miocene. Here, a small number of originally fully marine molluscan taxa, including *Dorsanum* of the Nassariidae and various Cardiidae, developed wide morphological variation in response to falling salinity caused by influx of fresh water from rivers draining into the basin. Such basins are characterized by faunas with comparatively few species showing wide variation and by a lack of exclusively marine groups such as corals, bryozoans and echinoderms. On the other hand, some of these, as well as brachiopods and cephalopods, are present in the diverse fauna of the shrinking Permian Zechstein Sea of north-western Europe, bordered by arid deserts and with rising salinity. Contrasting with the Zechstein, Runnegar & Newell (1971) recognized in the Permian of southern Brazil a relict fauna, which they compared with that of the present-day Caspian Sea and which lacked these typical marine elements.

Boltovsky (1958) suggested that the Caribbean had been the source of the fauna of the living fresh-water and low salinity foraminifera of the La Plata region. As they are absent from the Brazilian coast, he thought they had not reached the La Plata estuary by this route, but through the Continent. Among the various works he quoted in support of his ideas, he referred to Ihering (1927), whose Karte 1 postulated a connection between the Caribbean and Patagonia. Ihering's reconstruction, however, reflected his views of Upper Cretaceous palaeogeography, and his Eocene map (Karte 2) showed that this seaway had closed. It should be borne in mind, when reassessing relatively early palaeogeographic maps which were made without taking the theory of continental drift into account, that they were attempting to explain the distribution of faunas. Ihering's maps are therefore still of relevence in that he was postulating faunal separation of Patagonia and the Caribbean occurring near the beginning of the Tertiary. A further argument against Boltovsky's view is provided by the lack of foraminifera in the Pebasian, which would have straddled the route of his postulated migration. Although ostracods are well known from the Pebasian (Gardner 1927, Purper 1977, Sheppard & Bate 1980), no foraminifera have been found. None have been encountered by the present author, who provided Sheppard & Bate with the matrix yielding their fauna.

The discovery of the La Tagua faunas had immediately suggested a northward extension of the Upper Amazon, Pebasian, Basin, parallel to the still rising Andes, and it seems reasonable to postulate that to the east of the Andes chain, during the Tertiary, there lay a north–south trough up to 500 km wide, occupied by a continually shifting pattern of streams, swamps, and lakes of varying salinity and offering intermittent connections with the Caribbean. It would not seem to be necessary for the connection between the sea and the heart of the basin to be direct at any one time. A series of lakes continually splitting and merging with each other, or perhaps becoming reconnected by streams, would enable taxa to progress gradually from one area to another. Lake Titicaca, with its somewhat unusual, isolated, molluscan fauna (Haas 1955), presumably was once connected, in one of the ways suggested above, to other significantly large bodies of water in which the ancestors of its present faunas lived.

Few previous workers have supported the case for a Caribbean connection. Steinmann (1929: 207) devoted little more than a sentence to the proposition, whilst Oliveira & Leonardos (1943: 640) quoted Maury – without any reference to their actual source – as suggesting a link between the Pebasian Pliocene of the Upper Amazon and the Antilles. They may have been referring either to her views that this correlation was probable (Maury 1925*b*: 17–18) or to a later paper (Maury 1937: 12) in which she commented on Guppy's (1908) unillustrated work on the Comparo Road fauna of Trinidad. Guppy (1908: 114) had identified two Pebasian species, *Anodon batesi* Woodward and *Hemisinus sulcatus* Conrad, but it seems likely that these were misidentifications. Maury's own, more thorough, descriptions of Trinidad fossils (1925*b*) included descriptions of two new Comparo Road species, *Corbicula comparana* Maury, and *Hemisinus comparanus* Maury. Corbiculidae are not present in the Pebasian, whilst Maury's illustrations (1925*b*: pl. 46, figs 9, 10) of *Hemisinus comparanus* show it to differ markedly from any known Pebasian species. It is therefore concluded that there is no molluscan palaeontological evidence for this particular correlation, which Maury stated (1937: 12) had been accepted ever since in the Trinidad literature.

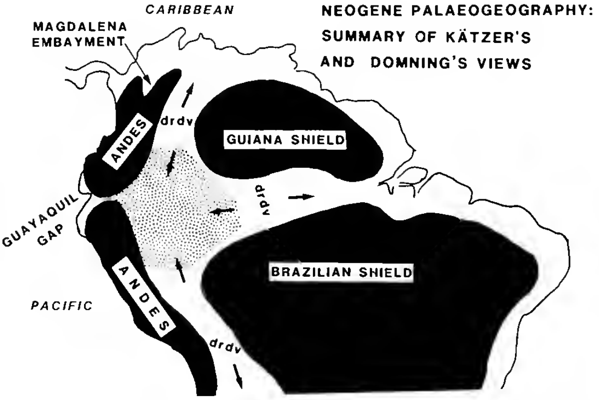


Fig. 453 Neogene palaeogeography, a summary of the views of Kätzer (1903) and of Domning (1984). Key; drdv, drainage divides; black arrows, direction of flow of rivers; stipple, inland brackish- to fresh-water sedimentary basin. The connection between the sedimentary basin and the Pacific Ocean through the Guayaquil Gap closed during the Neogene. In addition, the drainage divide in the present Amazon Valley was eliminated by headward erosion of rivers flowing eastwards as well as others flowing westwards; this resulted in the formation of the present-day Amazon system draining eastwards into the Atlantic Ocean after the closure of the connection with the Pacific. Note that the Magdalena Embayment is shown opening only northwards towards the Caribbean. Modified from Kätzer (1903) and Domning (1984) (compare Fig. 2, p. 170).

There has been more consistent support (Campbell 1970: 20; Domning 1982: 599, 607, 612, maps figs 8, 8a, 9; Fittkau 1974: 105–110, maps figs 10–13; Harrington 1962: 1801–1804, maps figs 27–30; Oliveira *in* Jenks 1956: 55) for Kätzer's (1903) hypothesis (Fig. 453) that there was a connection between the Pacific and the Amazon Basin through the so-called Marañón Portal, which was finally closed during the Miocene. Von Ihering (1927: 68–9) explained the presence of marine shells in the Pebas Beds (which he dated as Eocene) as being owing to the presence of an east–west 'Amazonsmeer' (Karte 2) bisecting the Continent. Grabert (1983), writing later when plate tectonics were generally accepted, referred to the Amazon – Bénoué Graben, stretching from the Pacific coast of South America, across the Atlantic Ocean and through west Africa from Mount Cameroon to Lake Chad.

Domning (1982: 612) gave a useful updated summary of Kätzer's views. Prior to the Miocene Andean orogeny, most of the western and central Amazon Basin drained into the Pacific and the Magdalena, Orinoco and La Plata Basins were separated by drainage divides. The only direct access to the western and central Amazon Basin was from the Pacific, and was eventually lost because of the mountain barriers formed during the Miocene orogeny. This connection is thought to have lain in the Peruvian–Ecuadorian border area, rather to the south of the Bay of Guayaquil. This created an initially brackish basin during the Miocene and Pliocene, with an internal drainage system. Headward erosion of streams eventually broke through the eastern divide which separated this basin from the eastern part of the Amazon Valley, thus initiating the present drainage system.

Domning's own palaeontological evidence does not necessarily support this view fully. He referred (1982: 600) to the presence of the manatee *Potamosiren magdalensis* Reinhart, 1951 in the La Venta fauna of the Miocene Honda Group in the Magdalena Basin of Colombia. He also referred to a probably Plio-Pleistocene specimen from the Jurua Valley (1982: 603–4), identified as cf. *Trichecus* sp., which resembled the modern west Indian rather than Amazonian species of manatee. Either of these could have reached their final destinations just as easily by migration from the Caribbean as through the Marañón Portal.

Campbell (1970: 20) referred to large lakes forming in the Oriente region of Ecuador during the Tertiary after the late Cretaceous Laramide uplift. He argued that there was some connection with the sea through the Marañón Portal because fossiliferous intercalations containing brackish-water faunas were locally present. However, it would seem equally likely that the presence of these faunas in the Oriente indicated some connection with either the Magdalena Basin of Colombia or with the Pebasian Basin, or with both. The main point in favour of the Pacific connection are the reports (Tschopp 1953: 2337–9) of foraminifera in the Tertiary of the Oriente. Foraminifera have not been reported from the Magdalena Valley, nor La Tagua, nor the Pebas Beds, so cannot have migrated from any of these.

Several factors now combine to suggest that there is not as yet any one clear-cut explanation of the history of the origin of the Pebasian Basin and its faunas. During the Tertiary, before the Panamanian land bridge between South and Central America came into being in Plio-Pleistocene times, there existed (Woodring 1965, 1966) a single marine province – termed the Tertiary Caribbean Province – stretching from the coastal strip of north-western Peru, through western Ecuador and Colombia to the Caribbean. Thus, it would be theoretically possible for a species to be distributed throughout this province and migrate into the Pebasian Basin by any route available to it, either from the Pacific or from the Caribbean. The molluscan and other palaeontological evidence is discussed below.

Mytilopsis, a member of the Dreissenacea, is tolerant of wide variation in salinity and may be found in habitats varying from fresh-water rivers to hypersaline, isolated stretches of water subject to reduction by evaporation. Some of its present-day distribution may be the result of introduction to new areas by man, but its fossil occurrences show that it has been capable of unaided migration across definitely marine water. The genus is known to occur in the European Eocene (p. 279) and its earliest western hemisphere occurrences are both probably in the late Oligocene. *M. trigalensis* Olsson, from western Peru, is here placed in the synonymy of the Pebasian species *M. scripta* (Conrad). This species is now also recognized as occurring at La Tagua and in the La Cira Formation of the Middle Magdalena Valley in Colombia. The second Oligocene species, *M. dalli* (Clerc *in* Joukowsky) was first described from the Pacific coastal side of Panama, and is here considered to be a synonym of the living Caribbean *M. sallei* (Recluz). This living species is now recorded (p. 283) from the Pebasian. The genus *Mytilopsis* is unknown from the Atlantic coastal belt of South America and therefore does not appear to have migrated to the Pebasian Basin either up the Amazon or northward from La Plata. At the present day, the most southerly Pacific coast records of the genus is from rivers in northern Ecuador (Olsson 1961, Keen 1971).

Thus, neither of these Oligocene records of *Mytilopsis*, from western Peru and Panama respectively, can be taken as supporting evidence of one possible migratory route into the Amazon Basin rather than another. It is hypothetically possible for the Peruvian *M. scripta* to have entered the basin *via* the Caribbean and for the Caribbean *M. sallei* to have entered from the Pacific coast. Furthermore, the spread of *Mytilopsis* within the basin itself cannot be monitored, because of both the paucity of records and inadequate knowledge of the stratigraphy. Although both species are quite variable, the specimens of *M. scripta* from La Tagua, lying on Rio Caqueta, and La Cira, in the Middle Magdalena Valley about 500 km to the north, are remarkably similar. This raises the possibility of migration southward from the Caribbean up the Magdalena Valley, rather than along a route to the east of the Cordillera Oriental. This by no means exhausts the possibilities: for instance, the faunas of the Oriente of Ecuador are barely known and, in consequence, the region seems not to have been seriously considered as part of a through route for faunal migration.

The recognition of the normally marine family Vitrinellidae in the Pebasian indicates nothing more than some undefined, and possibly distant, connection with the sea. At the present day, rather similar Vitrinellidae occur both in the Caribbean–western Atlantic and Pacific provinces, whilst the fossil record of the family is extremely sparse.

Neritina often has an intertidal distribution analogous to that of *Littorina* in temperate seas. Some *Neritina* species are fresh-water and have been found in mountain streams. At the present day, the genus occurs throughout the Caribbean (Warmke & Abbott 1961), and its range continues along the Atlantic coast to about 27° S in southern Brazil (Rios 1965). On the Pacific coast, it occurs from California southwards to northern Peru at about 5° S (Keen 1971). Records of the genus as fossils in deposits of the coastal strips surrounding South America are rare, probably largely because it was living in inshore habitats where its chances of fossilization were slim. It is apparently unknown in the Tertiary of the Buenos Aires region (Comacho 1966). On the basis of its known fossil and Recent distribution, the only route eliminated for its entrance into the Upper Amazon region is from the Rio de la Plata estuary. As explained on p. 183, *Neritina* *ortoni* Conrad of the Pebasian is not entirely typical of the genus. Its operculum, known only from one specimen, appears to be unusual and certain features of its ventral surface are reminiscent of the marine genera *Velates* (Eocene) and *Smaragdia* (Recent). Deductions made from the distribution of *Neritina* should therefore be viewed with some caution. Nevertheless, examination of all known fossil and living taxa suggests that the greatest resemblance to *N. ortoni* is shown by the single specimen from the Miocene of the Paraguana Peninsula of Venezuela, identified as *N.* aff. *woodwardi* Guppy by Jung (1965). Like *Mytilopsis*, this could have entered the Upper Amazon Basin from either the Caribbean or the Pacific. The only other fossil *Neritina* to be considered are those from the non-marine deposits of the Cuenca Basin, Ecuador. Unfortunately, they are too poorly preserved for worthwhile comparisons to be made with other species. However, enough of their characters can be seen to show that none are close to *N. ortoni*. No deductions can be made concerning their origins.

The Corbulidae are, in general, marine, though some species tolerate the reduced salinity encountered in, for example, estuarine areas. *Erodona*, whose hinge clearly shows it to be unrelated to *Pachydon*, lives in the Rio de la Plata estuary in such profusion that it sometimes forms shell banks. The presence of members of the Corbulidae in the Pebasian is a sure indication of connection with the sea at some stage in the evolution of the basin. All Corbulidae considered here are assigned to the Subfamily Pachydontinae, which is expanded to accommodate not only *Pachydon*, but also *Pebasia* and *Ostomya*, all three of which are extinct, as well as the living *Guianadesma*. *Pachydon* is one of the most important elements of typical Pebasian faunas, and until recently was thought to be endemic. Its recognition here in both the Magdalena Valley deposits and in the La Tagua Beds is crucial evidence for a connection between these three areas. *Pachydon hettneri* (Anderson), described from the Upper Magdalena Valley, occurs at La Tagua. This and other similarities between the faunas of these districts is taken as proof that the La Tagua Beds and the La Cira formation are contemporaneous and were laid down before the Andean orogeny destroyed the link between the Magdalena and Amazon Basins. The only record from the Cuenca Basin of *?Pachydon* sp. is based on a single not very informative mould misidentified as *Pachydon* cf. *iquitensis* (de Greve) by Parodiz *in* Bristow & Parodiz (1982), and here reidentified as *Corbicula cojitamboensis* Palmer, a common fossil species of the Cuenca Basin. The potentially valuable evidence of Rutsch (1952), who reported *Pachydon* in the Neogene of Venezuela, was unfortunately not backed by illustrations of the fossils. Rutsch had seen the material in an oil company's collections in Venezuela and had made his identification, presumably either with the aid of his memory or of notes, after his return to Switzerland and examining the fossils from Iquitos described by de Greve (1938) housed in PIMUZ.

None of the remaining molluscs provides evidence of a connection between the Upper Amazon Basin and the sea. Although they may well belong to families which have marine or brackish members, they themselves do not necessarily fall into those categories.

Both *Pebasia* gen. nov. (p. 315) and *Ostomya* are rare and endemic to the Pebasian. However, fossil species recognized here as belonging to *Guianadesma* have been wrongly assigned in the past to the clearly distinct *Ostomya*. All three of these genera are aberrant Corbulidae. *Pebasia* and *Pachydon* may well share common ancestry. *Ostomya* and *Guianadesma* may also share common ancestry but their connection with ordinary marine members of the family is obscure. *Guianadesma*, now living in rivers of the Guianas and tolerating brackish water, is now recognized fossil from the Neogene of Monogas State, northern Venezuela (Palmer 1945) and from rather poorly preserved material from the La Cira Formation of the Magdalena Valley (Pilsbry & Olsson, 1935). Its distribution suggests some link between these regions which does not necessarily involve areas to their south such as the Pebasian Basin and the Marañón Portal. The strength of this evidence, however, is undermined by the rarity of these genera and the poor preservation of the La Cira occurrence.

Some evidence for a fresh-water to possibly slightly brackish link with the Rio de la Plata estuary is provided by those members of the Hydrobiidae now assigned to the Lithoglyphinae, which is based on the living and Pleistocene European *Lithoglyphus*. The subfamily also occurs in North America. The Argentinian *Potamolithus* has also been assigned to it and may well be the closest living relative of endemic Pebasian genera such as *Eubora* and *Tropidobora*.

The Littoridininae are so ubiquitous that no conclusions can be drawn from their distribution pattern. Furthermore, their radiation in isolated areas such as Lake Titicaca suggests that they may be so subject to rapid morphological diversification that it becomes impossible to unravel their relationships. In contrast to the Littoridininae, the Cochliopinae are so poorly known in South America that their distribution pattern can hardly be used as a source of palaeogeographic evidence. *Nanivitrea*, described living on Cuba and Jamaica, is known from South America by a single Recent Venezuelan species and by *N. colombiana* sp. nov. (p. 213) from the La Tagua Beds.

The Unionacea and Mutelacea (swan mussels) and the river snails of the Thiaridae are nowadays distributed throughout the Amazon Valley as well as most of the other major river systems of the Continent, particularly those with Atlantic drainage. Tertiary fossil species, on the other hand, tend to be concentrated towards the west of the Continent, in the Pebasian, Cuenca and Magdalena Basins. This apparent change in distribution is of little significance beyond drawing attention to the fact that the main areas of non-marine deposition during the Tertiary lay in the north-western quadrant of the Continent.

The distribution of fossil molluscs provides not only evidence of connections between the Upper Amazon Basin and other regions, but also some indication of the extent of that basin. From earlier parts of this section, it has become apparent that there was a connection between the Pebasian Basin, the La Tagua Beds of the Rio Caqueta Valley and the deposits of the Middle and Upper Magdalena Valley. *Longiverena eucosmia* (Pilsbry & Olsson, 1935), described from the Middle Magdalena Valley, is now thought to occur at Iquitos in the Pebasian Basin and in the Cuenca Basin, whilst the rather similar *L. colombiana* sp. nov. occurs at La Tagua. *Pachydon* is known from all these deposits, though the Cuenca record is doubtful. Records of the genus from the Amazon Valley as far apart as Yurimaguas in the west and the Rio Inuya region of the upper Ucuyali Valley in the south (Willard 1966) give some indication that this basin extends well away from the classic Pebasian localities. An intriguing record of rocks 'crowded with *Tellina*' from Bolivia (Mather 1922) could possibly be of *Pachydon* and might mark a


454


455


456

Figs 454–455 *Dyris gracilis* Conrad. Pebasian; Canamá, Peru; Barrington Brown Colln. Front views, × 20. **454**, GG22416; **lectotype** (herein selected) of *Melania bicarinata* Etheridge (1879), originally figured by Etheridge (1879: pl. 7, fig. 7). **455**, GG22421; holotype of *Melania tricarinata* Etheridge (1879), originally figured by Etheridge (1879: pl. 7, fig. 6).

Fig. 456 *Liris scalarioides* (Etheridge). Pebasian; Canamá, Peru; Barrington Brown Colln. GG22419; **lectotype** (herein selected) of *Melania scalarioides* Etheridge (1879), originally figured by Etheridge (1879: pl. 7, fig. 8). Front view, × 20. (See also Fig. 139, p. 206).

southward extension of the basin towards Rio de la Plata, blocked further south by a drainage divide.

The eastern limit of the Pebasian Basin seems to be marked fairly closely by the long-known classic localities. So far, the most easterly Pebasian fossils known are those described from the neighbourhood of São Paulo da Olivença (Costa 1980). Brazilian geologists have mapped both the Pebasian deposits themselves and also apparently later beds stretching as far east as Manaus and encompassing deposits of the Rio Jurua as Solimões Formation. This problem is discussed in more detail in the section on Brazil. It is concluded, however, that they are not an extension of the Pebasian Basin and, where fossiliferous, contain different and younger faunas.

No Tertiary non-marine molluscan fossils have been named from the Oriente of Ecuador, though their presence was noted (Campbell 1970: 20, Tschopp 1953: 2338). The discussion on the Cuenca Basin deposits elsewhere in this work show that its molluscan faunas have far less in common with the Pebasian than formerly suggested (Bristow & Parodiz 1982). The presence of both *Liris* and *Longiverena eucosmia* suggest some connection. The Cuenca Basin is here regarded as part of the same general depositional area as the Pebasian. Differences in the fauna may be interpreted as signifying some difference in facies. It seems possible that the Ecuadorian Oriente provided links between many of the main faunas dealt with herein. It lies between the Cuenca and Pebasian basins, situated to its west and east respectively, and it also lies to the south of both the La Tagua region and the Magdalena Valley. Campbell (1970: 7) regarded it as the eastern margin of a much wider area of sedimentation before the last uplift of the Andes in the late Tertiary, pointing out that it thinned markedly to its east, where only a veneer of Tertiary sediments lay on basement rocks. He also wrote (1970: 8) that the Oriente had palaeogeographic connections with the Magdalena Basins, with a portal between the Central and Eastern Cordilleras of Colombia remaining open until the late Tertiary uplift. This portal probably lay (1970: 25) in the Mocoa area of the Putumayo district.

The palaeogeographic implications of manatee distribution (Domning 1982) has been discussed, p. 352. The occurrence of the crab *Necronectes proavitus* in the Cuenca basin (p. 349) is of particular interest. The species was described from the Gatun Formation (now probably best dated as late Miocene) of Panama. Moreover, *Necronectes* is an uncommon genus (S. F. Morris, BMPD, personal communication). The implication of this is that some connection between the Cuenca Basin and the sea existed and that the source of the *Necronectes* was the Neogene Caribbean Province, which extended down the Pacific Coast (Woodring 1966). Here again, this occurrence cannot be taken as positive proof of one migration route rather than another: the Pacific coast is, however, much closer than the Caribbean to the Cuenca Basin.

To conclude: as suggested above, p. 350, the evidence is that a connection between the Upper Amazon Basin and the sea was necessary in order to explain the character of its molluscan fauna. Sheppard & Bate (1980) provided confirmation of this by describing some ostracods, which they consider to be definitely marine. On balance, it appears that there may have been more than one such connection. One may have been through the Marañón Portal to the Pacific in the

Peruvian–Ecuadorian border region; the second would have been with the Caribbean, either through the Magdalena Valley, or further east, through areas from which such fossil faunas are completely unknown. A non-marine connection northwards towards the northern part of the Continent would help explain the distribution of some freshwater molluscs. In addition, other non-marine connections with the Lower Amazon Valley and with the Rio de la Plata region of Argentina are distinct possibilities.

Palaeoecological summary

As far as is known, the bulk of the material examined was not collected bed-by-bed with palaeoecological studies in mind. It must therefore be taken into account that the total fauna reported from any particular locality probably came from several different horizons. The faunas of more than one locality were sometimes combined by early collectors, such as Hauxwell and Steere, whose fossils were described in works by Conrad (1871*b*, 1874*a*) and Woodward (1871). Hartt (1872) quoted Steere's remarks that some bed was richer in bivalves than gastropods, or vice-versa. Brown (1879: 80) gave some details of specific associations that he had observed at Canamá, but sadly his efforts were largely nullified by the loss of many of his fossils, described in Etheridge (1879), with the result that it is not always possible to update their joint determinations. In some instances, the most reliable guides to co-occurrences and relative abundances of species are provided by the few hand specimens of sediment containing a selection of fossil specimens. Such samples may also show whether it was a life or death assemblage, for instance by the occurrence of bivalves with both valves together. More accurate details of specific associations are provided for some, but by no means all, localities in Pilsbry & Olsson (1935) for Magdalena Valley faunas, and in de Greve (1938) for the collection made by Peyer from Iquitos. Examples of modern, well documented collections are those of Bristow from the intermontane basins of Ecuador (Bristow & Parodiz 1982) and the CAE collections from La Tagua, made by Eden and his associates.

De Greve (1938: 117) lists the views on facies of all authors prior to that date who dealt with Pebasian faunas: these range from fresh-water through to marine. Wrong determinations have coloured such opinions, and even as late as 1970, von Buerlen (p. 334) referred to the presence of *Corbula, Tellina, Cerithium, Mesalia* and *Natica*, which he grouped as marine genera, occuring along with fresh-water *Anisothyris, Unio, Hydrobia, Melania* and others. The records of *Corbula, Tellina* and *Anisothyris* can all be referred to *Pachydon*, whilst *Dyris ortoni* was originally assigned to *Mesalia* by Gabb (1869). The fresh-water *Sheppardiconcha coronatum* was first described under *Cerithium* by Etheridge (1879). This species was described by Gardner (1927: 308) as a member of the *Potamides* group, which she stated is not known to penetrate the upper courses of rivers. The record of *Natica* can only have been based on the erroneous interpretation of a shell boring by Woodward (1871: 102) in a specimen now the holotype of *Eubora woodwardi* Kadolsky (p. 216). *Purpura woodwardi* Roxo (1924) from Três Unidos, belonging to a muricacean genus and not listed by von Buerlen (1970), was first recognized as belonging to *Verena* of the Hemisininae by Santos & Castro (1967). This change is recognized on p. 253: it is now suggested that Roxo's species is synonymous with *V. crenocarina* (Moricand), the type species of the genus and now living in the rivers of eastern Brazil.

Table 2 Habitat preferences of constituents of fossil faunas.

	L/E	if A	r	mm	br	fw	land
Neritina	L	–	C	*	*	*	–
Littoridininae	L	–	VC	*	*	*	–
Dyris, Liris	E	–	VC	–	(*)	(*)	–
Littoridina (s.str.)	L	A	–	–	?*	*	–
Heleobia	L	A	–	*	*	*	–
Cochliopinae	L	–	R	–	*	*	–
Nanivitrea	L	–	R	–	–	*	–
Lithoglyphinae	L	–	FC	–	–	*	–
Potamolithus	L	A	–	–	–	*	–
Eubora, Tropidobora	E	–	C	–	–	(*)	–
Toxosoma	E	–	C	–	–	(*)	–
Vitrinella	L	–	R	*	(*)	–	–
Hemisininae	L	–	FC	–	–	*	–
Sheppardiconcha	E	–	C	–	–	*	–
Basistoma	L	A	–	–	–	*	–
Hemisinus	L	–	R	–	–	*	–
Longiverena	L	–	FC	–	–	*	–
Verena	L	–	R	–	–	*	–
Aylacostoma	L	–	R	–	–	*	–
Hebetancylus	L	–	VR	–	–	*	–
Orthalicus	L	–	VR	–	–	–	*
Unionacea, Mutelacea	L	–	R	–	–	*	–
Mytilopsis	L	–	R	–	–	*	–
Corbulidae	L	–	VC	*	*	–	–
Corbula	L	A	–	*	*	–	–
Pachydon	E	–	VC	–	(*)	(*)	–
Pebasia	E	–	VR	–	(*)	(*)	–
Ostomya	E	–	VR	–	(*)	(*)	–
Guianadesma	L	–	VR	–	(*)	(*)	–

Key to Table:

Column 1,	Living or Extinct
Column 2,	A, if absent in fossil faunas (i.e., genera included for comparative purposes only)
Column 3,	r, rarity: VC, very common; C, common; FC, fairly common; R, rare
Columns 4–7	mm, marginal marine; br, brackish water; fw, fresh water; land. Asterisks denote known distribution of living taxa; asterisks in brackets, the inferred distribution of extinct taxa.

Most of the systematic changes reported above are at superfamilial or familial level. Their net result is the elimination of marine taxa in favour of those living predominantly in a non-marine environment. In addition, not only the Corbulidae but also *Neritina*, *Vitrinella*, and *Mytilopsis* are indicative of some past or present connection with the sea, with the attendant possibility of brackish conditions. Such taxa are of the utmost importance when considering the wider palaeogeographic implications: they are, however, not necessarily reliable guides when dealing with narrower problems such as the assessment of salinity at a particular locality.

Genera of Corbulidae, such as the widespread *Pachydon*, would have evolved from a marine, possibly inshore or even estuarine, ancestor. *Pachydon* possibly lived in a very similar environment to that of the present-day *Guianadesma*, found both in and above the tidal reaches of rivers in the Guianas. The Neritacea are predominantly marine, but include the fresh-water *Theodoxus*. *Neritina* itself is primarily a tropical intertidal genus; at the present day, several Central and South American and Caribbean species have invaded streams, and live in fresh water well away from the tidal zone. None, however, have been found at any considerable distance from the sea. *Mytilopsis* has a very wide salinity tolerance, but, like *Neritina*, and in common with other Dreissenacea, it appears to be absent from stretches of fresh water well away from the sea. The sea would appear to be a necessary part of any route whereby these two genera can establish a bridgehead when colonizing an entirely new area, such as the Tertiary inland basin of north-western South America.

Many of the localities under consideration have yielded faunas giving apparently contradictory evidence of facies, because their constituent species indicate a mixture of different environments. In some cases, this may well be the result of amalgamation of the faunas from different beds within the section, as discussed above. The proportions of the fauna indicating particular environments is always of importance: it would be reasonable to give more weight normally to evidence provided by the more common taxa, rather than to that to be deduced from the presence of rarities or of species only represented by possibly transported broken fragments. When two species occur with fairly similar frequencies, preference should clearly be given to the facies evidence provided by that species indicating a restricted environment rather than by a more tolerant species. Such criteria must be borne in mind when assessing the probable environment of extinct taxa. These points may be illustrated by the distribution of *Mytilopsis*, in particular with reference to its occurrence alongside fresh-water snails of the family Thiaridae, in different faunas.

An example of fresh-water occurrence of *Mytilopsis* is at the Rio Oponcito locality of the La Cira Formation of the Magdalena Valley. The fauna consists of *Mytilopsis* and *Guianadesma*, both of which can exist in a wide range of salinities, occurring with *Verena* and all four of the species of Unionacea and Mutelacea known from this Formation: all of these other taxa are exclusively fresh-water. *Pachydon*, which is present elsewhere in the La Cira Formation, is absent. (Determinations given by Pilsbry & Olsson (1935: 19), revised.)

In the Pebasian of Pichana, on the other hand, *Mytilopsis* is rare. The fauna is dominated by *Pachydon*, with *Neritina, Dyris* and *Liris* also important. None of the other genera present, mainly extinct Lithoglyphinae, are particularly common. Exclusively fresh-water taxa are rare. The Thiaridae and Mutelacea are represented only by the holotypes of *Hemisinus sulcatus* Conrad (*H. brasiliensis* herein, p. 244) and *Anodon batesi* Woodward (*Anodontites* herein), and the only Unionacea found are three juvenile *Diplodon*. Most of the ostracods are indicative of either brackish or marine conditions (Sheppard & Bate 1980), confirming the evidence suggested by the molluscan fauna, in which genera with known or probable wide salinity tolerance, such as *Pachydon*, *Neritina* and *Mytilopsis*, occur in a fauna almost totally lacking in fresh-water elements.

The Pebasian fauna of Iquitos, which includes *Mytilopsis*, is similar in most respects to that of Pichana except that fresh-water Thiaridae are important. *Sheppardiconcha tuberculifera* (Conrad) is reported as being represented by over 250 shells (Conrad 1874*b*, Pilsbry 1944). *S. coronata* (Etheridge), *Longiverena eucosmia* (Pilsbury & Olsson) and *Hemisinus kochi* (Bernardi) also occur (de Greve 1938). It may be suspected that the salinity here was less than at Pichana. Other Pebasian localities in which *Mytilopsis* occurs with abundant Thiaridae are Canamá, Três Unidos, and Puerto Nariño.

Table 3 Breakdown of elements of north-western South American fossil faunas by habitat and known distribution.

(1) Living marginal marine genera indicating links with sea.	*Neritina* *Mytilopsis* *Vitrinella*
(2) Typical modern South American fresh-water genera, with Recent distribution mainly on eastern side of continent.	*Hemisinus* *Verena* *Longiverena* *Aylacostoma* *Hebetancylus* *Diplodon* *Anodontites*
(3) Living in both brackish and fresh water in the Guianas.	*Guianadesma*
(4) Otherwise only known as living mainly in the Caribbean region except for one South American species (from Venezuela). Fresh-water, but with brackish-water relatives.	*Nanivitrea*
(5) Extinct genera first described from and endemic to Pebasian.	*Eubora* *Tropidobora* *Toxosoma* *Pebasia* *Ostomya*
(6) Extinct genera first described from Pebasian and since recognized in other South American fossil faunas.	*Dyris* *Liris* *Pachydon*
(7) Extinct genera first described from Cuenca Basin and since recognized in other South American fossil faunas.	*Sheppardiconcha* *Ecuadorea* (subgenus of *Diplodon*)

It thus appears that *Mytilopsis* occurs in sediments laid down in water of varying salinity: this reflects its present-day wide salinity tolerance. This, in turn, suggests that several of the extinct genera were also tolerant of a range of salinity. Of these, the most important is *Pachydon*, which occurs in many faunas, including all those used above to illustrate the example afforded by *Mytilopsis*. In fact, it might well be that different species of *Pachydon* – and perhaps this applies also to other genera – are indicative of particular salinities: however, I have not pursued this point. The remaining genera in these faunas are dealt with adequately in the palaeogeography section, above. Many occur at several fossil localities indicating a range of salinities, nearly all of which were probably rather low.

Finally, might not ostracods possibly change their facies preferences in a manner analogous to *Pachydon*? This genus, with presumed marine ancestry, has evolved and proliferated in brackish- to fresh-water environments in the Tertiary Upper Amazon Basin. Ostracods are generally accepted as excellent facies indicators, but in this basin their facies may be a matter of inference to a greater extent than usual. All but one of the species described from Pichana and La Tagua by Sheppard & Bate (1980) are new, and one of the supposedly marine genera, which is known from both localities, is also new.

ACKNOWLEDGEMENTS. I must first mention my debt of gratitude to Dr Michael J. Eden (Department of Geography, Royal Holloway and New Bedford College, London University, Egham, Surrey), who initiated this project by bringing to my attention fossils collected by himself and other members of the Colombian Amazonas Expedition from La Tagua. My thanks are due also to his colleagues, Dr D. F. M. McGregor of the same Department, and Dr J. A. Morelo V of Istituto Geografico 'Augustin Codazzi', Bogotá. Mr Nout Weeda, formerly with CAE, kindly forwarded additional collections from the La Tagua region and from Puerto Nariño, Colombia, at Eden's request.

I would also like to thank the many Curators who have kindly lent me material from the collections in their charge: Dr George M. Davis, Dr Robert Robertson, Mary Garback and Elizabeth Scott (ANSP); Dr Peter Jung (Basel NHM); Dr Barry Roth, Anthony Summers, Robert van Syoc (CAS); Dr Edouard Lanterno (Geneva NHM); Priv.-Doz. Dr Ernst Josef Fittkau, Dr Rosina Fechter (Munich); Dr Bruce Bell, Dr Edward Landing, Karin Young (NYSM); Dr K. A. Hünermann (PIMUZ); Dr Peter Hoover (PRI); Dr A. S. Tompa (Univ. Michigan); Dr Richard S. Houbrick (USNM). Dr Dan C. Marelli of Ecological Analysts Inc., 2150 John Glenn Drive, Concord, California, who had previously given specimens of *Mytilopsis sallei* (Recluz) from eastern Mexico, kindly collected a large sample of living *M. leucophaetus* (Conrad) from Florida on my behalf.

Among the many colleagues who have provided support and encouragement, I would specially like to mention: Dr John Whittaker (BMPD), for his advice on foraminiferal zonation; Mr Richard V. Melville (ICZN), for his helpful comments on the work of Spix & Wagner (1827); Mr George Bate of Honiton, Devon, for his help in sorting some of the micro-molluscan samples; Dr Noel Morris (BMPD), for his general interest in the work; Dr John Taylor and Dr David Brown (both BMZD), who read the manuscript; Dr Winston Ponder, for his expert advice on the Rissoacea; and Dietrich Kadolsky (Texaco), for his comments on the Dreisseniidae.

Particular thanks are due to the numerous members of staff of this Museum's Photographic Studio, under Mr Peter Green, who were responsible for all the light photographs, and to members of its Electron Microscope Unit, under Mr Don Claugher, for their help and advice. The author is responsible for the stereoscan electron micrographs used.

APPENDIX: GUIDES TO LOCALITIES

Entries marked * are dealt with in more detail in separate individual sections, at the pages indicated.

A. Peru

Aguaytia river valley. 110 km S of Contamana, 25 km W of Ucuyali valley. Bassler collected (as *Anisothyris*) *Pachydon erectus* Conrad, *P. carinatus* Conrad, *P. obliquus* Gabb and (as *Liris*) *Dyris tuberculata* (de Greve); det. Willard (1966: 69).

Ambayacú, Rio. 3° 19′ S, 71° 51′ W. Flows south into R. Marañón. Pebas and Old Pebas are near the mouth of this river.

Ampiyacú, Rio. Alternative spelling of above.

Barreiras Braga. Not in gazetteer. On Rio Javari, downstream from Canamá. Brown (1879: 78) reported shells similar to those of Canamá.

Cachiyacú, Quebrada. 7° 22′ S, 74° 52′ W. Tributary joining R. Ucuyali just S of Contamana. Good exposures of Ucuyali Formation (Kummel 1948: 1260).

Canamá (* p. 327).

Cocani, or **Coccani**, Quebrada. 10° 32′ S, 73° 58′ W. Lower part of Rio Inuya valley. Bassler collected in 1922 fossils identified (Willard 1966: 69) as *Anisothyris* sp. and *Calyptraea* sp. (The latter could, however, be a misidentification of *Tropidobora*.)

Cochaquinas (* under Pichana, p. 324).

Contamana. 7° 21′ S, 75° 03′ W. Ucayali Formation (Kummel 1948: pl. 1).

Contamana Group. Fossils collected by Singewald (1928) and described by Pilsbry (1944) from **Pachitea River** section (q.v.). Kummel (1948: 1259–60) stated that the folded Contamana Group, of probable Eocene to Miocene age, was overlain by flat-lying Pliocene beds, which he inferred might be the same as the Pebas Beds of the Amazon Valley between Iquitos and Tabatinga. He mentioned no fossils from these overlying beds, however, and later went on to discuss the **Ucayali Formation** (q.v.).

Cushabatay, Rio. Flows eastwards to join R. Ucayali N of Contamana. Good exposures of **Ucayali formation** (Kummel 1948: 1260).

Filipe del Acquia. 10 km upstream from Iquitos on Rio Marañón. Bassler collected in 1928 *Corbula* sp. (?=*Pachydon*), *Anisothyris* (=*Pachydon*) *obliqua* (Gabb), *A. carinata* Conrad, *A. hauxwelli* Woodward (=*A. tenua* Gabb), *Lunatia* sp. (?=*Eubora*), *Turbonilla* (=*Liris*) *minuscula* (Gabb), *Isaea* (=*Dyris*) *ortoni* Gabb; ident. Willard (1966: 65–6).

Inuya, Rio. 10° 41′ S, 73° 30′ W (see **Cocani**).

Iquitos. 3° 42′ S, 73° 42′ W (* p. 331; see also **Filipe del Acquia**).

Iquitos Formation. Rivera (1956: 49) referred to Iquitos Formación of Steinmann (1930: 213; not seen by me). In the first, German, edition of this work (1929: 206), Steinmann referred merely to the Neogene of Iquitos without erecting a Formation.

Machira Creek. Good exposures of **Ucayali Formation** (q.v.) 5 km S of Cachiyacú (7° 22′ S, 74° 57′ W), near Contamana (Kummel 1948: 1258, 1260).

Manseriche (see **Pongo de Manseriche**).

Mazan, Rio. Near confluence of Rio Mazan and Rio Napo (3° 28′ S, 73° 11′ W), 30 km N of Iquitos, Bassler collected in 1924 *Pachydon carinatus*, *P. amazonensis*, *P. obliquus*, *P. erectus*, *Neritina ortoni*, *N. etheridgei*, *Pseudolacuna macroptera*, *Hydrobia confusa* and *Liris minuscula*. (Willard 1966: 68). This fauna is Pebasian.

Negro Urca. On Rio Negro, 200 km NW of Iquitos (3° 05′ S, 72° 40′ W). Bassler collected in 1926: Serpulae (?), *Lingula, Triplodon latouri* (Pilsbry & Olsson 1935), *Pachydon cuneatus, P. obliquus, P. erectus, P. amazonensis, Neritina amazonensis, Eubora crassilabris, Hydrobia* sp. (internal casts only, ?= *Dyris*), *Longiverena tuberculifera*. (Willard 1966: 66). The fauna is Pebasian. The record of *Lingula* is surprising and has not been checked by me. It might be a fresh-water limpet of the Ferrisiidae.

Omaguas. 4° 08′ S, 73° 15′ W. Fossils reported by natives (Conrad 1871*b*: 192).

Pachitea, Rio. Section in Red Beds, now **Contamana Group** (q.v.). Singewald's collection (1928: 463) was identified by Pilsbry, and eventually described by him (1944). Apparently (Singewald 1928: 457) near Quebrada Pumayacú (9° 10′ S, 74° 40′ W). Also mentioned in Kummel (1948: 1259).

Paucarparta. On Rio Marañón (4° 13′ S, 73° 18′ W). Singewald collected species of *Diplodon*, described by Marshall (1928*a*) as *Prodiplodon singewaldi* and *P. paucarpartensis*. Assumed to be Pebasian.

Pebas. 3° 20′ S, 71° 49′ W (* p. 322; see also **Pichana**).

Pebas beds, Pebas clays. Terms used by Hartt (1872: 54).

Pebas Formation. Term introduced by Costa (1980: 635). The term Pebasian is used informally in this paper for Pebasian Fauna, Pebasian Age and Pebasian Basin. See discussion in Introduction, p. 169.

Pichana (* p. 324). Near **Cochaquinas** (q.v.), on S side (= right bank) of Rio Marañón (3° 31′ S, 71° 43′ W).

Pichua. Alternative, incorrect spelling of **Pichana**.

Pongo de Manseriche. 4° 20′ S, 77° 15′ W. (Pongo = canyon or gorge). Just below confluence of Rio Santiago and Rio Marañón, about 800 km above Iquitos. Singewald (1927: 491) referred to poorly preserved fossils, possibly similar to those from the Red Beds of Rio **Pachitea** (q.v.). Singewald also noted, outside the pongo, grey shale which included lignitic coal and brackish-water (un-named) Pliocene fossils, which he equated with those of Pebas.

Old Pebas (* under **Pichana**, p. 324). On left (north) bank of Rio Marañón, about 2 miles (*c*. 3 km) below mouth of Rio Ampiyacú.

Red Beds (see **Pachitea**).

Rumi Tuni. (2° 05′ S, 74° 27′ W). Valley of Rio Napo, 225 km N of Iquitos. Bassler (? 1925) collected *Pachydon amazonensis, P. obliquus, P. carinatus, P. erectus, Congeria?* (= *Mytilopsis*), nacreous bivalve fragments (? naiades) in coquina, *Neritina etheridgei, Hydrobia confusa, Longiverena tuberculifera* and '*Ampullina (Mesalina) ortoni* (Gabb)' (?= *Dyris ortoni*). Other collections from the neighbourhood yielded similar faunas and also *Arca* (?), *Triplodon latouri* (Pilsbry & Olsson), *Aperistoma* and *Eubora crassilabra*; det. Willard (1966: 66–68). Most of these species are typical of the Pebasian: the exceptions may well be misidentifications.

Santa Isabel (see **Yurimaguas**).

Sarayaquilla/Saroyaquilla, Rio. Flows eastwards to join Rio Ucayali (7° 00′ S, 75° 10′ W). Excellent exposures of Ucayali Formation (Kummel 1948: 1260).

Três Unidos (*p. 329). On Peruvian bank of Rio Javari, 4° 24′ S, 71° 13′ W.

Ucuyali Formation (Pliocene to Recent). About 30 m of horizontal clays etc., lying discordantly on Contamana Group in region of rivers Ucayali, Sarayaquilla and Cushabatay. Unnamed plant, fresh-water bivalve and gastropod fossils reported (Kummel 1946: 134; 1948: 1260). Fauna is possibly Pebasian (see **Aguaytia, Cocani** and **Ucayali Valley**).

Ucayali Valley. Willard (1966: 69) reported that between 1924 and 1926, Bassler collected a few isolated 'Pliocene' fossils including *Anisothyris* (=*Pachydon*) as well as *Ampullina* and *Natica*, which are almost certainly misidentified. Willard also tentatively identified a large conical gastropod as *Itaborahia*, a possible member of the pulmonate Superfamily Bulimulacea (tree snails). The genus is known only by its type species in the alleged Miocene of Brazil (Zilch 1960: 485). If *Pachydon* is truly present, then the age is likely to be Pebasian rather than later (Pleistocene or Holocene as in the case of the Porto Peter locality in Brazil, p. 359, whose age was reviewed by Simpson, 1961).

Yarina. Upstream from Isla Navarra, close to Rio Huallaga. Boss & Parodiz (1977: 118, figs 10, 11) described, figured and dated as Eocene an unidentifiable member of the Thiaridae or Pleuroceridae as *Doryssa corrosensis* (Pilsbry & Olsson, 1935), originally described from the Palaeogene Los Corros Formation of the Magdalena Valley, Colombia. The Yarina fossil might be of any age between Cretaceous and Quaternary.

Yurimaguas. 5° 54′ S, 76° 05′ W on Rio Huallaga. At Santa Isabel on Rio Paranapura, to the west of Yurimaguas, Bassler collected (? in 1925) many examples of small species identified by Willard (1966: 70) as *Semisinus* (=*Hemisinus*) and *Anisothyris* (=*Pachydon*).

B. Brazil

Both the classic localities of Canamá (Brown 1879, Etheridge 1879) and Três Unidos (Oliveira & Carvalho 1924, Roxo 1924) are on the Peruvian (north) bank of Rio Javari, and not, as is often indicated, in Brazil: see above. Several Brazilian localities, whose faunas have not been fully described, are mentioned in *Projeto Radambrasil* (published as *Levantamento Recurs. Nat.*, by Departamento Nacional da Produção Mineral (=DNPM).) in which the results of a multi-disciplinary study by numerous authors are published. The volumes of most relevance to the Pebasian are **14** (Fernandes *et al.* 1977), **15** (del'Arco *et al.* 1977) and **18** (Lourenço *et al.* 1978). All the localities in question, whether their faunas are Pebasian or not, were treated by them as Solimões Formation. Some are dealt with in some detail below. Several of the more interesting are discussed in the section on **Três Unidos**, p. 329.

Aquidaba. 6° 30′ S; 69° 40′ W, on Rio Jurua; see under **Três Unidos**. It has yielded fossils once thought to be Pebasian, but is now shown to have a very different fauna (del'Arco *et al.* 1977).

Atalaia do Norte. 4° 20′ S, 70° 12′ W. Right (south) bank of Rio Javari, about 20 km upstream from Benjamin Constant. Costa (1980) redescribed and figured several gastropod species, all belonging to the Rissoacea, from the State of Amazonas, Brazil. The following few species were recorded from this locality. No bivalves were included. The full extent of the fauna is unknown.

original determinations	**revised determinations**
Hydrobia ortoni (Gabb)	*Dyris ortoni* (Gabb)
Hydrobia lintea (Conrad)	*Dyris lintea* (Conrad)
Liris minuscula (Gabb)	*Liris scalarioides* (Etheridge)
Dyris gracilis Conrad	*Dyris gracilis* Conrad
Lacuna (Ebora) crassilabris (Conrad)	*Eubora* sp. (*woodwardi* Kadolsky or *crassilabris*)
Pseudolacuna macroptera Boettger	*Toxosoma eborea* Conrad

The genera *Toxosoma* and *Eubora* and all the species listed above are endemic to the Pebasian. All appear to occur equally with both brackish- and fresh-water elements of the Pebasian fauna at other localities.

Canamá (see p. 327; Peru, *not* Brazil).

Fracoas (Cachoera das). See under **Três Unidos** (p. 329), mis-spelling of **Tracoás** in Roxo (1924).

Igarapé da Extrema. (* p. 331.) See also under **Três Unidos** (Igarapé = stream).

Ipiranga or **Ypiranga**. 2° 59′ S, 69° 35′ W, on right (south) bank of Rio Içá, State of Amazonas. Section referred to, without mentioning fossils (Oliveira & Carvalho 1924: 73, map and perfil 21). Fernandes *et al.* (1977: 49 *et seqq.* and map) show this locality as Solimões Formation, and they list (1977: 72) *Hydrobia, Lacuna, Pseudolacuna, Neritina, Congeria, Pachydon cuneatus* Conrad and *P. tenuis* Gabb, along with *Chara*, ostracods and fish teeth, which were collected by Oliveira & Carvalhos in 1919, now in Departamento Nacional da Produção Mineral (*Projeta Radambrasil*). This fauna appears to be typical of the Pebasian and indicates brackish conditions. *Mytilopsis* is frequently misidentified as *Congeria*. Ipiranga and São Paulo da Olivença are probably among the two most easterly localities from which Pebasian fossils have been recorded.

Jesumira, Acré Territory. A small tributary of the Mõa, which in turn flows into the Juruá just above Cruzeira do Sul. The record of *Pachydon* (Maury 1937) is almost certainly incorrect (see **Porto Peter**).

Jutaí, Rio. Series of vertebrate localities in river banks, approximately 150 km SE of Benjamin Constant (see **Solimões Formation** and **Três Unidos**).

Poreré. 3° 20′ S, 67° 30′ W (Purper 1977: 355, map). Costa (1980) described from boring CPCAN II *Hydrobia tricarinata* Boettger (=*Dyris tricarinata*), *H. lintea* and *Dyris gracilis*. These indicate that the fauna is Pebasian. Purper (1977: 354) described ostracods, one of which was subsequently named *Cyprideis purperi purperi* by Sheppard & Bate (1980: 99). Its type locality is Pichana and it is only known from the Pebasian. It is thought to be a brackish-water species.

Porto Peter, Acré Territory. Simpson (1961) demonstrated that the small molluscan and plant biotas described from here were not Pebasian, but came from an infilling of an oxbow lake of either Recent or very late Pleistocene age. Maury (1937) had described poorly preserved bivalves from here and from **Jesumira** (q.v.) as *Anisothyris ACREANA* sp. nov. and *A.* cf. *ovata* (Conrad) respectively. According to Dr Dwight Taylor (U.S. Geol. Surv.), whose opinion Simpson (1961: 622) quoted, these were quite likely to belong to the Corbiculacea (found in the living Amazon fauna). It should be pointed out, however, that some of the reasons they gave for rejecting these fossils as members of the genus *Pachydon* (= *Anisothyris*) of the Corbulidae are oversimplified: some species of *Pachydon* are equivalve and do not have prominent beaks. On the other hand the roughly circular outline of these fossils probably points to the Corbiculacea rather than the Corbulidae.

Quixito, Rio. 4° 29′ S, 70° 18′ W (* p. 329, with **Três Unidos**).

Rebeiros. Not in Gazetteer; situated on southern (Brazilian) bank of Rio Solimões, about 32 km below confluence with Rio Javari; see section on **Canamá** (p. 327) for reports by Brown (1879) of fossiliferous clays.

São Paulo da Olivença. 3° 27′ S, 68° 48′ W (Purper 1977: 355, map). Costa (1980) described from borehole CPCAN III a very similar fauna to that occurring at Atalaia do Norte (q.v. for redeterminations): *Hydrobia tricarinata, H. lintea, Liris minuscula, Dyris gracilis, Lacuna (Ebora) crassilabris* and *Pseudolacuna macroptera*. Purper (1977) described ostracods subsequently named by Sheppard & Bate (1980) as *Cyprideis purperi purperi* (see **Poreré**) and (1980: 101) *Otarocyprideis elegans*, which is also a brackish-water species whose type locality is Pichana.

Solimões Formation. Vast areas of the Amazon Valley in Brazil, from the Peruvian and Colombian borders to as far east as Manaus were mapped as Solimões Formation in *Projeto Radambrasil* (see head of this section). This was dated as Pliocene and Pleistocene. Some localities have yielded Pebasian molluscan faunas: Três Unidos, Atalaia do Norte, Poreré and Tamanduá are among those mapped as Solimões Formation. However, at other localities mapped as this Formation (Aquidaba, Porto Peter), the molluscan fauna appears to be more like that of the present-day Amazon region. The Solimões vertebrate faunas have never been found with Pebasian molluscs and may be of entirely different ages (see **Jutaí**, Rio).

Tamanduá. 3° 57′ S, 68° 10′ W (Purper 1977: 355, map). Costa (1980) described from boring CPCAN I three Pebasian gastropods *Hydrobia lintea, Lacuna (Ebora) crassilabris* and *Pseudolacuna macroptera* (see Atalaia do Norte for redeterminations). *Otarocyprideis elegans* is among the few ostracods known from there (see **São Paulo da Olivença**).

Tracoás or **Tracoá** (Cachoera da). (* p. 330). Incorrectly spelt as Fracaos in Roxo (1924). See also under **Tres Unidos** (Cachoera = waterfalls or rapids).

Três Unidos (*p. 329). On Peruvian bank of Rio Javari.

Ypiranga (see **Ipiranga**).

REFERENCES

Aceñoloza, F. G. & Toselli, A. J. 1981. *Geologia del noroeste Argentino*. 212 pp., illustr. (unnumbered). San Miguel de Tucumán.

Adam, W. 1960. *Faune de Belgique, Mollusques*, **1**, *Mollusques terrestre et dulcioles*. 402 pp., pls A–D (colour), 163 text-figs. Inst. Roy. Sci. nat. Belge, Brussels.

Adams, A. 1860. On some new genera and species of Mollusca from Japan. *Ann. Mag. nat. Hist.*, London, (3) **5**: 405–413.

Adams, C. B. 1850. *Monograph of* Vitrinella, *a new genus of Turbinidae*. 10 pp. Amherst, Mass.

—— 1851. Descriptions of new fresh-water shells which inhabit Jamaica. *Contributions to Conchology* **1** (9): 174–175; and in *Ann. Lyc. nat. Hist.*, New York, **5**: 98–99.

Adams, H. 1860. Description of a new genus of freshwater bivalve Mollusca, belonging to the family Corbulidae, from the collection of Hugh Cuming, Esq., *Proc. zool. Soc. Lond.*, **28**: 203.

—— & **Adams, A.** 1854–58. *The genera of Recent Mollusca.* **2**, 661 pp.; **3**, 138 pls. London.

Agassiz, L. 1845. *Nomenclatoris zoologici, nomina systematica, generum animalium ... Mollusca.* xiii + 98 pp. Solothurn.

—— 1846–48. *Nomenclatoris zoologici ... index universalis.* viii + 393 pp. (1846); x + 1035 pp. (1848 reissue). Solothurn.

Ageitos de Castellanos, Z. J. 1967. Catalogo de los moloscos Marinos Bonaerenses. *Anales Comn. Invest. cient. Prov. B. Aires*, **8**: 1–365, pls 1–26.

Ahlfeld, F. & Branisa, L. 1960. *Geologia de Bolivia.* 245 pp., 89 text-figs, folding map. Instituto Boliviano del Petroleo, La Paz.

Albers, J. C. & Martens, E. von 1860. *Die Heliceën nach naturlicher Verwandschaft.* 2nd edn, 359 pp. Leipzig.

Altena, C. O. van Regteren 1966. Vitrinellidae (marine Mollusca, Gastropoda) from Holocene deposits in Surinam. *Zool. Meded.*, Leiden, **41**: 233–241, figs 1–6.

—— 1968. The Holocene and Recent marine bivalve Mollusca of Surinam. *Stud. Fauna Suriname and other Guyanas*, The Hague, **10**: 152–179, text-figs 145–152.

—— 1969–75. The marine Mollusca of Suriname (Dutch Guiana), Holocene and Recent. 1, General Introduction. *Zool. Verh. Leiden*, **101**. 49 pp., 4 pls, 4 tabs, 1 text-fig. (1969). 2, Bivalvia and Scaphopoda. *Loc. cit.*, **119**. 99 + 1 pp., 11 pls, 25 text-figs (1971). 3, Gastropoda and Cephalopoda. *Loc. cit.*, **139**. 104 pp., 11 pls, 43 text-figs (1975).

Ancey, C. F. 1888. Étude monographique sur le genre *Pyrgulopsis. Bull. Soc. malac. Fr.*, **5**: 185–202.

Anderson, F. M. 1927. Non-marine Tertiary deposits of Colombia. *Bull. geol. Soc. Am.*, New York, **39**: 591–644, pl. 14 (map), 15 text-figs.

—— 1928. Notes on Lower Tertiary deposits of Colombia and their molluscan and foraminiferal fauna. *Proc. Calif. Acad. Sci.*, **17**: 1–28, pl. 1, 9 text-figs.

—— 1929. Marine Miocene and related deposits of northern Colombia. *Proc. Calif. Acad. Sci.*, **18**: 73–212, pls 8–23.

Andrussov, N. 1897–98. Fossile und lebende Dreissensiidae eurasiens. *Trudy̆ S. Petersb. Obshch. Estest. (Sect. Geol. Min.)*, **25**. 683 + 115 pp. (1898); 25 pls (1897). [In Russian with German summary].

Arco, J. O. del' *et al.* 1977. Folha S. B. 19 Juruá, 1-Geologia. *Levantamento Recurs. Nat.*, Rio de Janeiro, **15**: 1–88, 12 pls, 16 text-figs, coloured folding map.

Baker, F. (with contribution by **Pilsbry, H. A.**). 1914. The land and fresh-water mollusks of the Stanford expedition to Brazil. *Proc. Acad. nat. Sci. Philad.*, **65**: 618–672, pls 21–27.

Baker, H.B. 1956. Family names in the Pulmonata. *Nautilus, Philad.*, **69**: 128–139.

—— 1963. Type land snails in the Academy of Natural Sciences of Philadelphia. Part II. Land Pulmonata, exclusive of North America north of Mexico. *Proc. Acad. nat. Sci. Philad.*, **115**: 191–259.

Bartsch, P. 1907. New mollusks of the family Vitrinellidae from the West coast of America. *Proc. U. S. nat. Mus.*, **32**: 167–176, 11 text-figs.

Beneden, P. J. van 1835. Histoire naturelle et anatomique du *Dreissena polymorpha* ... genre nouveau dans la famille de mytilacées. *Bull. Acad. r. Belge*, Brussels, **2**: 25–26, 44–47, 166–169.

Bernardi, A. C. 1856. Description de coquilles nouvelles. *J. Conch. Paris*, **5**: 82–84, pl. 3, figs 6, 7.

Binder, E. 1968. Répartition des mollusques dans la lagune Ébrié (Côte d'Ivoire). *Cah. O.R.S.T.M. sér. Hydrobiol.*, Paris, **2** (3–4): 2–34, 5 text-figs.

Binney, W. G. 1865. Land and fresh water shells of North America, part III. *Smithson. Misc. Collns*, **144**. viii + 120 pp., 232 figs.

Blainville, H. M. D. de 1825–27. *Manuel de malacologie et de Conchyliologie.* 664 pp., 1 table (1825); 87 pls (1827). Paris.

Blow, W. H. 1969. Late Middle Eocene to Recent planktonic foraminiferal biostratigraphy. *In* Bronnimann, P. & Renz, H. H. (eds), *Proceedings of the first international conference on planktonic microfossils*, Geneva, 1967, **1**:199–422; 54 pls, 43 text-figs. Leiden, 1969.

Boettger, O. 1878. Die Tertiarfauna von Pebas am oberen Marañón. *Jahrb. K.-K. geol. Reischsanstalt Wien*, **28**: 485–540, pls 13, 14.

Bold, W. A. van den 1976. Distribution of species of the tribe Cypreidini (Ostracoda, Cytherideidae) in the Neogene of the Caribbean. *Micropaleont.*, New York, **22**: 1–42, pls 1–5, 18 text-figs.

Boltovsky, E. 1958. The foraminiferal fauna of the Rio de la Plata and its relation to the Caribbean area. *Contr. Cushman Fdn foramin. Res.*, **9** (1): 17–21, 2 text-figs.

Bonarelli, G. 1927. Fósiles de la Formación Petrolifera. *Boln. Acad. nac. Cienc. Córdoba*, **30**: 51–115, 6 pls.

Bonetto, A. A. 1967. La superfamilia Unionacea en la Cuenca Amazonica. *Atas do Simpôsio sôbre a biota Amazonica*, Rio de Janeiro, **3** (Limnologia): 63–82, 10 text figs.

Borello, A. V. (ed.) 1966. See Comacho, H. H.

Boss, K. J. & Parodiz, J. J. 1977. Paleospecies of neotropical ampullariids and notes on other fossil non-marine South American gastropods. *Ann. Carneg. Mus.*, **46** (9): 107–127, 18 figs.

Bosworth, T. O. 1922. See Woods, H.

Bristow, C. R. 1973. *Guide to the geology of the Cuenca Basin, Southern Ecuador.* 54 pp., 3 figs. The Ecuadorian Geological and Geophysical Society, Quito.

—— 1981. An annotated bibliography of Ecuadorian geology. *Overseas Geol. Miner. Resour.*, London, **58**. 38 pp.

—— & **Hoffstetter, R.** 1977. *Lexique Stratigraphique International* **5**. *Amérique Latine*, Fasc. **5a** (2), *Ecuador.* 410 pp., 10 figs. Centre National de la Recherche Scientifique, Paris.

—— & **Parodiz, J. J.** 1982. The stratigraphical paleontology of the Tertiary non-marine sediments of Ecuador. *Bull. Carnegie Mus. nat. Hist.*, **19**. 53 pp., 24 text-figs, 1 table, 1 map.

Brot, A. 1870. Catalogue of the Recent species of the family Melaniidae. *Am. Jl Conch.*, **6** (2) Appendix: 271–325.

—— 1872. *Notices sur les Mélanies de Lamarck, conservées dans le Museé Delessert et sur quelques espèces nouvelles ou peu connues.* 55 pp., 4 pls. Geneva.

—— 1874–79. Die Melaniaceen (Melaniidae). *In* Küster, H. C. (ed.), *Systematisches Conchylien-Cabinet von Martini und Chemnitz.* 488 pp., 49 pls. Nürnberg.

Brown, A. P. & Pilsbry, A. A. 1914. Fresh water mollusks of the Oligocene of Antigua. *Proc. Acad. nat. Sci. Philad.*, **66**: 209–213, pl. 9.

Brown, C. B. 1879. On the Tertiary deposits on the Solimões and Javary rivers in Brazil (with an appendix by R. Etheridge). *Q. Jl geol. Soc. Lond.*, **35**: 76–88, pl. 7.

—— & **Lidstone, W.** 1878. *Fifteen thousand miles on the Amazon and its tributaries.* 520 pp., illustr., map. London.

Bruguière, J. G. 1792*a*. Catalogue des coquilles envoyées de Cayenne, à la Société d'histoire naturelle de Paris par M. Le Blond. *Act. Soc. Hist. nat. Paris*, **1** (1): 126.

—— 1792*b*. Sur une nouvelle espèce de mulète. *J. Hist. nat.*, Paris, **1**: 107, pl. 6, figs 3, 4.

—— 1792*c*. Sur une nouvelle coquille du genre de l'*anodontite. J. Hist. nat.*, Paris, **1**: 131–136, pl. 8, figs 6, 7.

Buerlen, K. 1970. *Geologie von Brasilien.* 444 pp., 76 text-figs, 6 text-tables & 1 map, 1 table, 2 pullouts. Berlin and Stuttgart.

Burch, J. B. 1976. Outline of classification of Australian terrestrial molluscs (native and introduced). *Jl malac. Soc. Australia*, **3** (3): 127–156.

Bush, K. J. 1897. Revision of gastropods referred to *Cyclostrema, Adeorbis, Vitrinella*, and related genera; with descriptions of some new genera and species belonging to the Atlantic fauna of America. *Trans. Conn. Acad. Arts Sci.*, **10**: 97–144, pls 22, 23, 10 text-figs.

Butler, J. W. 1939. Geology of Middle and Upper Magdalena Valley. *World Petroleum*, New York, **10**: 95–100, 2 text-figs (un-numbered), 1 table.

—— 1942. Geology of Honda District, Colombia. *Bull. Am. Ass. Petrol. Geol.*, Chicago, **26** (5): 793–837, 14 text-figs.

Campbell, C. J. 1970. *Guidebook to the Puerto Napo area, eastern Ecuador with notes on the regional geology of the Oriente Basin.* 39 pp., 7 text-figs. Ecuadorian Geological and Geophysical Society, Quito.

—— & **Bürgl, H.** 1965. Section through the eastern Cordillera of Colombia, South America. *Bull. geol. Soc. Am.*, **76**: 567–590, 1 pl. (folding section), 6 text-figs.

Chenu, J. C. 1858. *Illustrations conchyliologiques*, **2**. 58 pls. Paris.

—— 1859–62. *Manuel de conchyliologie et de paléontologie conchyliologique.* **1** (1859), vii + 508 pp., 3707 text-figs. **2** (1862), 327 pp., 1236 text-figs. Paris.

Clarke, J. M. 1906. List of type specimens of Tertiary fossils from the Pebas on the Maranhao River, Brazil, described by T. A. Conrad in the American Journal of Conchology, 1871. *Rep. N.Y. St. Mus. nat. Hist.*, Albany, **58** (1) (for 1904): 131–133.

Clerc, M. 1906. See Joukowsky.

Clessin, S. See Miller.

Collins, J. S. H. & Morris, S. F. 1976. Tertiary and Pleistocene crabs from Barbados and Trinidad. *Palaeontology*, London, **19** (1): 107–131, pls 17–20.

Comacho, H. H. 1966. *In* Borello, A. V. (ed.), *Paleontografia bonaerense*, **3**. *Invertebrados.* xxv + 159 pp., 19 pls. La Plata.

Conrad, T. A. 1831. Description of fifteen new species of Recent and three of fossil shells, chiefly from the coast of the United States. *Jl Acad. nat. Sci. Philad.*, **6**: 256–268, pl. 11.

—— 1853. Synopsis of the family of naiades of North America. *Proc. Acad. nat. Sci. Philad.*, (**1853**): 243–269.

—— 1858. Description of a new genus of the family Dreissenidae. *Proc. Acad. nat. Sci. Philad.*, (**1857**): 167.

—— 1871*a*. Report of the meeting of October 6th 1870. *Am. Jl Conch.*, **6** (3): 14 (published 4th April 1871).

—— 1871*b*. Descriptions of new fossil shells of the upper Amazon. *Am. Jl Conch.*, **6**: 192–198, pls 10, 11.

—— 1874*a*. Remarks on the Tertiary clay of the Upper Amazon with descriptions of new shells. *Proc. Acad. nat. Sci. Philad.* (**1874**): 25–32, pl. 1.

—— 1874*b*. Description of two new fossil shells of the Upper Amazon. *Proc. Acad. nat. Sci. Philad.* (**1874**): 82–83, pl. 12, figs 4, 5.

Cooke, C. W. 1919. Tertiary mollusks from the Leeward Island and Cuba. *In* Vaughan, T. W., Contributions to the geology and palaeontology of the West Indies. *Publs Carnegie Instn, Washington*, **291** (Contrib. no 4): 105–156, 16 pls.

Cossmann, M. 1906–21. *Essais de Paléoconchologie Comparée*, **7**; 261 pp., 14 pls, 22 text-figs (1906); **8**; 248 pp., 4 pls, 78 text-figs (1909); **10**; 292 pp., 12 pls, 63 text-figs (1915); **12**; 348 pp., 6 pls, text-plates A–C, 121 text-figs (1921). Paris.

Costa, E. V. 1980. Gastrópodes Cenozóicos do Alto Amazonas (Estado do Amazonas), Brasil. *Anais Acad. bras. Cienc.*, Rio de Janeiro, **52**: 867–891, pls 1–3, 2 text-figs.

—— 1981. Revisão gastrópodes fósseis da localidade do Três Unidos, Formação Pebas, Plioceno do Alto Amazonas, Brasil. *Anais II Congresso Latino-Americano Paleontologia, Porto Alegre, Abril 1981*: 635–649, 1 pl., 1 text-fig.

Cox, L. R. 1969. General features of Bivalvia. *In* Moore, R. C. (ed.) 1969, *Treatise on Invertebrate Paleontology*, N, Mollusca **6** (1): N2–N129, figs 1–86. Lawrence, Kansas.

Cuvier, G. L. C. F. D. 1834 (translated F. S. Voigt). *Das Thierreich, geordnet nach seiner Organisation*, **3** *Mollusken*. xviii + 621 pp. Leipzig.

Dall, W. H. 1872. Note on the genus *Anisothyris*, Conrad, with a description of a new species. *Am. J. Conch.*, **7**: 89–92, pl. 16, figs 14–15.

—— 1898. Tertiary Fauna of Florida. *Trans. Wagner free Inst. Sci. Philad.*, **3** (4): vii, 571–947, pls 23–35.

Davies, A. M. 1971–75. See Morley Davies, A.

Davis, G. M. & Pons da Silva, M. C. 1984. *Potamolithus*: morphology, convergence, and relationships between hydrobioid snails. *Malacologia* **25** (1): 73–108, 20 text-figs.

de Folin, 1867. See Folin.

de Gregorio, 1890. See Gregorio.

de Greve, 1938. See Greve.

d'Orbigny, 1835*a*, 1835–47, 1850. See Orbigny.

de Porta, 1965, 1966, 1974. See Porta.

del'Arco *et al.*, 1977. See Arco.

Doering, A. 1884. Apuntos sobre la fauna de moluscos de la República Argentina. *Boln Acad. nac. Cienca Córdoba*, **7**: 457–474, 2 text-figs.

Domning, D. P. 1982. Evolution of Manatees: a speculative history. *J. Paleont.*, **56**: 599–619, 9 text-figs.

Dunker, W. 1848. Diagnoses molluscorum novorum. *Z. malakozool.*, Hannover, **5**: 177–186.

—— 1853. Neue Mytilaceen. *Z. malakozool.*, Hannover, **10**: 82–92.

—— 1855. *De septiferis genere Mytilaceorum et de Dreisseniis*. 26 pp. Marburg.

Eames, F. E. 1953. The Miocene–Oligocene boundary and use of the term Aquitanian. *Geol. Mag.*, London, **90** (6): 388–392.

—— 1971–75. See Morley Davies, A.

Eden, M. J., McGregor, D. F. M. & Morelo V, J. A. 1982. Geomorphology of the middle Caqueta basin of eastern Colombia. *Z. Geomorph.*, Berlin and Stuttgart, (N.F.) **26**: 343–364, 7 text-figs, 5 tables, 3 photos.

Escarbassiere, R. M. & Almeida, P. 1976. Aspectos biologicos y ecologicos de *Mytilopsis sallei* Recluz (Bivalvia – Eulamellibranchia) en areas adyacentes a la Laguana de Unare (Estado Anzoategui, Venezuela). *Acta biol. venez.*, Caracas, **9**: 165–193, 16 text-figs.

Etheridge, R. 1879. Notes on the Mollusca collected by C. Barrington Brown, Esq., A. R. S. M., from the Tertiary deposits of Solimões and Javary Rivers, Brazil. *Q. Jl geol. Soc. Lond.*, **35**: 82–88, pl. 7.

Eydoux, F. 1841–52. See Souleyet, F. L. A.

Fechter, R. 1983*a*. Liste des Typenmaterials der von J. B. v. Spix in Brasilien gesammelten. Gastropoda. *Spixiana*, Munich, Suppl. **9**: 221–223.

—— 1983*b*. Das Typenmaterial der von J. B. v. Spix in Brasilien gesammelten. Unionacea. *Spixiana*, Munich, Suppl. **9**: 225–255, pls A–M.

Fernandes, P. E. *et al.* 1977. Folha SA. 19 Içа, 1-Geologia. *Levantamento Recurs. Nat.*, Rio de Janeiro, **14**: 1–123, pls 1–23, text-figs 1–27.

Fischer, P. 1858. Enumeration monographique des expèces du genre *Dreissena*. *J. Conch. Paris*, **7**: 123–134.

Fischer, P. H. 1880–87. *Manuel de conchyliologie et de paléontologie conchyliologique*. xxiv + 1369 pp., frontisp., pls 1–2, map, text-figs. Paris.

—— **& Crosse, H.** 1880–1902. *Études sur les mollusques terrestres et fluviatiles du Mexique et du Guatemala. Mission Scientifique au Mexique et dans l'Amérique centrale. Recherches Zoologiques*. **2** (7). 731 pp., 72 pls. Paris.

Fittkau, E. J. 1974. Zur ökologischen Gliederung Amazoniens, I. Die erdgeschichtliche Entwicklung Amazoniens. *Amazoniana*, Kiel, **5** (1): 77–134, 15 text-figs.

Fleming, J. 1822. *The philosophy of zoology*. **1**, l + 432 pp., 5 pls; **2**, 618 pp. Edinburgh and London.

—— 1828. *A history of British animals*. xxiii + 565 pp. Edinburgh.

Flores, C. & Cáceres, R. 1973. La familia Neritidae (Mollusca: Archaeogastropoda) en las aguas costeros de Venezuela. *Boln Inst. oceanograf. Cumana*, **12** (2): 3–13, pls 1–3, 1 text-fig.

Folin, L. de 1867. *Les méléagrinicoles, espèces nouvelles*. 74 pp., 6 pls. Le Havre.

Forcart, L. 1948. Beschreibungen neuer Schnecken von Celebes, Rotti, Neu Guinea und Venezuela. *Verh. Naturf. Ges. Basel*, **49**: 45–54, pl. 1.

Fryer, G. 1961. The developmental history of *Mutela bourguignati* (Ancey) (Mollusca: Bivalvia). *Phil. Trans. R. Soc. Lond.*, **244B**: 259–298, 78 figs.

Gabb, W. M. 1869. Descriptions of fossils from the clay deposits of the Upper Amazon. *Am. J. Conch.*, **4**: 197–200, pl. 16.

Gaillard, M. C. 1974*a*. Una nueva *Littoridina* de Albufera. *Neotropica*, Buenos Aires, **20** (62): 104–106, 3 text-figs.

—— 1974*b*. Sobre nuevas *Littoridina* de la Republica Argentina. *Neotropica*, Buenos Aires, **20** (63): 140–143, 9 text-figs.

Gardner, J. A. 1927. A recent collection of late Pliocene invertebrates from the head-waters of the Amazon. *J. Wash. Acad. Sci.*, **17** (20): 505–509.

—— 1948. Mollusca from the Miocene and Lower Pliocene of Virginia and North Carolina. Part 2, Scaphopoda and Gastropoda. *Prof. Pap. U. S. geol. Surv.*, **199B**: 179–310, pls 24–38.

Germeraad, J. H., Hopping, C. A. & Muller, J. 1968. Palynology of Tertiary sediments from tropical areas. *Rev. Palaeobot. Palynol.*, Amsterdam, **6**: 189–348, 18 pls, 17 text-figs.

Gill, T. N. 1871. Arrangement of the families of mollusks. *Smithson. Misc. Collns*, **10** (227). xvi + 49 pp.

Goldfuss, G. A. 1820. *Handbuch der Zoologie*, **1**. xlvi + 696 pp., 2 pls. Nürnberg.

Grabert, H. 1983. Das Amazonas-Entwässerungssystem in Zeit und Raum. *Geol. Rdsch.*, Stuttgart, **72** (2): 671–683, 2 text-figs, 1 table.

Gray, J. E. 1834. Mollusca. pp. 1–138, pls 1–40, index 595–601. *In* Griffith, E. & Pidgeon, E., *The Mollusca and Radiata arranged by the Baron Cuvier with supplementary additions to each order*. London.

—— 1840. *Synopsis of the contents of the British Museum*, 42nd edn, ... *Eastern zoological gallery*: 88–152. London.

—— 1847. A list of the genera of Recent Mollusca, their synonyms and types. *Proc. Zool. Soc. Lond.*, **15**: 129–219.

—— 1854. *List of the shells of South America in the collection of the British Museum, collected and described by M. Alcide d'Orbigny, in the Voyage dans l'Amerique Méridionale*. 89 pp., London.

—— 1840. *In* Turton, W., *A manual of the land and fresh-water shells of the British Islands with figures of each of the kinds*. ix + 324 pp., 12 pls, text illustr. (numerous unnumbered figs). London.

Gregorio, A. de 1890. Monographie de la faune Eocènique de l'Alabama. *Annls Géol. Paléont.*, Palermo, **7**: 1–156, pls 1–17 (Jan). **8**: 157–316, pls 18–46 (April).

Greve, L. de 1938. Eine Molluskenfauna aus dem Neogen von Iquitos am Oberen Amazonas in Peru. *Abh. schweiz. palaont. Ges.*, Basel, **61**. 133 pp., 10 pls, 25 text-figs.

Gundlach, J. *In* **Poey** 1865, 1866; see Poey.

Guppy, R. J. L. 1866. On the Tertiary Mollusca of Jamaica. *Q. Jl geol. Soc. Lond.*, **22**: 281–295, pls 16–18.

—— 1908. On some fossil shells from Comparo Road, Trinidad. *Bull. misc. Inf. R. bot. Gdns Trin.*, **59**: 114–115. (See Harris, G. D., 1921, reprinted).

Haas, F. 1949*a*. Land- und Susswasser mollusken aus dem Amazonas-Gebiete. *Arch. Molluskenk.*, Frankfurt a.M., **78**: 149–156, pl. 7.

—— 1949*b*. On fresh water mollusks from the Amazonian region. *Anales Inst. Biol. Univ. México*, **20**: 301–314, 6 figs.

—— 1950. Some land and fresh water mollusks from Pará State, Brazil. *Nautilus*, *Philad.*, **64**: 4–6.

—— 1952. South American non-marine shells: further remarks and descriptions. *Fieldiana, Zoo.*, Chicago, **34** (9): 107–132, text-figs 14–26.

—— 1955. The Percy Sladen Trust Expedition to Lake Titicaca in 1937. Part xvii, Mollusca: Gastropoda. *Trans. Linn. Soc. Lond.*, (3) **1** (3): 275–308, 28 text-figs.

—— 1969*a*. Superfamilia Unionacea. *Das Thierreich* **88**. x + 663 pp. Berlin.

—— 1969*b*. Superfamily Unionacea. *In* Moore, R. C. (ed), 1969. *Treatise on Invertebrate Paleontology*, N, Mollusca **6** (1): N411–N467, figs D15–D57. Kansas.

Hammen, T. van der 1957. Periodicidad climática yevolución de floras suramericanas del Maestrichtiana y del Terciario. *Boln. geol. Bogota*, **5** (2): 5–48, 1 pl., 9 text-figs.

—— 1961. Estratigrafia del Terciario y Maestrichtiano Continentales y tectogenesis de Los Andes Colombianos. *Boln. geol. Bogota*, **6**: 73–128, 7 pls.

Hanley, S. 1842–56. *Illustrated and descriptive catalogue of Recent bivalve shells*. xviii + 392 pp., 24 pls. London.

Harrington, H. J. 1962. Palaeogeographic development of South America. *Bull. Am. Ass. Petrol. Geol.*, **46** (10): 1773–1814, 34 text-figs.

Harris, G. D. 1921. (See Guppy, R. J. L., 1908). A reprint of the more inaccessible paleontological writings of Robert John Lechmere Guppy. *Bull. Am. Paleont.*, **8**: III, IV, 149–346, pls 5, 14, frontisp.

Hartt, C. F. 1872. On the Tertiary basin of the Marañón. *Am. J. Sci. Arts*, (3) 4: 53–58.

Hemming, F. (ed.) 1956. See ICZN.

Herrmannsen, A. N. 1846–52. *Indicis generum malacozoorum primordia*. **1**: i–xxvii, 1–637 (1846–7); **2**: xxviii–xlii, 1–717 (1847–9); index: i–v, 1–140 (1852). Cassel.

Hershler, R. 1985. Systematic revision of the Hydrobiidae (Gastropoda: Rissoacea) of the Cuatro Cienegas Basin, Coahuila, Mexico. *Malacologia*, **26** (1–2): 31–123, 52 text-figs.

Hertlein, L. G. & Hanna, G. D. 1949. Two new species of *Mytilopsis* from Panama and Fiji. *Bull. Sth Calif. Acad. Sci.*, **48**: 13–18, pl. 4.

Hidalgo, J. G. 1868. Description d'espèces nouvelles. *J. Conch. Paris.*, **16**: 352–353, pl. 13, figs 5, 6.

Hopping, C. A. 1967. Palynology and the oil industry. *Rev. Palaeobot. Palynol.*, Amsterdam, **2**: 23–48, 2 pls, 12 text-figs.

Hubendick, B. 1955. The Percy Sladen Trust Expedition to Lake Titicaca. Part xviii, the Anatomy of the Gastropoda. *Trans. Linn. Soc. Lond.*, (3) **1**: 309–327, 95 text-figs.

Hubricht, L. 1940. A subterranean snail from an artesian well. *Nautilus, Philad.*, **54**: 34–35.

I. C. Z. N., Direction 41. 1956. I(a) DREISSENIDAE (correction of DREISSENADAE) Gray, (J. E.), 1840 (type genus: *Dreissena* van Beneden, 1835) (first published in correct form as DREISSENIDAE by Gray (J. E.), 1847). (Class Pelecypoda) (Opinion 351) (Name no. 76). *Opin. Decl. int. Commn zool. Nom.*, London. (Hemming, F., ed.)

Ihering, H. von 1890. Revision der von Spix in Braisilien gesammelten Najaden. *Arch. Naturgesch.*, Berlin, **(1890)**: 117–170, pl. 9.

—— 1893. Najaden von S. Paulo und die geographische Verbreitung der Susswasser-Faunen von Sudamerika. *Arch. Naturgesch.*, Berlin, **(1893)**: 45–140, pls 3, 4.

—— 1902. As Melanias do Brazil. *Revta Mus. paul.*, São Paulo, **5**: 653–682, 5 text-figs.

—— 1907. Les mollusques fossiles du Tertiare et du Crétacé Supérieur de l'Argentine. *An. Mus. nac. Hist. Nat. B. Aires* (3) **7**. xiii + 611 pp., 18 pls.

—— 1910. Descriptions of two new species of *Potamolithus*. *Nautilus, Philad.*, **24**: 15.

—— 1927. *Die Geschichte des Atlantischen Ozeans*. vii + 256 pp., 9 maps. Jena.

Jaume, M. L. & Abbott, R. T. 1948. A new Cuban species of the amnicolid genus *Nanivitrea*. *Revta Soc. malac. Carlos de la Torre*, Havana, **6** (1): 5–8, 4 text-figs.

Jenks, W. F. (ed.) 1956. Handbook of South American geology. An explanation of the geologic map of South America. *Mem. geol. Soc. Am.*, **65**. xviii + 378 pp., numerous maps and text-figs.

Johnson, R. I. 1971. The types and figured specimens of Unionacea (Mollusca: Bivalvia). *Bull. Br. Mus. nat. Hist.* (Zool.), **20** (3): 75–108, pls 1, 2.

—— 1974. Lea's unionid types. *Spec. Occ. Publs Dep. Moll. Mus. Comp. Zool. Harv.*, **2**. 159 pp.

—— **& Baker, H. B.** 1973. The types of Unionacea (Mollusca: Bivalvia) in the Academy of Natural Sciences of Philadelphia. *Proc. Acad. nat. Sci. Philad.*, **125**: 145–186, pls 1–10.

Jonas, J. H. 1844. Beschreibung neuer Melanien. *Z. Malakozool.*, Hannover, **(1844)**: 49–52.

Jones, M. L. & Rutzler, K. 1975. Invertebrates of the upper chamber, Gatun Locks, Panama Canal, with emphasis on *Trochospongilla leidii* (Porifera). *Mar. Biol. Wash.* **33**: 57–66, 6 text-figs.

Joukowsky, E. & Clerc, M. 1906. Sur quelques affleurements nouveaux de roches tertiares dans l'Isthme de Panama. *Mém. Soc. Phys. Hist. nat. Genève*, **35** (2): 155–178, pls 6, 7, 5 text-figs.

Jung, P. 1965. Miocene Mollusca from the Paraguana Peninsula, Venezuela. *Bull. Am. Paleont.*, Ithaca, **49** (223): 387–652, pls 50–79.

—— 1969. Miocene and Pliocene mollusks from Trinidad. *Bull. Am. Paleont.*, **55** (247): 293–657, pls 13–60, 4 text-figs.

Kadolsky, D. 1980. On the taxonomic position, the species and the paleoecological significance of the genera *Eubora*, *Toxosoma* and *Littoridina* (?) in the Pliocene Pebas Formation of the Upper Amazon region (Gastropoda: Prosobranchia). *Veliger*, **22**: 364–375, 15 text-figs.

Kätzer, F. 1903. *Grundzüge der Geologie des unteren Amazonas gebietes (des Staates Pará in Brasilien)*. 296 pp., 16 pls, 261 figs. Leipzig.

Keen, M. 1960. Superfamily Neritacea Rafinesque, 1815. *In* Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology*, **I** (Mollusca 1): 1275–290, figs 179–189. Lawrence, Kansas.

—— 1968. West American mollusk types in the British Museum (Natural History), IV. Carpenter's Mazatlan collection. *Veliger*, **10** (4): 389–439, pls 55–59, 171 text-figs.

—— 1969. Dreissenacea: N643–644, fig. E125; Myacea: N690–699, figs E153–159; Pandoracea: N843–852, figs F21–27. *In* Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology*, N, Mollusca **6** (2). Lawrence, Kansas.

—— 1971. *Sea shells of tropical West America*, edn 2. x + 1064 pp., 22 col. pls, 3292 figs, 8 text-figs, 6 maps. Stanford.

Keferstein, W. *In* Bronn, H. G. & Keferstein, W. 1862–66. *Die Klassen und Ordnungen des Thier-Reichs wissenschaftlich dargeskellt in Wort und Bild. Malacozoa* 3 (2): 521–1500, pls 45–135, text-figs 35–136. Leipzig & Heidelberg.

Kummel, B. 1946. Estratigrafía de la región de Santa Clara. *Boln. Soc. geol. Peru*, Lima, **19**: 133–142, 4 photo, 3 maps (lam.).

—— 1948. Geological reconnaisance of the Contamana region, Peru. *Bull. geol. Soc. Am.*, New York, **59** (12): 1217–1265, 6 pls, 11 text-figs.

Küster, H. C. 1839–62. Die Flussperlmuscheln (*Unio* et *Hyria*). *Systematisches Conchylien-Cabinet von Martini und Chemnitz*. (Küster edition). 318 pp., 100 pls. Nürnberg.

—— (continued by **Clessin, S.**). 1838–76. Die Gattung *Anodonta*. *Systematisches Conchylien-Cabinet von Martini und Chemnitz*. (Küster edition). 288 pp., pls A, 1–87. Nürnberg.

—— (——). 1840–90. Die Familie der Mytilidae. *Systematisches Conchylien-Cabinet von Martini und Chemnitz*. (Küster edition). 170 pp., 36 pls. Nürnberg.

Lamarck, J. B. P. A. de 1809. *Philosophie zoologique*, **1**. xxv + 428 pp. Paris.

—— 1818. *Histoire naturelle des animaux sans vertèbres*, **5**. 612 pp. Paris.

—— 1822. *Histoire naturelle des animaux sans vertèbres*, **6**, part 2. 232 pp. Paris.

Lea, I. 1831–34. Observations on the Naiades, and descriptions of new species of that and other families. *Trans. Am. phil. Soc.*, (n.s.) 4: 63–121, pls 3–18.

—— 1852. Description of a new genus (*Basistoma*) of the family Melaniana, together with some new species of American Melaniae. *Trans. Am. phil. Soc.*, (n.s.) **10**: 295–302, pl. 30.

—— 1859. Descriptions of twenty-one new species of exotic Unionidae. *Proc. Acad. nat. Sci. Philad.*, **(1859)**: 151–154.

—— 1860. Descriptions of exotic Unionidae. *J. Acad. nat. Sci. Philad.*, (2) **4**: 235–273, pls 33–45.

Liddle, R. A. & Palmer, K. v. W 1941. The geology and paleontology of the Cuenca–Azogues–Biblian region, Provinces of Canar and Azuay, Ecuador. *Bull. Am. Paleont.*, **26**: 357–418, pls 50–59.

Lourenço, R. S. *et al.* 1978. Folha SA. 20 Manaus, 1-Geologia. *Levantamento Recurs. Nat.*, Rio de Janeiro, **18**: 1–164, pls 1–40, text-figs 1–28, col. map.

Macsotay, O. 1968. Edad y paleoecologia de las formaciones Tuy y Siquire, a base de su fauna de moluscos fosiles. *Boln Geol. Minist. Minas Venez.*, Caracas, **9** (19): 297–307, pl. 1.

Marcus, E. & E. 1963*a*. Mesogastropoden von der Küste São Paulos. *Abh. math.-naturw. Kl. Akad. Wiss. Mainz*, (1963) **1**. 105 pp., 18 pls, 95 text-figs.

—— —— 1963*b*. On Brazilian supralittoral and brackish water snails. *Bolm Inst. Oceanogr. S. Paulo*, **13** (2): 41–52, 9 text-figs.

Marelli, D. C. & Berrend, R. E. 1978. A new species record for *Mytilopsis sallei* (Récluz) in Central America (Mollusca: Pelecypoda). *Veliger*, **21** (1): 144.

—— **& Gray, S.** 1983. Conchological redescriptions of *Mytilopsis sallei* and *Mytilopsis leucophaeta* (Bivalvia: Dreissenidae) of the brackish Western Atlantic. *Veliger*, **25** (3): 185–193, 1 pl., 6 text-figs.

Marinescu, F. 1973. Les mollusques pontiens de Tirol (Banat Roumain). *Memle Inst. geol. Rom.*, Bucharest, **18**: 7–56, 12 pls.

Marshall, W. B. 1917. New and little-known species of South American freshwater mussels of the genus *Diplodon*. *Proc. U. S. natn. Mus.*, **53** (2209): 381–388, pls 50–55.

—— 1925. Microscopic sculpture of pearly fresh-water mussel shells. *Proc. U. S. natn. Mus.*, **67** (4): 1–14, pls 1–4.

—— 1928*a*. New fossil pearly fresh-water mussels from deposits of the Upper Amazon of Peru. *Proc. U. S. natn. Mus.*, **74** (3): 1–7, 1 pl.

—— 1928*b*. New fresh-water and marine bivalve species from Brazil and Uruguay. *Proc. U. S. natn. Mus.*, **74** (17): 1–7, pls 1–4.

—— 1931*a*. *Ruganodontites*, a new sub-genus of South American pearly, freshwater mussels. *Nautilus, Philad.*, **45**: 16–21.

—— 1931*b*. *Ruganodontites*, a genus of South and Central American and Mexican pearly fresh-water mussels. *Proc. U. S. natn. Mus.*, **79** (23): 1–16, pls 1, 2.

—— 1934. Two new species of pearly fresh-water mussels. *J. Wash. Acad. Sci.*, **24**: 78–81, 6 text-figs.

—— **& Bowles E. O.** 1932. New fossil fresh-water mollusks from Ecuador. *Proc. U. S. natn. Mus.*, **82** (5). 7 pp., 1 pl.

Martens, E. von 1863–79. Die Gattung *Neritina*. *Systematisches Conchylien-Cabinet von Martini und Chemnitz*. (Küster edition). 303 pp., pls A, 1–23. Nürnberg.

—— 1873. Die Binnenmollusken Venezuelas. *In: Festschrift zur feier des hundertjahrigen Bestehens der Gesellschaft Naturforschender Freunde zu Berlin*: 157–225, pls 1, 2.

—— 1884. *Zoological Record (Mollusca)*. (**1883**). 113 pp., London.

—— 1890–1901. Land and Freshwater Mollusca. 706 pp., 44 pls. *Biologia centam.*, London.

Martinez Escarbassiere & Almeida. 1976. See Escarbassiere, R. M. & Almeida, P.

Mather, K. F.. 1922. Front ranges of the Andes between Santa Cruz, Bolivia and Embarcacion, Argentina. *Bull. geol. Soc. Am.*, 33: 703–764, 21 text-figs.

Matthews, S. C. 1973. Notes on open nomenclature and on synonymy lists. *Palaeontology*, **16**: 713–719.

Maury, C. J. 1917. Santo Domingo type sections and fossils. *Bull. Am. Paleont.*, **5** (29): 165–413, pls 29–65.

—— 1925*a*. Fosseis terciarios do Brazil com descripção de novas formas cretaçeas. *Monografias Serv. Geol. Min. Brasil*, Rio de Janeiro, **4**. v + 711 pp., 24 pls.

—— 1925*b*. A further contribution to the paleontology of Trinidad (Miocene horizons). *Bull. Am. Paleont.*, **10** (42): 1–250 (152–402), pls 1–43 (12–51).

—— 1937. Argillas fossiliferas do Pliocenio do Territorio do Acre. *Bolm Serv. geol. miner. Bras.*, Rio de Janeiro, 77. 29 pp., 2 unnumbered plates.

Meek, F. B. 1876. A report on the invertebrate Cretaceous and Tertiary fossils of the Upper Missouri country. *Rep. U. S. geol. geogr. Surv. Territ.*, **9**. lxi + 629 pp., pls 1–45.

Mermod, G. 1956. Les types de la collection Lamarck au Muséum de Genève. Mollusques vivantes III. *Rev. Suisse Zool.*, Geneva, **59**: 23–97, 59 text-figs.

Miller, K. 1879. Die Binnenmollusken von Ecuador. *Malakozool. Bl.*, Cassel, (n.s.) **1**: 117–203, pls 4–15.

Modell, H. 1942. Das naturlijke System der Najaden. *Arch. Molluskenk.*, Frankfurt a.M., **74**: 161–191, pls 5–7.

—— 1950. Südamerikanische Najaden der Gattungen *Castalia, Schleschiella* und *Ecuadorea*. *Arch. Molluskenk.*, Frankfurt a.M., **79**: 135–146.

Moore, D. R. 1972. *Cochliolepis parasitica*, a non-parasitic marine gastropod, and its place in the Vitrinellidae. *Bull. mar. sci.*, Coral Gables, **22** (4): 881–899, 12 figs.

Moricand, J. 1860. Note sur le *Melanopsis brasiliensis*. *J. Conch. Paris*, **8**: 301–304, pl. 12, figs 6, 7.

Moricand, S. 1838. Premier supplément au mémoire sur les coquilles terrestres et fluviatiles de la Province de Bahia, envoyées par M. Blanchet. *Mém. Soc. Phys. Hist. nat. Genève*, **8** (1): 139–148, pl. 3.

—— 1841. Second supplément au mémoire sur les coquilles terrestres et fluviatiles de la Province de Bahia. *Mém. Soc. Phys. Hist. nat. Genève*, **9**: 57–64, pl. 4.

Morlet, L. 1884. Description d'espèces nouvelles de coquilles recueillies par M. Pavie, au Cambodge. *J. Conch. Paris*, **32**: 386–403, pls 11–13.

—— 1892*a*. Diagnoses molluscorum novorum in Indo-China collectorum. *J. Conch. Paris*, **40**: 82–86.

—— 1892*b*. Description d'espèces nouvelles provenant de l'Indochine. *J. Conch. Paris*, **40**: 315–329, pls 6–8.

Morley Davies, A. 1971, 1975. *Tertiary faunas*, revised edn by Eames, F. E. **1** (1971), 571 pp. **2** (1975), 447 pp., illustr. London.

Morrison, J. P. E. 1939. Notes on the genera *Potamopyrgus* and *Lyrodes*. *Nautilus, Philad.*, **52**: 87–88.

—— 1943. A new type of fresh-water clam from British Guiana. *Nautilus, Philad.*, **57** (2): 46–52, pl. 8.

—— 1945. *Durangonella*, a new hydrobiine genus from Mexico, with three new species. *Nautilus, Philad.*, **59**: 18–23; pl. 3, figs 1–10.

—— 1946. The nonmarine mollusks of San José Island, with notes on those of Pedro González Island, Pearl Islands, Panama. *Smithson. Misc. Collns*, **106** (6). 49 pp., 3 pls.

—— 1952. World relations of the melanians (an abstract). *Rep. Am. malac. Un. Pacif. Div.*, Buffalo, N.Y., (**1951**): 6–9 (not seen).

—— 1954. The relationships of old and new world melanians. *Proc. U. S. natn. Mus.*, **103**: 357–394.

Morton, B. 1970. The evolution of the heteromyarian condition in the Dreissenacea (Bivalvia). *Palaeontology*, **13**: 563–572, 8 text-figs.

—— 1981. The biology and functional morphology of *Mytilopsis sallei* (Recluz) (Bivalvia: Dreissenacea) fouling Visakhapatnam Harbour, Andhra Pradesh, India. *J. moll. Stud.*, **47**: 25–42, 12 text-figs.

Moura, P. de & Wanderley, A. 1938. Noroeste de Acre. Reconheçimentos geologicos para petróleol. *Bolm Dep. nac. Prod. min. Rio de J.*, **26**: 1–116.

Müller, O. F. 1774. *Vermium terrestrium et fluviatilium, seu animalium infusoriorum, helminthicorum, et testaceorum, non marinorum succinta historia*. **2**. xxxci + 214 pp., indexes (10 pp., unpaginated). Copenhagen and Leipzig.

New York State Museum 1906. See Clarke, J. M.

Newton, R. B. 1891. *Systematic list of the Frederick E. Edwards collection of British Oligocene and Eocene Mollusca in the British Museum (Natural History)*. xxviii + 365 pp. London.

Neumayr, M. 1884. Zur Morphologie des Bivalvenschlosses. *Sber. Akad. Wiss. Wien*, **88** (1) (1883): 385–419, 2 pls.

Oliveira, A. I. de 1956. Brazil. *In* Jenks, W. F. (ed.), Handbook of South American geology, an explanation of the geologic map of South America. *Mem. geol. Soc. Am.*, **65**: 1–62, tabs 1–7, map.

—— **& Carvalho, P. G. de** 1924. Linhito no Alto-Solimões. Estudos geologicos na fronteira com o Peru. *Bolm Serv. geol. miner. Bras.*, Rio de Janeiro, 8: 53–76, map, 2 text-figs.

—— **& Leonardos, O. H.** 1943. *Geologia do Brazil*, 2nd edn. xxvi + 813 pp., 212 text-figs, and numerous unnumbered illustrations, folding map. Rio de Janeiro.

Oliveira, P. E. 1940. Fósseis do Território do Acre e do Estado do Amazonas. *Mineraç. Metall.*, Rio de Janeiro, 5 (27): 118.

Oliveira Roxo, M. G. de. See Roxo, M. G. de Oliveira.

Olsson, A. A. 1931–32. Contributions to the Tertiary paleontology of northern Peru. Part 4, the Peruvian Oligocene. *Bull. Am. Paleont.*, Ithaca, **17**: 99–260, pls 13–33 (1931). Part 5, The Peruvian Miocene. *Loc. cit.* **19**: 1–272, pls 1–24, 3 text-figs (1932).

—— 1961. *Panamic-Pacific pelecypoda*. 574 pp., 86 pls. Pal. Res. Inst., Ithaca, N.Y.

—— **& Harbison, A. *et al.*** 1953. Pliocene Mollusca of Southern Florida with special reference to those from North Saint Petersburg. *Monogr. Acad. nat. Sci. Philad.*, 8. 457 pp., 65 pls.

—— **& McGinty T. L.** 1958. Recent marine mollusks from the Caribbean coast of Panama with the description of some new genera and species. *Bull. Am. Paleont.*, **39** (177): 1–58, pls 1–5.

d'Orbigny, A. 1835*a*. Synopsis terrestrium et fluviatilium molluscorum in suo per Americam meridionalem itinere ab A. d'Orbigny collectorum. *Mag. Zool. Paris, Classe V, Mollusques*, **61, 62**. 44 pp.

—— 1835–47. Mollusques. *In: Voyage dans l'Amérique Meridionale éxecuté penant les années 1826–1833*. **5**. xliii + 758 pp.; Atlas, **9** (2), 85 pls. Paris.

—— 1850. *Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés*. **2**. 427 pp. Paris.

Ortmann, A. E. 1911. The anatomical structure of certain exotic Naiades compared with that of the North American forms. *Nautilus, Philad.*, **24**: 103–108; 114–130; 127–131, pls 6, 7.

—— 1921. South American naiades; a contribution to the knowledge of the freshwater mussels of South America. *Mem. Carneg. Mus.*, **8** (3): 451–684, pls 34–48, 4 text-figs.

Padron, J. L. 1956. Vénézuéla. *Léxique strat. int.*, Paris, **5** Amérique Latine (3). 740 pp.

Pain, T. 1956. Revision of the Melaniidae of British Guiana and Surinam. *Basteria*, Lisse, **20**: 91–105, 11 text-figs.

Palmer, K. v. W. 1945. Fossil fresh-water Mollusca from the State of Monogas, Venezuela. *Bull. Am. Paleont.*, Ithaca, **31**: 1–34, pls 1–3.

Parodiz, J. J. 1969. The Tertiary non-marine Mollusca of South America. *Ann. Carneg. Mus.*, Pittsburgh, **40**. 242 pp., 19 pls, 7 maps.

—— **& Bonetto, A. A.** 1963. Taxonomy and zoogeographic relationships of the South American Naiades (Pelecypoda: Unionacea and Mutelacea). *Malacologia*, **1**: 179–213, 17 text-figs, 2 maps.

Partsch, P. 1835. Über die sogenannten Versteinerten Ziegenklauen aus dem Platensee in Ungarn, und ein neues, urweltliches geschlecht zweischaliger Conchylien. *Annln Wien. Mus. Naturg.*, **1** (1): 95–101, pls 11, 12.

Petzall, C., Stainforth, R. M., González de Juana, C. & Martín Belliza, C. *et al.* 1978. Vénézuéla (2nd edn). *Lexique strat. int.*, Paris, **5** Amérique Latine (3A). 715 pp., 1 text-fig., 4 tables, 3 maps.

Pfeiffer, L. 1860–66. *Novitates conchologicae*, Ser. 1, *Mollusca extramarina* **2** (1): 139–160, pls 37–42. Cassel.

Philippi, R. A. 1847–48. *Melania* (**2**: 169–177, pl. 4), 1847; *Unio* (**3**: 79–81, pl. 5), 1848. *Abbildungen und Beschreibungen neuer oder weinig gekannter Conchylien*. Cassel.

Pilsbry, H. A. 1896. Notes on new series of Amnicolidae collected by Dr Rush in Uruguay. *Nautilus, Philad.*, **10** (8): 86–89.

—— 1899–1902 (continuing from Tryon, G. W.). *Manual of Conchology, Second Series: Pulmonata*. **12**. 258 pp., 64 pls. (1899). Classification of Bulimulidae and index of Vols 10–14, pp. i–xcix. (1902). Philadelphia.

—— 1911. The non marine Mollusca of Patagonia. *Rep. Princeton Univ. Exped. Patagonia*, **3** (Zoology) (5): 513–633, pls 38–47, 29 text-figs.

—— 1914. See Baker, F.

—— 1920. Mollusca from Central America and Mexico. *Proc. Acad. nat. Sci. Philad.*, **72**: 195–202, 7 text-figs.

—— 1924. South American land and fresh-water mollusks: notes and descriptions. Part II, The South American genera of Ancylidae. *Proc. Acad. nat. Sci. Philad.*, **76**: 54–59, text-fig. 4.

—— 1932. A Jamaican fluviatile *Neritina*. *Proc. Acad. nat. Sci. Philad.*, **84**: 12–13, text-figs 1, 2.

—— 1939. Fresh-water Mollusca and Crustacea from near El Molino, Bolivia. *Johns Hopkins Univ. Stud. Geol.*, **13**: 69–72, pl. 9.

—— 1944. Molluscan fossils from the Rio Pachitea and vicinity in Eastern Peru. *Proc. Acad. nat. Sci. Philad.*, **96**: 137–153, pls 9–11, 3 text-figs.

—— 1946. Land Mollusca of North America (north of Mexico), 2 (1). *Monogr. Acad. nat. Sci. Philad.*, 3. vi + 520 pp., 281 text-figs, col. frontispiece.

—— 1953. Vitrinellidae. *In* Olsson, A. A. & Harbison, A., Pliocene Mollusca of southern Florida with special reference to those from North Saint Petersburg. *Monogr. Acad. nat. Sci. Philad.*, **8**: 411–438, pls 49–56.

—— **& Becquaert, J.** 1927. The aquatic mollusks of the Belgian Congo, with a geographical and ecological account of Congo malacology. *Bull. Am. Mus. nat. Hist.*, **53**: 69–602, pls 10–77, 15 maps, 93 text-figs.

—— **& Ferris, J. H.** 1906. Mollusca of the Southwestern States II. *Proc. Acad. nat. Sci. Philad.*, **58**: 123–175, pls 5–9.

Pilsbry, H. A. & McGinty, T. 1945–50. 'Cyclostrematidae' and Vitrinellidae of Florida. 1. *Nautilus, Philad.*, **59**: 1–13, pls 1, 2 (1945); 2. *loc. cit.* **59**: 52–59, 72, pl. 6; 3. *loc. cit.* **59**: 77–83, pl. 8 (1946); 4. *loc. cit.* **60**: 12–18, pl. 2 (1947); 5. *loc. cit.* **63**: 85–87, pl. 5 (1950).

—— **& Olsson, A. A.** 1935. Tertiary fresh-water mollusks of the Magdalena embayments, Colombia. *Proc. Acad. nat. Sci. Philad.*, **7**: 7–39, pls 2–5, map.

—— —— 1941. Moluscos terciarios de Agua dulce en el valle de Magdalena, Introducion y descripcion de las especies. *Rev. Acad. Colomb. Cienc. exact. fis. nat.*, Bogotá, **4**: 410–417 (translation of 1935 paper).

—— —— 1945–52. Vitrinellidae and similar gastropods of the Panamic Province. *Proc. Acad. nat. Sci. Philad.*, **97**: 249–278, pls 22–30 (1945); **104**: 35–88, pls 2–13 (1952).

Poey, F. 1865–66. Descripcion de tres moloscos terrestres de la Isla de Cuba. *Repertorio fisico-natural de la Isla de Cuba*, Havana, **1**: 69–70.

Pompeckj, J. 1930. See Wenz, W.

Ponder, W. F. 1982. Hydrobiidae of Lord Howe Island (Mollusca: Gastropoda: Prosobranchia). *Aust. J. mar. freshwater Res.*, **33**: 89–159, 122 text-figs.

—— 1986. Glacidorbidae (Glacidorbacea: Basommatophora), a new family and superfamily of operculate freshwater gastropods. *Zool. J. Linn. Soc. Lond.*, **87**: 53–83, 22 text-figs.

Pons da Silva, M. C. & Davis, G. M. 1983. D'Orbigny's type specimens of *Paludestrina* (Gastropoda: Prosobranchia) from southern South America. *Proc. Acad. nat. Sci. Philad.*, **135**: 128–146.

Porta, J. de 1965. Estratigrafía del Cretácico Superior y Terciario en el extremo S del Valle Medio del Magdalena. *Boln Geol. Fac. Petrol. Univ. ind. Santander*, **19**: 5–50, 13 text-figs.

—— 1966. Geología del extremo S del Valle medio del Magdalena entre Honda y Guataqui (Colombia). *Boln Geol. Fac. Petrol. Univ. ind. Santander*, **22–23**: 5–347, 36 text-figs, 48 photo pls.

—— 1974. Colombie (deuxième partie), Tertiare et Quaternaire. *Lexique strat. int.*, Paris, **5** Amérique Latine (4B). 692 pp., 13 text-figs, 11 tables.

Prezant, R. S. 1981. Comparative shell ultrastructure of lyonsiid bivalves. *Veliger*, **23** (4): 289–299, 87 text-figs.

Purper, I. 1977. Some Ostracods from the Upper Amazon Basin, Brazil. Environment and age. *In*: Löffler, H. & Danielopol, D. (eds), *Aspects of ecology and zoogeography of Recent and fossil Ostracoda. Proceedings of the 6th International Symposium on Ostracods, Saalfelden (Salzburg), July 30–August 18, 1976*: 353–367, 4 pls, 1 map. The Hague.

Rafinesque, C. S. 1815. *Analyse de la Nature ou tableau de l'univers et des corps organisés*. 224 pp. Palermo.

Rathbun, M. J. 1919. Decapod crustaceans from the Panama Region. *Bull. U.S. natn Mus.*, **103**: 123–184, pls 54–66.

Recluz, C. A. 1849. Description de quelques nouvelles espèces de coquilles. *Rev. Mag. Zool.*, Paris, (2) **1**: 64–71.

—— 1852. Description de coquilles nouvelles. *J. Conch. Paris.*, **3**: 249–256, pl. 10.

Reeve, L. A. 1857–58. Monograph of the genus *Mytilus*. *Conchologica Iconica: or, illustrations of the shells of molluscous animals*, **10**. 11 pls, 61 spp. London.

—— 1859–61. Monograph of the genus *Melania*. *Conchologica Iconica: or, illustrations of the shells of molluscous animals*, **12**. 59 pls, 473 spp. London.

—— 1860. Monograph of the genus *Hemisinus*. *Conchologica Iconica: or, illustrations of the shells of molluscous animals*, **12**. 6 pls, 26 spp. London.

Rehder, H. A. 1945. *Buccinum zebra* Müller, the type of *Orthalicus*. *Nautilus, Philad.*, **59**: 29–31.

Richards, H. G. 1968. Catalogue of the invertebrate fossil types at the Academy of Natural Sciences of Philadelphia. *Spec. Publs Acad. nat. Sci. Philad.*, **8**. 222 pp.

Ridewood, W. G. 1903. On the structure of the gills of the Lamellibranchia. *Phil. Trans. Roy. Soc. Lond.*, **195 (B)**: 147–284, 61 text-figs.

Rios, E. C. 1975. *Brazilian marine mollusks, iconography*. 331 pp., 91 pls. Museu Oceanográfico, Universidade do Rio Grande.

—— 1985. *Sea shells of Brazil*. 328 pp., 102 pls. Rio Grande.

Rivera, R. 1956. Peru. *Lexique strat. int.*, Paris, **5** Amérique Latine (5B). 132 pp., map.

Roxo, M. G. de Oliveira 1924. Breve noticea sobre os fosseis terciario do Alto Amazonas. *Bolm Serv. geol. miner. Brasil*, Rio de Janeiro, **11**: 41–52, 1 pl.

—— 1937. Fosseis pliocenios do rio Jurua, Estado do Amazonas. *Notas prelim. Estud. Serv. Geol. min. Bras.*, Rio de Janeiro, **9**: 4–13.

Ruegg, W. & Rosenzweig, A. 1949. Contribución a la geologia de las formaciones modernas de Iquitos y de la Amazonia superior. *(Boln) Soc. geol. Perú*, Lima, Volumen Jubilar, XXV Anniv., **II** (3). 26 pp., 2 pls.

Runnegar, B. & Newell, N. D. 1971. Caspian-like relict molluscan fauna in the South American Permian. *Bull. Am. Mus. nat. Hist.*, New York, **146**: 1–66, 27 text-figs.

Russell, H. D. 1941. The Recent mollusks of the family Neritidae of the Western Atlantic. *Bull. Mus. Comp. Zool. Harv.*, **88** (4): 347–404, 7 pls, 4 text-figs.

Rutsch, R. F. 1952. Die paläogeographische Bedeutung der Fauna von Iquitos im oberen Amazonasbecken. *Eclog. geol. Helv.*, Lausanne & Basel, **44** (1951): 447–450.

Salvador, A. 1964. Proposed simplification of the stratigraphic nomenclature in Eastern Venezuela. *Boln inf. Asoc. Venezol. Geol. Min. Petról.*, Caracas, **7** (6): 153–202, 7 text-figs.

Santos, M. E. C. M. & Castro, J. S. 1967. Moluscos cenozóicos de agua dolce do Alto Amazonas. *Atas Simp. Biota Amazonica., Geoci. Belém*, **1**: 411–423, 11 text-figs.

Schepman, M. M. 1887. Bijdrage tot de Kenntnis der Molluskenfauna van der Schelpritsen van Suriname. *Samml. geol. Reichsmus. Leiden*, (2) **1**: 150–168.

Schmidt, A. 1855. Der Geschlechtsapparat der Stylommatophoren in taxonomischer Hinsicht. *Abh. naturw. Ver. Halle*, **1**: 1–52, pls 1–14.

Sheppard, G. 1934. Geology of the Interandine basin of Cuenca, Ecuador. *Geol. Mag.*, **71**: 356–370, 7 text-figs.

Sheppard, L. M. & Bate, R. H. 1980. Plio-Pleistocene ostracods from the Upper Amazon of Colombia and Peru. *Palaeontology*, **23** (1): 97–124, pls 7–13, 6 text-figs.

Sherborn, C. D. & Woodward, B. B. 1901. Notes on the dates of publication of the natural history portions of some French voyages. Part 1 'Amérique méridionale'; 'Indes orientales'; 'Pôle Sud' ('Astrolabe' and 'Zelée'); 'La Bonite'; 'La Coquille'; and 'L'Uranie et Physicienne'. *Ann. Mag. nat. Hist.*, (7) **7**: 388–392.

Simpson, C. T. 1900. Synopsis of the Naiades, or pearly fresh-water mussels. *Proc. U. S. natn Mus.*, **22**: 501–1075.

—— 1914. *A descriptive catalogue of the Naiades or pearly fresh-water mussels*. viii + 1540 pp. Ann Arbor.

Simpson, G. G. 1961. The supposed Pliocene Pebas Beds of the Upper Juruá River, Brazil. *J. Paleont.*, **35** (3): 620–624, 1 text-fig.

Singewald, J. T. 1927. Pongo de Manseriche. *Bull. geol. Soc. Am.*, **38**: 479–492, 9 text-figs.

—— 1928. Geology of the Pichis & Pachitea River, Peru. *Bull. geol. Soc. Am.*, **39**: 447–464, 11 text-figs.

Snelling, N. J. (1974). *Unpublished report on K:Ar age determinations on andesite from Descanso, Ecuador*. Institute of Geological Sciences, London.

Souleyet, F. L. A. 1841–52. Mollusques. *In* Eydoux, F., *Voyage autour du monde exécuté pendant ... 1836 et 1837 sur la corvette 'La Bonite' commandée par M. Vaillant, Capitaine de Vaisseau*. **2**: i–xxxix; 1–106 (1841), 107–328 (1842). Atlas: 2–8, 45 pls (1846–1849?). Paris. (Dates from Sherborn & Woodward 1901: 391).

Sowerby, G. B. 1864–68. Monograph of the genus *Unio*. *Conchologica Iconica: or, illustrations of the shells of molluscous animals*, **16**. 96 pls, 525 spp.

—— 1867–70. Monograph of the genus *Anodon*. *Conchologica Iconica: or, illustrations of the shells of molluscous animals*, **17**. 37 pls, 154 spp.

Sowerby, J. & J. de C. 1826–29. *The mineral conchology of Great Britain*, **6**: 1–230, pls 504–609. London.

Spix, J. B. von & Wagner, J. A. 1827. *Testacea fluviatilia Brasiliensia*. iv + 36 pp., 29 pls. Munich.

Stainforth, R. M. 1948. Description, correlation, and paleoecology of Tertiary Cipero Marl Formation, Trinidad, B. W. I. *Bull. Am. Ass. Petrol. Geol.*, **32** (7): 1292–1330, 2 text-figs.

Steinmann, G. *et al.* 1929. *Geologie von Peru*. xii + 488 pp. 9 pls, folding map, 271 text-figs. Heidelberg.

—— 1930. *Geología del Perú*. 448 pp., 1 geol. map. Heidelberg. (Not seen).

Stimpson, W. 1858. On *Cochliolepis parasitica* (gen. et sp. nov.). *Proc. Boston Soc. nat. Hist.*, **6**: 307–309, 1 text-fig.

—— 1865*a*. Diagnoses of newly discovered genera of gastropods, belonging to the sub-family Hydrobiinae, of the family Rissoidae. *Am. J. Conch.*, **1**: 52–54, pl. 8, fig. 1.

—— 1865*b*. Researches upon the Hydrobiinae and allied forms: chiefly made from materials in the Museum of the Smithsonian Institution. *Smithson. Misc. Collns*, Washington, (Art. 201) **7** (4): i–ii, 1–59, 29 text-figs.

Stirton, R. A. 1953. Vertebrate paleontology and continental stratigraphy in Colombia. *Bull. geol. Soc. Am.*, New York, **64** (6): 603–622, 13 text-figs.

Strebel, H. 1909. Revision der Unterfamilie der Orthalicinen. *Jb. Hamburg. Wiss. Anst.*, **26** (1908): 1–191, pls 1–38.

Swainson, W. 1840. *A treatise on malacology*. 419 pp., 130 text-figs. London.

Taylor, D. W. 1966. A remarkable snail fauna from Coahuila, Mexico. *Veliger*, **9**: 152–228, pls 8–19, 25 text-figs.

—— **& Sohl, N. F.** 1962. An outline of gastropod classification. *Malacologia* **1** (1): 7–32.

Taylor, J. D., Kennedy, W. J. & Hall, A. 1969. The shell structure of the Bivalvia – Introduction; Nuculacea–Trigonacea. *Bull. Brit. Mus. nat. Hist.* (Zool.) Suppl. 3. 125 pp., 29 pls, 77 text-figs.

——— ——— ——— 1973. The shell structure and mineralogy of the Bivalvia. II, Lucinacea–Clavagellacea; Conclusions. *Bull. Br. Mus. nat. Hist.* (Zool.). **22** (9): 253–294, 15 pls, 19 tabs, 33 text-figs.

Tello, J. 1975. *Catálogo de la fauna Venezolana, VIII. Mollusca.* xx + 599 pp. Caracas.

Thiele, J. 1928. Revision des Systems der Hydrobiiden und Melaniiden. *Zool. Jb. Abt. Syst. ökol. u. Geog.*, Jena, **55**: 351–402, pl. 8, 63 text-figs.

—— 1929–35. *Handbuch der systematischen Weichtierkunde*, **1**: 1–376 (1929); 377–778 (1931); **2**: 779–1022 (1934); 1023–1153 (1935), 114 text-figs. Jena.

Thompson, F. G. 1964. A new aquatic snail of the family Amnicolidae from Costa Rica. *Revta Biol. trop.*, San José, **12** (1): 97–105, 2 text-figs.

—— 1977. The hydrobiid snail genus *Marstonia*. *Bull. Fla. St. Mus. biol. Sci.*, Gainesville, **21** (3): 113–158, 25 figs.

—— 1984. North American freshwater snail genera of the hydrobiid subfamily Lithoglyphinae. *Malacologia*, **25** (1): 109–141, 84 text-figs.

Tillier, S. 1980. Gastéropodes terrestres et fluviatiles de Guyane française. *Mém. Mus. natn Hist. nat. Paris*, N. S. (A, Zool.) **118**. 188 pp., 6 pls, 124 text-figs.

Tryon, G. W. 1863. Descriptions of new species of fresh-water Mollusca, belonging to the families Amnicolidae, Valvatidae and Limnaeidae, inhabiting California. *Proc. Acad. nat. Sci. Philad.*, (**1863**): 147–150, pl. 1.

—— 1866*a*. Monograph of the Terrestrial Mollusca of the United States. *Am. J. Conch.*, **2**: 218–277, 306–327.

—— 1866*b*. Description of a new species of *Septifer*. *Am. J. Conch.*, **2**: 302; pl. 20, fig. 8.

Tschopp, H. J. 1953. Oil explorations in the Oriente of Ecuador, 1938–1950. *Bull. Am. Ass. Petrol. Geol.*, **37** (10): 2303–2347, 7 text-figs.

Turton, W. 1840. See Gray *in* Turton.

Vernhout, J. H. 1914. The non-marine molluscs of Surinam. *Notes Leyden Mus.*, **36**: 1–48; pl. 1, figs 1–14; pl. 2; 1 text-fig.

Vokes, H. E. 1945. Supraspecific groups of the pelecypod family Corbulidae. *Bull. Am. Mus. nat. Hist.*, **86** (1). 32 pp., 4 pls.

Wagner 1827. See Spix, J. B. von & Wagner, J. A. 1827.

Walker, B. 1917. A revision of the classification of the North American patelliform Ancylidae, with descriptions of new species. *Nautilus, Philad.*, **31** (1): 1–10, pls 1–3.

Warmke, G. L. & Abbot, R. T. 1961. *Caribbean sea shells.* x + 346 pp., 44 pls, 19 maps, 34 text-figs. Narberth, Pennsylvania.

Weeks, L. G. 1948. Paleogeography of South America. *Bull. geol. Soc. Am.*, **69**: 249–282, 16 pls, 1 fig.

Weisbord, N. E. 1962. Late Cenozoic gastropods from northern Venezuela. *Bull. Am. Paleont.*, **42**. 672 pp., 48 pls.

—— 1964. Late Cenozoic pelecypods from northern Venezuela. *Bull. Am. Paleont.*, **45**. 564 pp., 59 pls, 8 figs.

Wellman, S. S. 1970. Stratigraphy and Petrology of the non-marine Honda Group (Miocene), Upper Magdalena Valley, Colombia. *Bull. geol. Soc. Am.*, **81**: 2353–2374, 13 text-figs.

Wenz, W. 1925. Zur Nomenklatur tertiärer Land- und Susswasser-gastropoden VII. *Senckenbergiana*, Frankfurt a.M., **7**: 124–125.

—— 1926–30. Gastropoda extramarina tertiaria. **32** (vii): 1863–2230 (1926); **40** (ix): 2503–2886 (1929); **46** (xi): 3015–3387 (1930). *In*: Pompeckj, J. F. (ed.), *Fossilium catalogus*, **1**: *Animalia*. Berlin.

—— 1939–40. Gastropoda, Allgemeiner Teil/Prosobranchia. *In*: Schindewolf, O. H. (ed.), *Handbuch der Paläozoologie*, **6** (1) Lieferung 3: 481–720, text-figs 1236–2083 (1939); Lieferung 4: 721–960, text-figs 2084–2787 (1940). Berlin (reprinted 1961).

Wheeler, O. C. 1935. Tertiary stratigraphy of the Middle Magdalena Valley. *In*: Pilsbry, H. A. & Olsson, A. A., Tertiary fresh-water mollusks of the Magdalena embayment, Colombia. *Proc. Acad. nat. Sci. Philad.*, **87**: 21–39, geol. map.

Willard, B. 1966. *The Harvey Bassler collection of Peruvian fossils.* 255 pp., 75 pls, 9 text-figs. Bethlehem, Pennsylvania.

Windhausen, A. 1931. *Geologia Argentina, 2 parte, Geologia histórica y regional del territorio Argentino.* 645 pp., 58 pls, 214 text-figs, 1 geol. map. Buenos Aires.

Wolff, W. J. 1969. The Mollusca of the estuarine region of the rivers Rhine, Meuse and Scheldt in relation to the hydrography of the area. II. The Dreissenidae. *Basteria*, Lisse, **33**: 93–103, 3 text-figs.

Wood, W. 1828. *Supplement to the Index Testaceologicum or catalogue of shells.* iv + 59 pp., 8 pls. London.

Woodring, W. P. 1925. Miocene mollusks from Bowden, Jamaica. Pelecypods and scaphopods. *Publs Carnegie Instn*, **366**. 221 pp., 28 pls.

—— 1928. Miocene mollusks from Bowden, Jamaica, Part II. Gastropods and discussion of results. *Publs Carnegie Instn*, **385**. vii + 564 pp., 40 pls, 2 text-figs.

—— 1957–59. Geology and paleontology of the Canal Zone and adjoining parts of Panama. *Prof. Pap. U. S. geol. Surv.*, **306–A**: 1–145, pls 1–23, 4 text-figs (1957); *loc. cit.* **306–B**: 147–239, pls 24–38 (1959).

—— 1965. Endemism in Middle Miocene Caribbean molluscan faunas. *Science, N.Y.* **148** (no. 3672, May 14 1965): 961–963, 1 text-fig.

—— 1966. The Panamá Land bridge as a sea barrier. *Proc. Am. phil. Soc.*, **110** (6): 425–433, 3 text-figs, 5 tables.

Woods, H. 1922. *In*: Bosworth, T.O., *Geology of the Tertiary and Quaternary periods in the north-west part of Peru*: 51–111, pls 1–20. London.

Woodward, H. 1871. The Tertiary shells of the Amazons valley. *Ann. Mag. nat. Hist.*, London, (4) **7**: 59–64, 101–109, pl. 5.

Zilch, A. 1959–60 (continuing from **Wenz, W.**). Gastropoda, 2, Euthyneura. *In*: Schindewolf, O. H. (ed.), *Handbuch der Paläozoologie*, **6**. 834 pp., 2515 figs. Berlin.

GENERAL INDEX

Biology, Collectors, Gazetteer, Geography, Geology, Maps, non-molluscan Phyla. * Figure.

SYSTEMATIC INDEX

Asterisks denote illustrations.

Bulletin of the British Museum (Natural History)

Geology Series

Most earlier Geology *Bulletins* are still in print. A full list of available titles can be obtained from Publication Sales (address inside front cover).

Vol. 36 No. 1 Middle Cambrian trilobites from the Sosink Formation, Derik–Mardin district, south-eastern Turkey. W. T. Dean. 1982. Pp. 1–41, 68 figs. £5.80

Vol. 36 No. 2 Miscellanea: Dinantian terebratulids—New microfossils—*Neseuretus*—*Archaeocidaris whatleyensis*—Carboniferous dasyclad—*Nanjinoporella*—Toarcian bryozoans—Drybrook Sandstone plants—British fossil bintoniellids—*Uraloporella*. 1982. Pp. 43–155. £19.80

Vol. 36 No. 3 The Ordovician Graptolites of Spitsbergen. R. A. Cooper & R. A. Fortey. 1982. Pp. 157–302, 6 plates, 83 figs, 2 tables. £20.50

Vol. 36 No. 4 Campanian and Maastrichtian sphenodiscid ammonites from southern Nigeria. P. M. P. Zaborski. 1982. Pp. 303–332, 36 figs. £4.00

Vol. 37 No. 1 Taxonomy of the arthrodire *Phlyctaenius* from the Lower or Middle Devonian of Campbellton, New Brunswick, Canada. V. T. Young. 1983. Pp. 1–35, 18 figs. £5.00

Vol. 37 No. 2 *Ailsacrinus* gen. nov., an aberrant millericrinid from the Middle Jurassic of Britain. P. D. Taylor. 1983. Pp. 37–77, 48 figs, 1 table. £5.90

Vol. 37 No. 3 Miscellanea: Permian *Glossopteris* in Turkey—Wealden *Theriosuchus*—Wealden conifer—Permian plants of Saudi Arabia—Carboniferous Edrioasteroidea—British cicadas—Dittonian cephalaspids. 1983. Pp. 79–171. £13.50

Vol. 37 No. 4 The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. B. G. Gardiner. 1984. Pp. 173–428, 145 figs, 4 plates. 0 565 00967 2. £39.00

Vol. 38 No. 1 New tertiary pycnodonts from the Tilemsi valley, Republic of Mali. A. E. Longbottom. 1984. Pp. 1–26, 29 figs, 3 tables. 0 565 07000 2. £3.90

Vol. 38 No. 2 Silicified brachiopods from the Viséan of County Fermanagh, Ireland. (III) Rhynchonellids, Spiriferids and Terebratulids. C. H. C. Brunton. 1984. Pp 27–130, 213 figs. 0 565 07001 0. £16.20

Vol. 38 No. 3 The Llandovery Series of the Type Area. L. R. M. Cocks, N. H. Woodcock, R. B. Rickards, J. T. Temple & P. D. Lane. 1984. Pp. 131–182, 70 figs. 0 565 07004 5. £7.80

Vol. 38 No. 4 Lower Ordovician Brachiopoda from the Tourmakeady Limestone, Co. Mayo, Ireland. A. Williams & G. B. Curry. 1985. Pp. 183–269, 214 figs. 0 565 07003 7. £14.50

Vol. 38 No. 5 Miscellanea: Productacean growth and shell shape—Jurassic alga *Palaeosiphonium*—Upper Ordovician brachiopods and trilobites—Lower Devonian Osteostraci from Podolia—*Hipparion* from Diavata—Preparation and study of Singa skull—Carboniferous and Permian bryozoa—Lower Eocene trionychid—Montsech fossil insects. 1985. Pp. 271–412. 0 565 07004 5. £24.00

Vol. 39 No. 1 Upper Cretaceous ammonites from the Calabar region, south-east Nigeria. P. M. P. Zaborski. 1985. Pp. 1–72, 66 figs. 0 565 07006 1. £11.00

Vol. 39 No. 2 Cenomanian and Turonian ammonites from the Novo Redondo area, Angola. M. K. Howarth. 1985. Pp. 73–105. 33 figs. 0 565 07006 1. £5.60

Vol. 39 No. 3 The systematics and palaeogeography of the Lower Jurassic insects of Dorset, England. P. E. S. Whalley. 1985. Pp. 107–189, 87 figs, 2 tables. 0 565 07008 8. £14.00

Vol. 39 No. 4 Mammals from the Bartonian (middle/late Eocene) of the Hampshire Basin, southern England. J. J. Hooker, 1986. Pp. 191–478, 71 figs, 39 tables. 0 565 07009 6. £49.50

Vol. 40 No. 1 The Ordovician graptolites of the Shelve District, Shropshire. I. Strachan. 1986. Pp. 1–58, 38 figs. 0 565 07010 X. £9.00

Vol. 40 No. 2 The Cretaceous echinoid *Boletechinus*, with notes on the phylogeny of the Glyphocyphidae and Temnopleuridae. D. N. Lewis. 1986. Pp. 59–90, 11 figs, 7 tables. 0 565 07011 8. £5.60

Vol. 40 No. 3 The trilobite fauna of the Raheen Formation (upper Caradoc), Co. Waterford, Ireland. A. W. Owen, R. P. Tripp & S. F. Morris. 1986. Pp. 91–122, 88 figs. 0 565 07012 6. £5.60

Vol. 40 No. 4 Miscellanea I: Lower Turonian cirripede—Indian coleoid *Naefia*—Cretaceous–Recent Craniidae—Lectotypes of Girvan trilobites—Brachiopods from Provence—Lower Cretaceous cheilostomes. 1986. Pp. 125–222. 0 565 07013 4. £19.00

Vol. 40 No. 5 Miscellanea II: New material of *Kimmerosaurus*—Edgehills Sandstone plants—Lithogeochemistry of Mendip rocks—Specimens previously recorded as teuthids—Carboniferous lycopsid *Anabathra*—*Meyenodendron*, new Alaskian lepidodendrid. 1986. Pp. 225–297. 0 565 07014 2. £13.00

Vol. 41 No. 1 The Downtonian ostracoderm *Sclerodus* Agassiz (Osteostraci: Tremataspididae), P. L. Forey. 1987. Pp. 1–30. 11 figs. 0 565 07015 0. £5.50

Vol. 41 No. 2 Lower Turonian (Cretaceous) ammonites from south-east Nigeria. P. M. P. Zaborski. 1987. Pp. 31–66. 46 figs. 0 565 07016 9. £6.50

Vol. 41 No. 3 The Arenig Series in South Wales: Stratigraphy and Palaeontology. I. The Arenig Series in South Wales. R. A. Fortey & R. M. Owens. II. Appendix. Acritarchs and Chitinozoa from the Arenig Series of South-west Wales. S. G. Molyneux. 1987. Pp. 67–364. 289 figs. 0 565 07017 7. £59.00

Vol. 41 No. 4 Miocene geology and palaeontology of Ad Dabtiyah, Saudi Arabia. Compiled by P. J. Whybrow. 1987. Pp. 365–457, 54 figs. 0 565 07019 3. £18.00

Vol. 42 Cenomanian and Lower Turonian Echinoderms from Wilmington, south-east Devon. A. B. Smith, C. R. C. Paul, A. S. Gale & S. K. Donovan. 1988. 244 pp., 80 figs, 50 pls. 0 565 07018 5. £46.50

Vol. 43 A Global Analysis of the Ordovician–Silurian boundary. Edited by L. R. M. Cocks & R. B. Rickards. 1988. 394 pp., figs. 0565 07020 7. £70.00

Vol. 44 No. 1 Miscellanea: Palaeocene wood from Mali—Chapelcorner fish bed—*Heterotheca* coprolites—Mesozoic Neuroptera and Raphidioptera. 1988. Pp. 1–63. 0 565 07021 5. £12.00

Vol. 44 No. 2 Cenomanian brachiopods from the Lower Chalk of Britain and northern Europe. E. F. Owen. 1988. Pp. 65–175. 0 565 07022 3. £21.00

Vol. 44 No. 3 The ammonite zonal sequence and ammonite taxonomy in the *Douvilleiceras mammillatum* Superzone (Lower Albian) in Europe. H. G. Owen. 1988. Pp. 177–231. 0 565 07023 1. £10.30

Vol. 44 No. 4 Cassiopidae (Cretaceous Mesogastropoda): taxonomy and ecology. R. J. Cleevely & N. J. Morris. 1988. Pp. 233–291. 0 565 07024 X. £11.00

Vol. 45 No. 1 Arenig trilobites—Devonian brachiopods—Triassic demosponges—Larval shells of Jurassic bivalves—Carboniferous marattialean fern—Classification of Plectambonitacea. 1989. Pp. 1–163. 0 565 07025 8. £40.00

CONTENTS

A review of the Tertiary non-marine molluscan faunas of the Pebasian and other inland basins of north-western South America. By P. C. Nuttall

Bulletin British Museum (Natural History)
GEOLOGY SERIES
Vol. 45, No. 2, March 1990

Bulletin British Museum (Natural History)

Geology Series

Mid-Cretaceous Ammonites of Nigeria; new amphisbaenians from Kenya; English Wealden Equisetales; Faringdon Sponge Gravel Bryozoa

VOLUME 46 NUMBER 1 31 MAY 1990

The *Bulletin of the British Museum (Natural History)*, instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

The Geology Series is edited in the Museum's Department of Palaeontology
Keeper of Palaeontology: Dr L. R. M. Cocks
Editor of the Bulletin: Dr M. K. Howarth
Assistant Editor: Mr D. L. F. Sealy

Papers in the *Bulletin* are primarily the results of research carried out on the unique and ever-growing collections of the Museum, both by the scientific staff and by specialists from elsewhere who make use of the Museum's resources. Many of the papers are works of reference that will remain indispensable for years to come.

A volume contains about 400 pages, made up by two numbers: published Spring and Autumn. Subscriptions may be placed for one or more of the series on an Annual basis. Individual numbers and back numbers can be purchased and a Bulletin catalogue, by series, is available. Orders and enquiries should be sent to:

Sales Department,
Natural History Museum Publications,
British Museum (Natural History),
Cromwell Road,
London SW7 5BD

Telephone: 01-938 9386
Telex: 929437 NH PUBS G
Fax: 01-938 8709

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Geol.)

ISBN 0 565 07027 4
ISSN 0007–1471

Geology Series
Vol 46 No 1 pp 1–152

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 31 May 1990

Bull. Br. Mus. nat Hist (Geol.) 46 (1): 1–18

Issued 31 May 1990

The Cenomanian and Turonian (mid-Cretaceous) ammonite biostratigraphy of north-eastern Nigeria

P. M. P. ZABORSKI

Department of Geology and Mining, University of Jos, P.M.B. 2084, Jos, Nigeria

CONTENTS

Synopsis. The Cenomanian–Turonian ammonite biostratigraphy of the Pindiga Formation and its age equivalents was investigated at a number of localities in north-eastern Nigeria. Five biozones were found to be recognizable in the main limestone-bearing sequences of the region as a whole: a Zone of *Nigericeras gadeni* (Chudeau) at the base, a Zone of *Vascoceras cauvini* Chudeau, a Zone of *Vascoceras proprium* (Reyment), a Zone of *Pseudotissotia nigeriensis* (Woods) and a Zone of *Wrightoceras wallsi* Reyment above. The Gadeni and Cauvini Zones are Late Cenomanian in age while the Nigeriensis and Wallsi Zones are Early Turonian. The Cenomanian–Turonian boundary lies within or at the top of the Proprium Zone. The Wallsi Zone at Dukul is overlain by a condensed horizon containing *Fagesia* sp., *Neoptychites cephalotus* (Courtiller), *Wrightoceras munieri* (Pervinquière) and *Hoplitoides ingens* (von Koenen), ammonites ranging from Lower to Middle Turonian. The youngest Turonian zone recognizable is that of *Coilopoceras discoideum* Barber. A broadly similar ammonite succession occurs in the Algerian Sahara, while correlation of these Nigerian zones with those in Israel is good, especially in the Upper Cenomanian. Local subsidence history had a profound effect on the age, thickness and lithological character of the ammonite-bearing sequences in north-eastern Nigeria; all these factors vary significantly.

INTRODUCTION

The Cenomanian–Turonian limestones of north-eastern Nigeria have long been noted for their prolific vascoceratid-dominated ammonite faunas. Elements were first described by Woods (1911), but following the accounts of Reyment (1954, 1954*a*, 1955) and Barber (1957, 1960) the full wealth of these assemblages became evident. This area has subsequently assumed major importance in mid-Cretaceous Tethyan biostratigraphy. The ammonite-bearing beds outcrop widely but in its details the geology of the region is rather complex, a fact reflected by the multiplicity of lithostratigraphical and palaeogeographical terms applied to it. Cretaceous sedimentation in north-eastern Nigeria was, for its greater part, strongly influenced by a number of important strike-slip faults trending NE–SW (Benkhelil 1982, Benkhelil & Robineau 1983, Popoff *et al.* 1983, Maurin *et al.* 1986; Fig. 1). Two major sedimentary basins are present, the Chad Basin to the north and the Lau Basin (Benue Basin of Carter *et al.* (1963), Lamurde Basin of Ojo & Pinna (1982)), comprising the distal part of the Benue Trough, to the south. The area between, termed the 'Zambuk Ridge' by Carter *et al.* (1963), is characterized by strong faulting which resulted in the development of several differentially subsiding basins (Ojo & Pinna 1982, Maurin *et al.* 1986). Following the first systematic geological mapping of the region, Carter *et al.* (1963) referred the Cenomanian–Turonian limestone-shale sequence in the western part of the Chad Basin to the Gongila Formation, that in the Lau Basin to the Dukul Formation and that in the remaining area to the Pindiga Formation. These marine formations overlie a transitional sandstone-shale sequence (the Yolde Formation) over most of north-eastern Nigeria. The earliest sediments are a thick but varied fluviatile and

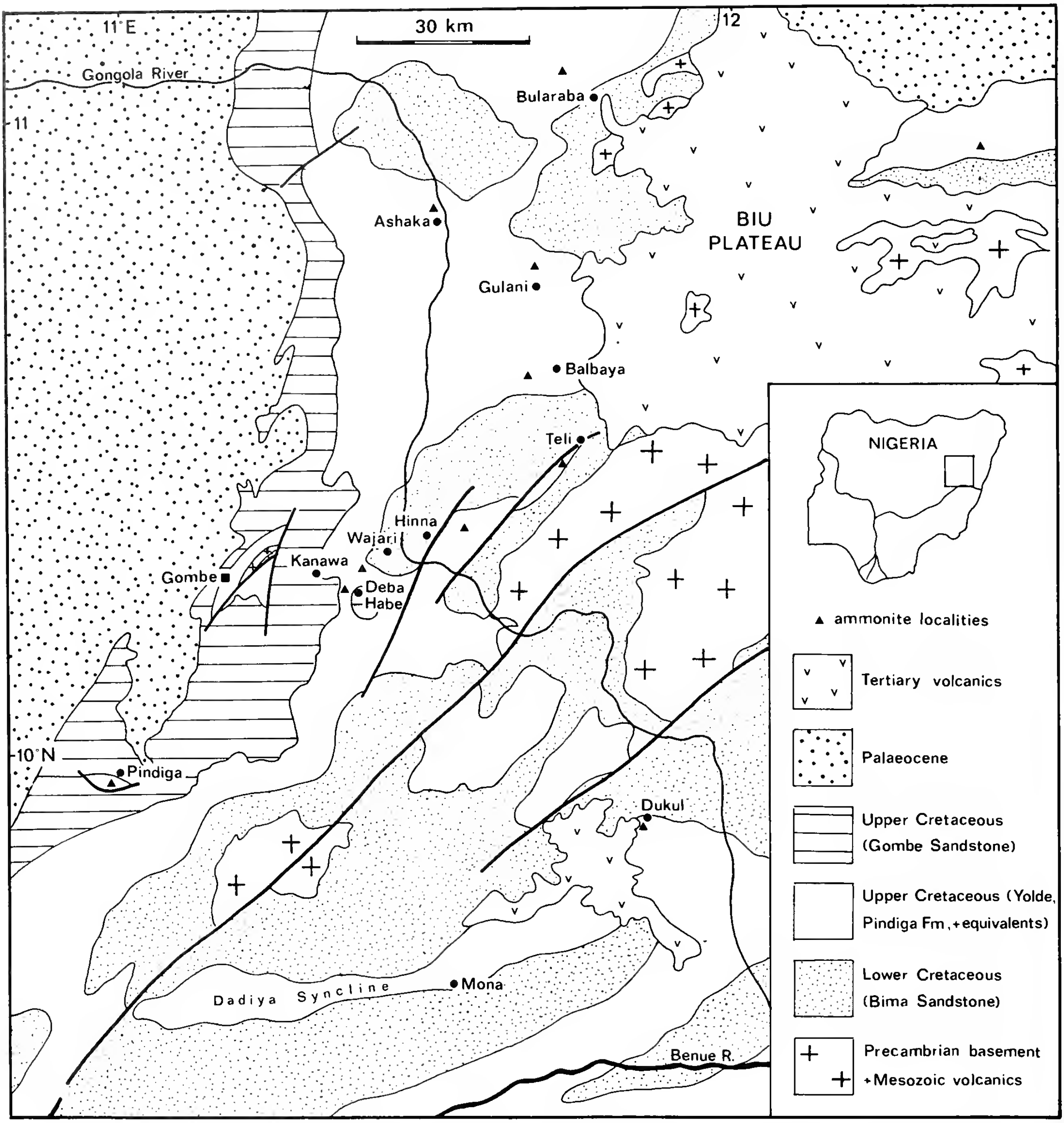


Fig. 1 Simplified geological map of part of north-eastern Nigeria showing ammonite localities mentioned in the text.

lacustrine succession, the Bima Sandstone of Aptian to Albian age (Allix *et al.* 1981, Doyle *et al.* 1982) which underlies the entire area.

Woods (1911) established the presence of Turonian deposits in north-eastern Nigeria but Reyment (1954) proposed the first subdivision of this stage in Nigeria, regarding the vascoceratid-dominated faunas as characteristic of his 'Oldest Beds' (of the Turonian). These beds he subsequently referred to as the 'Zone of *Pachyvascoceras costatum* Reyment' and, later, as the 'Zone of *Pseudotissotia* (*Wrightoceras*) *wallsi* Reyment' (Reyment 1956, 1965). Barber (1957), however, proposed three zones for this sequence in north-eastern Nigeria: a Zone of *Vascoceras bulbosum* (Reyment) below, a Zone of *Paravascoceras costatum* (Reyment) and a Zone of *Pseudotissotia* (*Bauchioceras*) *nigeriensis* above. All were assigned to the Lower Turonian, though Barber noted the Cenomanian affinities of elements of his Bulbosum Zone fauna. Wozny & Kogbe (1983) later proposed a 'Zone of *Gombeoceras gongilense* Reyment' between Barber's Costatum and Nigeriensis Zones. These three zones they referred to the Lower Turonian, regarding Barber's Bulbosum Zone as Upper Cenomanian. Most recently, Popoff *et al.* (1986) reinvestigated the Gongila Formation at Ashaka Quarry and the Pindiga Formation at its streamside type locality (see Fig. 1). They divided the ammonite-bearing levels into seven zones, as follows:

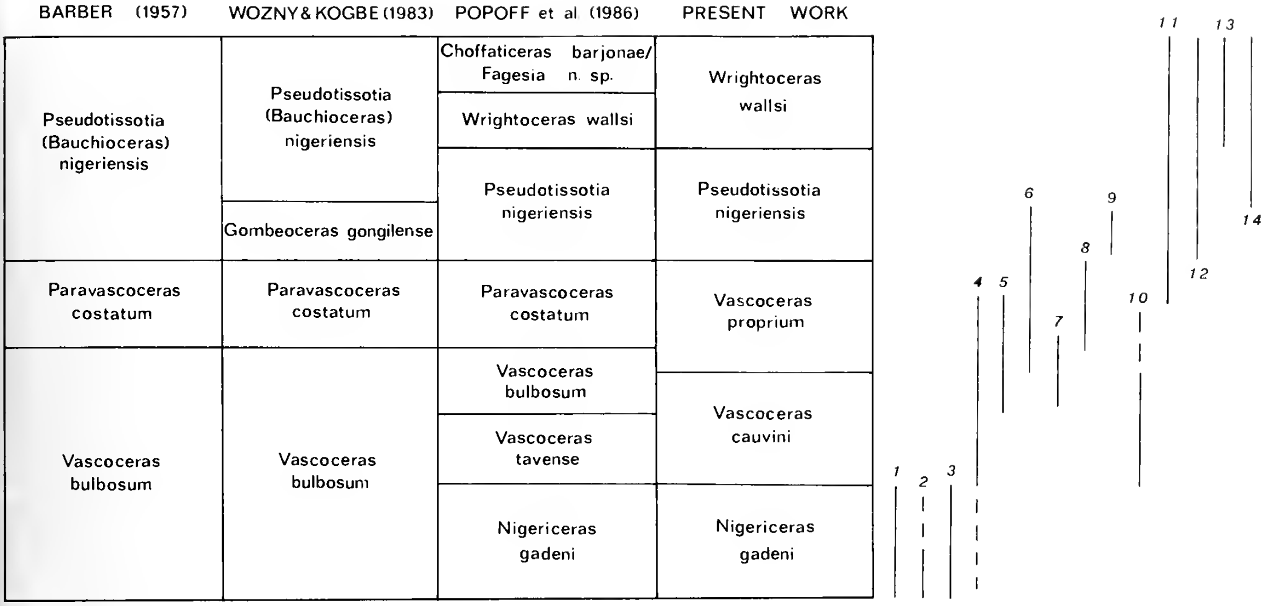


Fig. 2 Present and previous proposals for a biostratigraphical subdivision of the Upper Cenomanian and Lower Turonian in north-eastern Nigeria based on ammonites. The stratigraphical ranges of selected forms are shown at right: 1, *Metengonoceras dumbli*. 2, *Metoicoceras geslinianum*. 3, *Nigericeras gadeni*. 4, *Vascoceras cauvini*. 5, *V. nigeriense*. 6, *V. proprium*. 7, *V.* sp. juv. 8, '*Paramammites*' sp. 9, *Pseudaspidoceras* cf. *flexuosum*. 10, *P.* cf. *pseudonodosoides*. 11, *Thomasites gongilensis*. 12, *Pseudotissotia nigeriensis*. 13, *Wrightoceras wallsi*. 14, *Eotissotia simplex*.

7. Zone of *Choffaticeras barjonae* (Choffat)/*Fagesia* n. sp. (youngest)
6. Zone of *Wrightoceras wallsi*
5. Zone of *Pseudotissotia nigeriensis*
4. Zone of *Paravascoceras costatum*
3. Zone of *Vascoceras bulbosum*
2. Zone of *Vascoceras tavense* Faraud
1. Zone of *Nigericeras gadeni* (Chudeau) (oldest).

Zones 1–3 were dated Late Cenomanian, the Costatum Zone Early Turonian and zones 5–7 Middle Turonian.

There has, therefore, been a divergence of opinion regarding the biostratigraphical subdivision and precise ages of these beds. One of the main problems in dealing with vascoceratid faunas is ascertaining the limits of individual species which are frequently represented by a large array of morphotypes (see, for example, Schöbel 1975, Renz 1982, Hirano 1983, Berthou *et al.* 1985, Kennedy *et al.* 1987). The taxonomic approaches adopted by previous authors have strongly influenced their biostratigraphical and palaeobiogeographical interpretations of the Nigerian faunas. The purpose of this contribution is not to attempt a complete taxonomic revision of these ammonites but rather to propose a biostratigraphy effective in correlation both within and outside north-eastern Nigeria. Inevitably, however, certain taxonomic remarks are necessary especially in regard to those species that have been selected as zonal indices.

PROPOSED BIOZONATION

The following ammonite biozones are proposed for the main part of the Late Cenomanian and Early Turonian limestone-bearing sequences in north-eastern Nigeria:

5. Zone of *Wrightoceras wallsi* (youngest)
4. Zone of *Pseudotissotia nigeriensis*
3. Zone of *Vascoceras proprium* (Reyment)
2. Zone of *Vascoceras cauvini* Chudeau
1. Zone of *Nigericeras gadeni* (oldest).

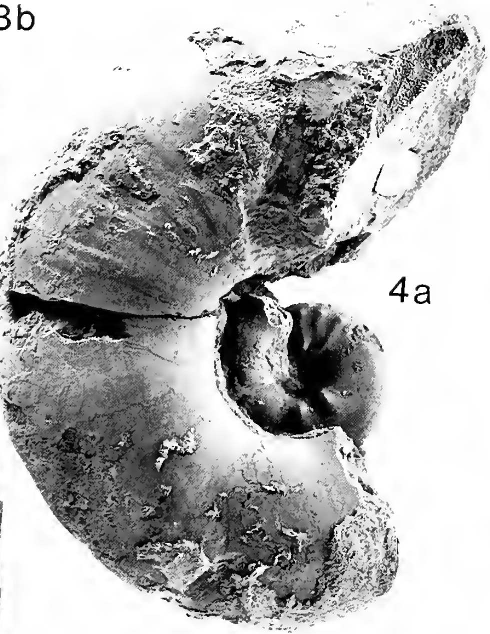
This scheme has been found to be applicable over the region as a whole. Zones 1–4 are interval zones, defined at their bases by the appearances of the index species. Zone 5 is a range zone based on the local occurrence of *W. wallsi*. The relationship of these zones to previously proposed schemes is shown in Fig. 2. As discussed below, the Wallsi Zone is locally overlain by a fauna containing, amongst others, *Hoplitoides*. At Mona and Bularaba (Fig. 1) still younger Turonian beds contain *Coilopoceras discoideum* Barber.

The *Nigericeras gadeni* Zone

A Zone of *Nigericeras gadeni* was first proposed by Popoff *et al.* (1986) for the earliest ammonite-bearing beds in north-eastern Nigeria. Although ammonites are generally scarce in this zone, *N. gadeni* occurs in some numbers and has a wide geographical distribution in the region. In this study it has not been found outside the Gadeni Zone, but Popoff *et al.* (1986: 348) reported it from Ashaka Quarry as high as beds included here in the *Vascoceras proprium* Zone. Faunas characteristic of the Gadeni Zone can be recognized in the lowest limestone bed at Pindiga (unit 1 of Barber 1957: table 3; unit 3 of Popoff *et al.* 1986: 354); at Ashaka Quarry (units 2 and 3 of Popoff *et al.* 1986: 347; the former, contrary to their statement, being exposed in a drainage cut in the eastern part of the quarry); in the lowest limestone bed exposed at Deba Habe; in the region between Kanawa and Hinna; at Teli; and to the north-east of the Biu basalt plateau (see Fig. 1). At the last two localities the Gadeni Zone is the only ammonite biozone present.


3a


3b


4a


4b


5a

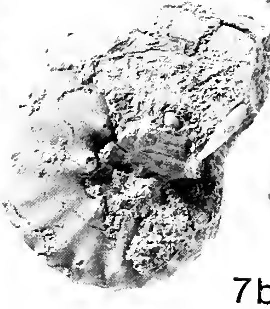

5b


8a


8b

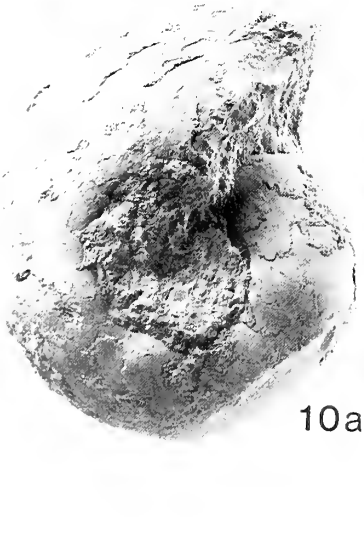

6a

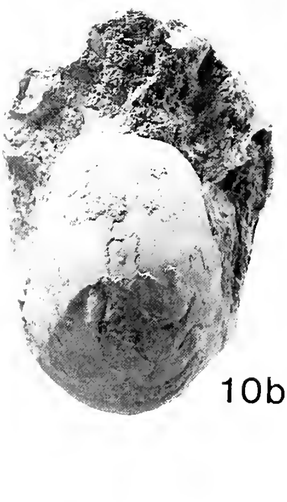

6b


7a


7b


9


10a


10b


11a


11b

Material of *N. gadeni* from north-east Nigeria is variable as regards strength and persistence of the juvenile ornamentation (Figs 4–7). Numerous specimens resemble in particular *N. lamberti* Schneegans (1943: 121; pl. 6, figs 1–5, 7). In agreement with Schöbel (1975) and Wright & Kennedy (1981), *N. lamberti*, *N. gignouxi* Schneegans (1943: 119; pl. 5, figs 10–15) and *N. jacqueti* Schneegans (1943: 125; pl. 6, fig. 8; pl. 7, fig. 1) are here regarded as synonyms of *N. gadeni* (Chudeau 1909: 71; pl. 3, fig. 6), making up a series varying mainly in the ornamental details mentioned above. The Gadeni Zone has also yielded *Metengonoceras dumbli* (Cragin) at Pindiga and Deba Habe. East of Kanawa a single specimen of *Metoicoceras geslinianum* (d'Orbigny) (Fig. 3) was found in scree which otherwise produced only rare *Metengonoceras dumbli*, more frequent *Nigericeras gadeni* and a poorly preserved fragment of *Vascoceras*. A fragment of a compressed *Vascoceras*, perhaps referrable to *V. cauvini*, was also found in the lowermost limestone bed at Pindiga. Two further, rather better preserved, immature specimens of *Vascoceras* (Figs 9, 10) were collected from the same bed. One of these (Fig. 10) shows broad, clavate umbilical tubercles similar to those discernible in the holotype of *V. bulbosum* (Reyment 1954*a*: pl. 4, figs 2a, b). The Pindiga individual is more inflated but is linked to the latter specimen by an ammonite referred to *V. bulbosum* by Barber (1957: pl. 6, fig. 8; Fig. 11 here). The Pindiga material mentioned above may be conspecific with *V. bulbosum* which itself is a possible synonym of *V. cauvini* Chudeau (see below). If *V. cauvini* is confirmed at this stratigraphical level in Nigeria, the Cauvini Zone can be extended downwards to include those beds here referred to as the Gadeni Zone, with the latter possibly being retained as a subzone. Popoff *et al.* (1986) reported *Eotissotia* Barber from the Gadeni Zone at Pindiga. This genus is otherwise found only at much higher stratigraphical levels in the Nigeriensis and Wallsi Zones. Finally, a fragment of a depressed ammonite with an acanthoceratid ornament (British Museum (Natural History) C.91294), possibly referrable to *Euomphaloceras*, was found in the Gadeni Zone at Pindiga.

The *Vascoceras cauvini* Zone

The base of this zone is marked by the appearance of *Vascoceras cauvini*, which can at present be drawn in the middle of unit 3 of Barber (1957: table 3), that is unit 4 of Popoff *et al.* (1986: 354), at Pindiga, and at the base of unit 4 of Popoff *et al.* (1986: 348) at Ashaka. It encompasses the greater part of the '*Vascoceras bulbosum* Zone' of Barber (1957) and the '*Vascoceras tavense* Zone' and lower part of the '*Vascoceras bulbosum* Zone' of Popoff *et al.* (1986) (see Fig. 2).

The Cauvini Zone is characterized by the common occurrence of moderately involute, compressed *Vascoceras*, generally smooth or nearly so in the juvenile whorls but sometimes with broad umbilical bullae. Such forms were referred by Barber (1957) to *V. bulbosum* (see Barber 1957: pl. 6, figs 6, 8) and *V. depressum* Barber (1957: 19; pl. 6, fig. 5). Only immature specimens have been found at Pindiga (Figs 8, 15). At other localities, notably Ashaka Quarry, the later growth stages are well represented and show the characteristic ventral ribbing of *V. cauvini* Chudeau (1909: 68; pls 1–2; pl. 3, figs 1, 2, 4) to which these specimens are here referred. A series of specimens at different growth stages is shown in Figs 12–14. *V. bulbosum* itself is based on a rather more inflated specimen than these (C.47295; see Reyment 1954*a*: pl. 4, figs 2a, b) showing broad, clavate umbilical ornamentation. It is, however, closely matched in whorl proportions by a specimen from Damergou included in *V. cauvini* by Chudeau (1909: pl. 3, figs 4a, b). This individual was refigured by Schneegans (1943: pl. 4, fig. 1) as *Paravascoceras nigeriensis* (Woods), apparently because of its early loss of umbilical tuberculation. Both Reyment (1954*a*: 256) and Barber (1957: 15) also tentatively referred it to this species. Contrary to the impression given by Woods (1911), however, rapid loss of ornamentation is by no means a characteristic feature of *Vascoceras nigeriense*. Certain specimens retain umbilical tubercles, often becoming bullate, to diameters of 70 mm or more (Fig. 25). It is possible that Chudeau's individual mentioned above is a true *V. cauvini* of which *V. bulbosum* may be a synonym. A list of further possible synonyms has been given by Schöbel (1975).

At Pindiga the uppermost part of the Cauvini Zone and the lowermost part of the overlying Proprium Zone consist of two thin calcareous beds separated by 50 cm of shales with gypsum (unit 5 of Barber 1957: table 3). These calcareous beds contain a stratigraphically important but taxonomically problematical assemblage of juvenile *Vascoceras* (Figs 17–18, 20). At Deba Habe a comparable association (Figs 16, 21) again occurs in an equivalent stratigraphical position. Barber (1957: 27) noted the similarity of some of these forms to *V. nigeriense* but, uncertain of their precise affinities, left them in open nomenclature as '*Vascoceras* sp. juv.' These individuals are consistently rather evolute and ventrally are either smooth or with only broad, low ribs. Their umbilical ornament, however, is highly variable. In some (Fig. 20) there are comparatively small, rounded umbilical tubercles. More commonly prominent, highly bullate umbilical tubercles are present, giving off single or paired indistinct ribs which fade over the venter (Figs 17, 21). This range of ornament is reminiscent of that in *Vascoceras diartianum* (d'Orbigny) (see Kennedy & Juignet 1977) and in particular of an assemblage from the Upper Cenomanian of southern Germany described by Förster *et al.* (1983: 133; pl. 3, figs 1–5). Others still show large, frequently paired, umbilical bullae (Fig. 18). Such massive tuberculation recalls that in *V. silvanense* Choffat (1898: 57; pl. 8, fig. 5; pl. 21, fig. 9), a form based on a juvenile of uncertain affinity (Berthou *et al.* 1985: 68). Although, within the Nigerian faunas, *V. nigeriense* is closest in whorl proportions to these juveniles, their variability precludes assignment to this species with confidence, if indeed they are all conspecific. It should also be noted that

---

Figs 3a, b *Metoicoceras geslinianum* (d'Orbigny). Pindiga Formation (Gadeni Zone), between Kanawa and Wajari. C.91205, × 1.

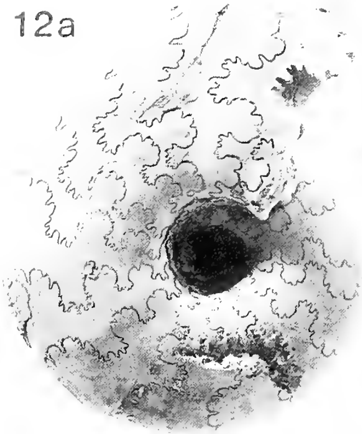
Figs 4–7 *Nigericeras gadeni* (Chudeau). Pindiga Formation (Gadeni Zone). Figs 4a, b, C.91209, × 1. North-east of Biu plateau. Figs 5a, b, C.91212, × 1. Teli. Figs 6a, b, C.91215, × 1. Between Kanawa and Wajari. Figs 7a, b, C.91216, × 1. Between Kanawa and Wajari.

Figs 8a, b *Vascoceras cauvini* Chudeau. Pindiga Formation (Cauvini Zone), Pindiga. C.91285, × 1.

Figs 9, 10 *Vascoceras* sp. Pindiga Formation (Gadeni Zone), Pindiga. Fig. 9, C.91225, × 1. Figs 10a, b, C.91224, × 1.

Figs 11a, b *Vascoceras bulbosum* (Reyment). Pindiga Formation, Pindiga. C.47667, × 1 (see also Barber 1957: pl. 6, fig. 8).

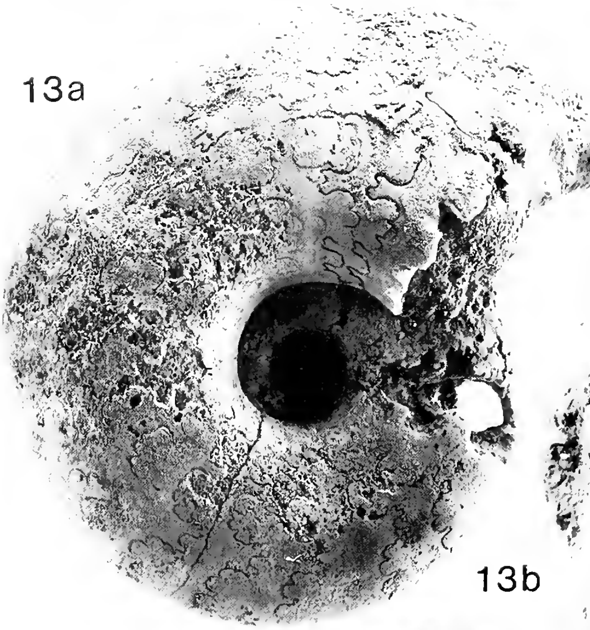
All specimens are housed in the British Museum (Natural History), London.



12a

12b

14



13a

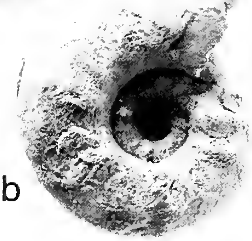
13b

15a

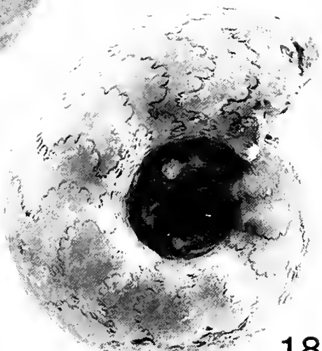
15b

17a

16



17b



18a

18b

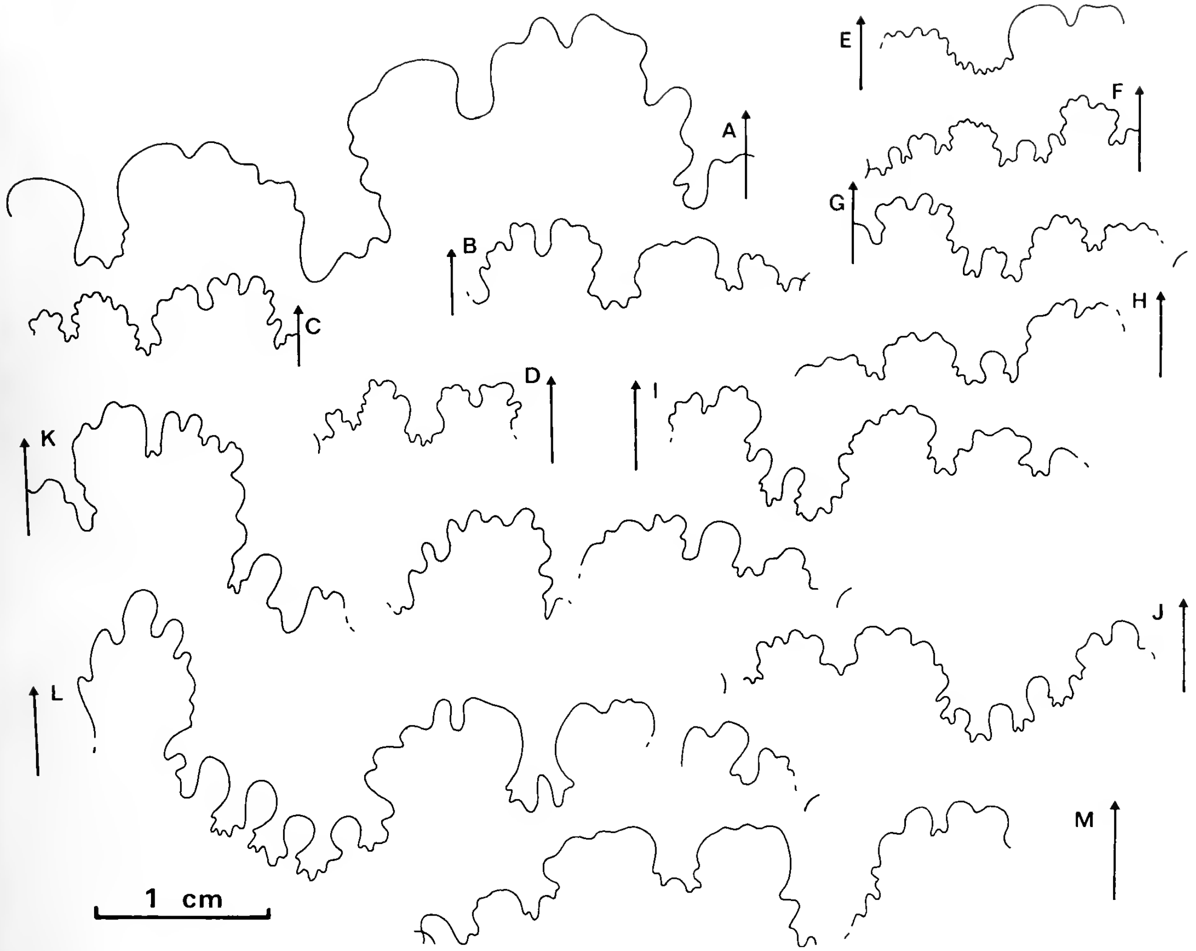


Fig. 19 Sutures in: A–D, *Nigericeras gadeni* (Chudeau), Gadeni Zone, Pindiga Formation. A, C.91222, basal limestone bed, Ashaka Quarry. B, C.91207, north-east of Biu plateau. C, C.91211, Teli. D, C.91212, Teli. E, *Eotissotia simplex* Barber, C.91235, upper Dukul Formation, Dukul. F–K, *Hoplitoides ingens* (von Koenen), upper Dukul Formation, Dukul. F, C.91251; G, C.91250; H, C.91247; I, C.91245; J, C.91248; K, C.91246. L, *Coilopoceras discoideum* Barber, C.91227, Pindiga Formation, Bularaba. M, *Wrightoceras munieri* (Pervinquière), C.91237, upper Dukul Formation, Dukul. All specimens are housed in the British Museum (Natural History), London. × 2·4

dissection of several adult *V. nigeriense* failed to reveal juvenile whorls with the highly bullate umbilical tubercles which are common in these forms.

Vascoceras cf. *evolutum* (Schneegans 1943: 130; pl. 8, fig. 2) is common in the Cauvini Zone at Ashaka and Pindiga; it occurs associated with *Pseudaspidoceras pseudonodosoides* (Choffat). At Dukul the stratigraphically lowest ammonite collected belongs to the latter genus (Fig. 22). This form is conspecific with the '*Pseudaspidoceras* sp.' of Barber (1957: 11; pl. 25, fig. 8) which, while losing all but the umbilical ornament early in ontogeny, shows the robust, rectiradiate ribbing of *P. pseudonodosoides* in its juvenile and middle growth stages. The Dukul specimen occurs below scree levels containing ammonites typical of the Proprium and Nigeriensis Zones (Fig. 28), suggesting a stratigraphical position high in the Cauvini Zone. Barber's material, however, came from Bularaba, where the ammonite-bearing beds begin in the Proprium Zone (see below), indicating that *Pseudaspidoceras* of *pseudonodosoides* type extend into this part of the sequence.

Popoff *et al.* (1986) proposed a 'Zone of *Vascoceras tavense*' for beds at Pindiga and Ashaka making up the lower part of the Cauvini Zone as here defined. As Freund & Raab (1969: 23–24) pointed out, *V. tavense* Faraud (1940: 43; pl. 1, fig. 1; pl. 5, fig. 1; pl. 8, fig. 2) is a very poorly defined species. Berthou *et al.* (1985: pl. 3, figs 11, 12) refigured the corroded holotype photographically and showed its inadequacy as the basis of a new species. They remarked upon similarities with *Spathites* (*Jeanrogericeras*) Wiedmann, 1960 but regarded *V. tavense* as a *nomen dubium*. A Zone of *V. tavense* is not

---

Figs 12–15 *Vascoceras cauvini* Chudeau. Figs 12–14, Pindiga Formation, Ashaka Quarry. Figs 12a, b, C.91272, × 1. Figs 13a, b, C.91271, × 1. Fig. 14, C.91274, × ⅔. Figs 15a, b, Pindiga Formation (Cauvini Zone), Pindiga. C.91278, × 1.

Figs 16–18 *Vascoceras* sp. juv. Fig. 16, Pindiga Formation (Cauvini Zone), Deba Habe. C.91256, × 1. Figs 17–18, Pindiga Formation (Cauvini Zone), Pindiga. Figs 17a, b, C.91263, × 1. Figs 18a, b, C.91264, × 1.

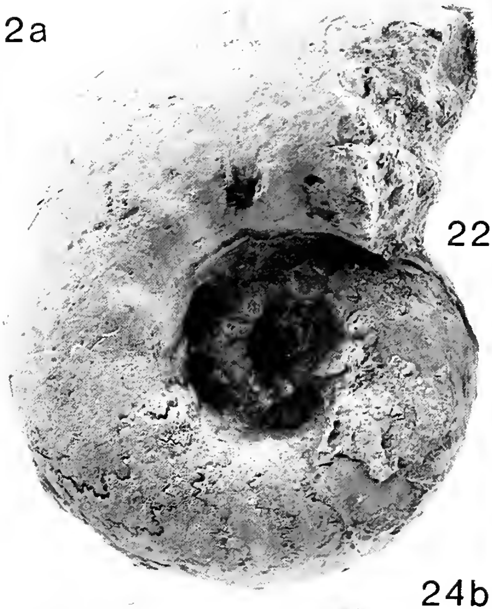
All specimens are housed in the British Museum (Natural History), London.

20

21

22a

22b



23

24a

24b

26

27a

27b

25

adopted here; all the *Vascoceras* occurring at these stratigraphical levels can be referred to *V. cauvini*.

The Cauvini Zone can be recognized at Pindiga, Ashaka and Deba Habe. The upper part is probably represented in the lower Dukul Formation at Dukul.

The *Vascoceras proprium* Zone

This zone encompasses the uppermost part of the *Vascoceras bulbosum* Zone and the *Paravascoceras costatum* Zone as applied by Barber (1957) and Popoff *et al.* (1986) (see Fig. 2). Its base is defined at the appearance of *V. proprium* which at Pindiga is the upper 'crystalline limestone' of Barber's (1957: table 3) unit 5. At Ashaka the base occurs at the bottom of unit 5 of Popoff *et al.* (1986: 348).

Paravascoceras costatum (Reyment 1954*a*: 257; pl. 3, fig. 6; pl. 4, fig. 3; pl. 5, fig. 2; text-figs 3a, b, 5), previously employed as a zonal index in north-eastern Nigeria, has recently been listed, along with *Pachyvascoceras* (=*Vascoceras*) *globosum* Reyment (1954*a*: 259; pl. 3, fig. 3; pl. 5, fig. 4; text-figs 3c, 7), as a synonym of *Vascoceras proprium* (Reyment 1954*a*: 258; pl. 5, figs 1a, b; text-figs 3d, 6) by Kennedy *et al.* (1987: 46). The Proprium Zone is condensed at Ashaka and in the region around Gulani and Bularaba (Fig. 1). It contains an enormous array of rather compressed to highly depressed *Vascoceras* in these areas, mainly referred to *V. globosum* and *Paravascoceras costatum* by Barber (1957). These faunas are in need of detailed revision but, in agreement with Kennedy *et al.* (1987), it has not proved possible to distinguish *P. costatum* as a discrete species. It is a variant of *V. proprium* with suppressed umbilical tuberculation but ventral ribbing in the adult stages. *V. cauvini* and *V. nigeriense* extend into the Proprium Zone, along with the juvenile *Vascoceras* mentioned above in connection with the upper part of the Cauvini Zone. *Thomasites gongilensis* appears in the Proprium Zone. The various forms referred to *Paramammites* Furon and *Nigericeras* Schneegans by Barber (1957) occur in the Proprium Zone. They are not, however, typical members of either of these genera. Similar material is common at Ashaka and shows an ornament characteristic of the Euomphaloceratinae Cooper, 1978 in the early and middle growth stages with seven rows of tubercles and much multiplied ventral ribbing. Unlike true *Paramammites* there are marked siphonal tubercles persisting to diameters as high as 70 mm. The suture lacks the square, bifid first lateral saddle typical of *Nigericeras* (Figs 19A–D), its elements being more elongate and the lateral lobe wider, while these forms show stronger and more persistent ornament. They often resemble *Nigericeras ogojaense* Reyment (1955: 62; pl. 13, fig. 6; pl. 14, fig. 3; text-fig. 28) and, to a lesser extent, *N. scotti* Cobban (1971: 18; pl. 9, figs 1–4; pl. 18, figs 1–9; text-figs 15–19). These species also show divergence from the type species, *N. gignouxi* Schneegans, 1943, in the characters mentioned above. Finally, Wozny & Kogbe (1983) reported *Metengonoceras dumbli* from their *Paravascoceras costatum* Zone (= Proprium Zone as employed here), although in the present study it has been found only in the Gadeni Zone.

The Proprium Zone can be recognized at Pindiga, Ashaka, Balbaya, Gulani and Bularaba (Fig. 1). Characteristic members of its fauna are present in surface scree at Deba Habe and Dukul. In the area between Balbaya and Bularaba it makes up the basal part of the limestone-bearing beds.

The *Pseudotissotia nigeriensis* Zone

As employed here, the *Pseudotissotia nigeriensis* Zone corresponds with that of Popoff *et al.* (1986), its base being marked by the appearance of *P. nigeriensis. Thomasites gongilensis* reaches its acme in the lower half of this zone where it may occur in very large numbers. Wozny & Kogbe (1983) proposed a 'Zone of *Gombeoceras gongilense*' for these horizons. As noted by Popoff *et al.* (1986), however, *Thomasites* [= *Gombeoceras*] *gongilensis* occurs both lower and higher and, following these authors, a separate zone is not distinguished here. At Pindiga and Ashaka the acme of *T. gongilensis* coincides with the occurrence of *Pseudaspidoceras* of *P. flexuosum* Powell, 1963 type (Figs 23, 24). *Vascoceras proprium* extends into the lower part of the Nigeriensis Zone, while *Neoptychites*, *Choffaticeras* and *Mammites*? occur as rarities. *Eotissotia simplex* Barber is common in its upper part. At several localities, notably Dukul, the more compressed and smoother varieties of *Pseudotissotia nigeriensis* occur higher in the zone, the earlier members resembling, indeed merging with, *Thomasites gongilensis*.

The Nigeriensis Zone can be recognized at Pindiga, Ashaka, Deba Habe, Dukul, Balbaya, Gulani and Bularaba.

The *Wrightoceras wallsi* Zone

A 'Zone of *Wrightoceras wallsi*' was first proposed for north-eastern Nigeria by Reyment (1965) but was intended to include the entire sequence from Gadeni to Wallsi Zone as employed here. Popoff *et al.* (1986) used the zone in a more restricted sense for beds including the upper part of the range of *Pseudotissotia nigeriensis*. Wherever the stratigraphical relationships have been seen (Pindiga, Ashaka, Deba Habe, Dukul and Bularaba), *W. wallsi* occurs only at these high levels. Apart from the index species, the Wallsi Zone contains *P. nigeriensis* and *Eotissotia simplex*, both of which are common.

Popoff *et al.* (1986) proposed a 'Zone of *Choffaticeras barjonae*' for the uppermost ammonite-bearing beds at Pindiga and a 'Zone of *Fagesia* n. sp. aff. *spheroidalis* Pervinquière' for those at Ashaka. These zones were correlated with one another even though, in fact, they contain no ammonites in common. A form similar to *Fagesia superstes* var. *spheroidalis* Pervinquière (1907: 324; pl. 20, figs 3a, b, 4, A) also occurs at Dukul (see below, Figs 32, 33) but in beds younger than those

---

Figs 20, 21 *Vascoceras* sp. juv. Fig. 20, Pindiga Formation (Cauvini Zone), Pindiga. C.91262, × 1. Fig. 21, Pindiga Formation (Cauvini Zone), Deba Habe. C.91257, × 1.

Figs 22a, b *Pseudaspidoceras* cf. *pseudonodosoides* (Choffat). Lower Dukul Formation, Dukul. C.91232, × 1.

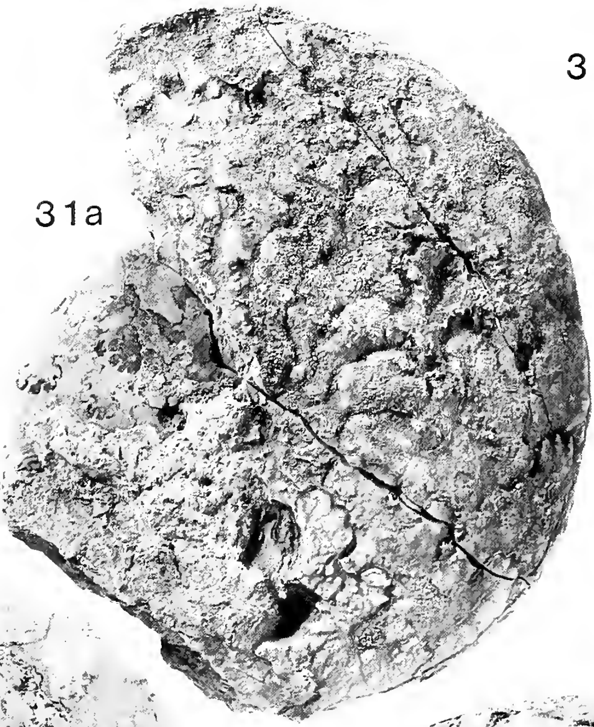
Figs 23, 24 *Pseudaspidoceras* cf. *flexuosum* Powell. Fig. 23, Pindiga Formation (lower part of Nigeriensis Zone), Ashaka Quarry. C.91275, × ¾. Figs 24a, b, Pindiga Formation (lower part of Nigeriensis Zone), Pindiga, C.91276, × 1.

Fig. 25 *Vascoceras nigeriense* Woods. Pindiga Formation (Proprium Zone), Ashaka Quarry. C.91277, × ¾.

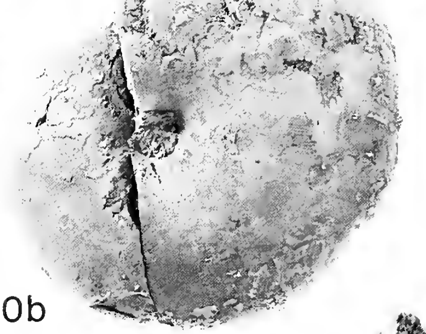
Figs 26, 27 *Hoplitoides ingens* (von Koenen). Upper Dukul Formation, Dukul. Fig. 26, C.91247, × 1. Figs 27a, b, C.91246, × 1.

All specimens are housed in the British Museum (Natural History), London.

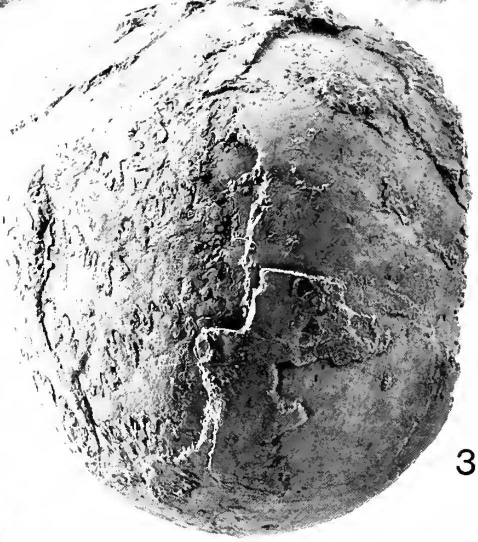

29

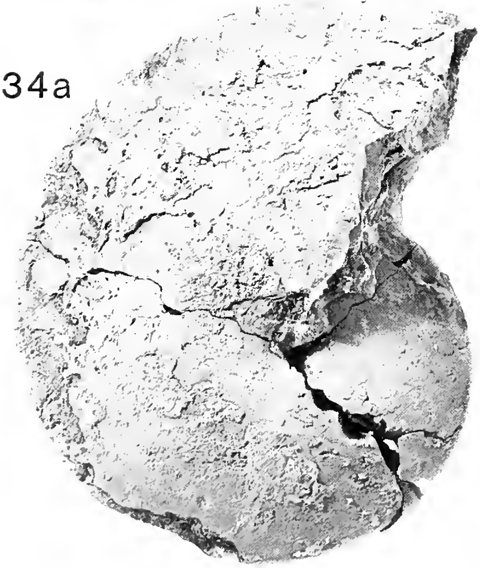

31a


31b


30a

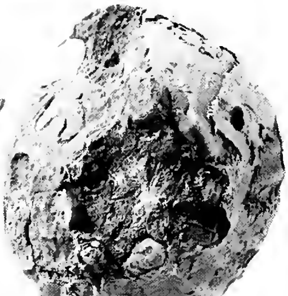

30b


32


34a


34b


33a


33b

at Ashaka. Nowhere else in the region have the index species of Popoff *et al.* been found. *Wrightoceras wallsi* persists throughout their Zone of *Fagesia* n. sp. at Ashaka. Their Barjonae Zone at Pindiga also contains species (*Eotissotia simplex* and *Thomasites gongilensis*) persisting from below. These two zones cannot yet be applied over north-eastern Nigeria as a whole and they are not differentiated here from the Wallsi Zone. It is, however, possible that in the future a discrete zone might be recognized at this stratigraphical level.

The Wallsi Zone outcrops at Pindiga, Ashaka, Deba Habe, Dukul and Bularaba. The index species has also been reported from Gulani and south-east of Numan (Barber 1957, Carter *et al.* 1963).

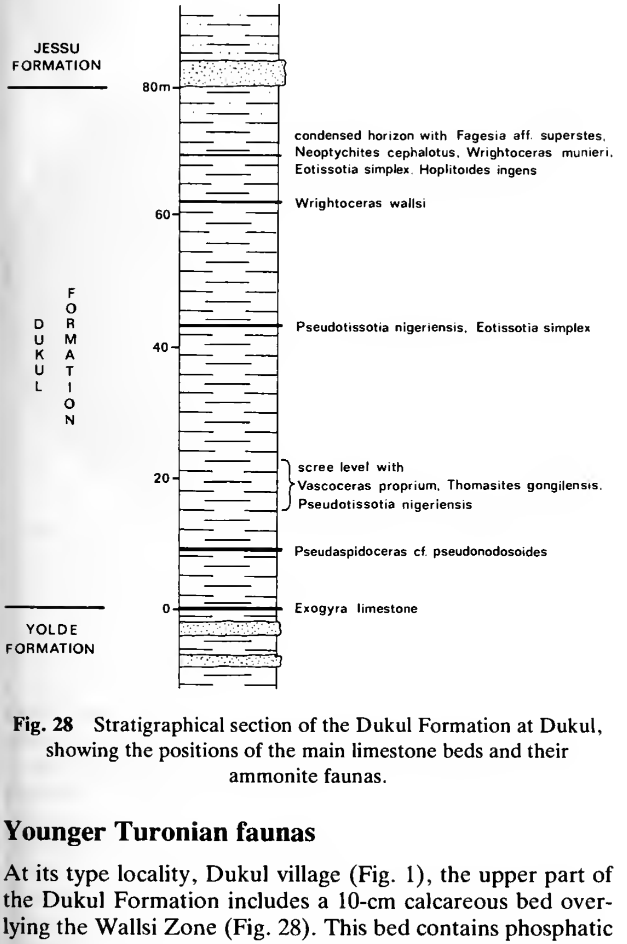


Fig. 28 Stratigraphical section of the Dukul Formation at Dukul, showing the positions of the main limestone beds and their ammonite faunas.

Younger Turonian faunas

At its type locality, Dukul village (Fig. 1), the upper part of the Dukul Formation includes a 10-cm calcareous bed overlying the Wallsi Zone (Fig. 28). This bed contains phosphatic pebbles and laths, comminuted vertebrate remains and phosphatized gastropod moulds. Numerous ammonites also occur, with the exception of one specimen of *Fagesia*, all those recovered being wholly or partially phosphatized and some showing signs of reworking. The fauna includes rare *Eotissotia simplex* (Figs 19E, 37) and *Neoptychites cephalotus* (Courtiller) (Fig. 31) with more common *Wrightoceras munieri* (Pervinquière) (Figs 19M, 29, 30). Also present are scarce *Fagesia* (Figs 32, 33), similar to *F. superstes* (Kossmat 1897: 26; pl. 6, fig. 1) in the early whorls and later developing a highly globular shell shape like that in *F. superstes* var. *spheroidalis* Pervinquière. The Nigerian form, however, has peculiar, highly clavate umbilical tubercles, in places forming an almost continuous flange on the umbilical shoulder. The commonest ammonite in this fauna, though, is *Hoplitoides ingens* (von Koenen, 1897) (Figs 19F–K, 26, 27, 34). The timing of the transition from a truncated to an acute venter is variable in this material but all the variants are matched by specimens of *H. ingens* in a fauna from Wadatta in central Nigeria described by Reyment (1955: 79–81). Being highly condensed, no formal biostratigraphical unit is proposed for this bed; its fauna may eventually be found to span more than one biozone. It is, however, of great significance in allowing an upper age limit to be placed upon the Wallsi Zone (see below).

To the north of Bularaba (Bularafa) (Fig. 1) the Proprium to Wallsi Zones are present in the main limestone development of the Pindiga Formation. The immediately overlying strata are not exposed but some distance above the Wallsi Zone thin shelly limestones and calcareous sandstones occur containing *Coilopoceras discoideum* Barber, 1957 (Figs 19L, 35, 36) and *Placenticeras* aff. *cumminsi* Cragin, 1893 (Fig. 38). An assemblage zone characterized by these two ammonites is here proposed for these beds. *C. discoideum* is otherwise known only from the Mona region (Barber 1957, Grant 1965) some 150 km to the south (Fig. 1).

AGES AND CORRELATION

Correlation outside Nigeria

The Nigerian faunas discussed here are predominantly composed of members of the characteristically Tethyan family Vascoceratidae. Ammonite faunas of the Upper Cenomanian and Lower Turonian in north-west Europe, including the type areas, are, on the other hand, mainly Boreal in nature with the Mammitinae especially important. Problems of provinciality at these levels in the Cretaceous are well known. Sufficient data, however, are accumulating from various parts of the world to allow a reasonably reliable correlation with northern Nigeria.

The oldest ammonite-bearing beds in north-eastern Nigeria, the *Nigericeras gadeni* Zone, contain, west of Wajari, *Metoicoceras geslinianum*. These beds can therefore be firmly assigned to the Upper Cenomanian as previously suggested by Hancock & Kennedy (1981), Wozny & Kogbe (1983), Popoff *et al.* (1986) and Kennedy *et al.* (1987). They correlate with the *M. geslinianum* Zone of north-west Europe, now included in the Cenomanian (see, for example, Kennedy & Juignet 1973, Wright & Kennedy 1981, Hancock & Kennedy 1981). There are no ammonite faunas in north-eastern Nigeria of age equivalent to those with *Neolobites* Fischer which underlie beds of Geslinianum Zone age in many parts of the

---

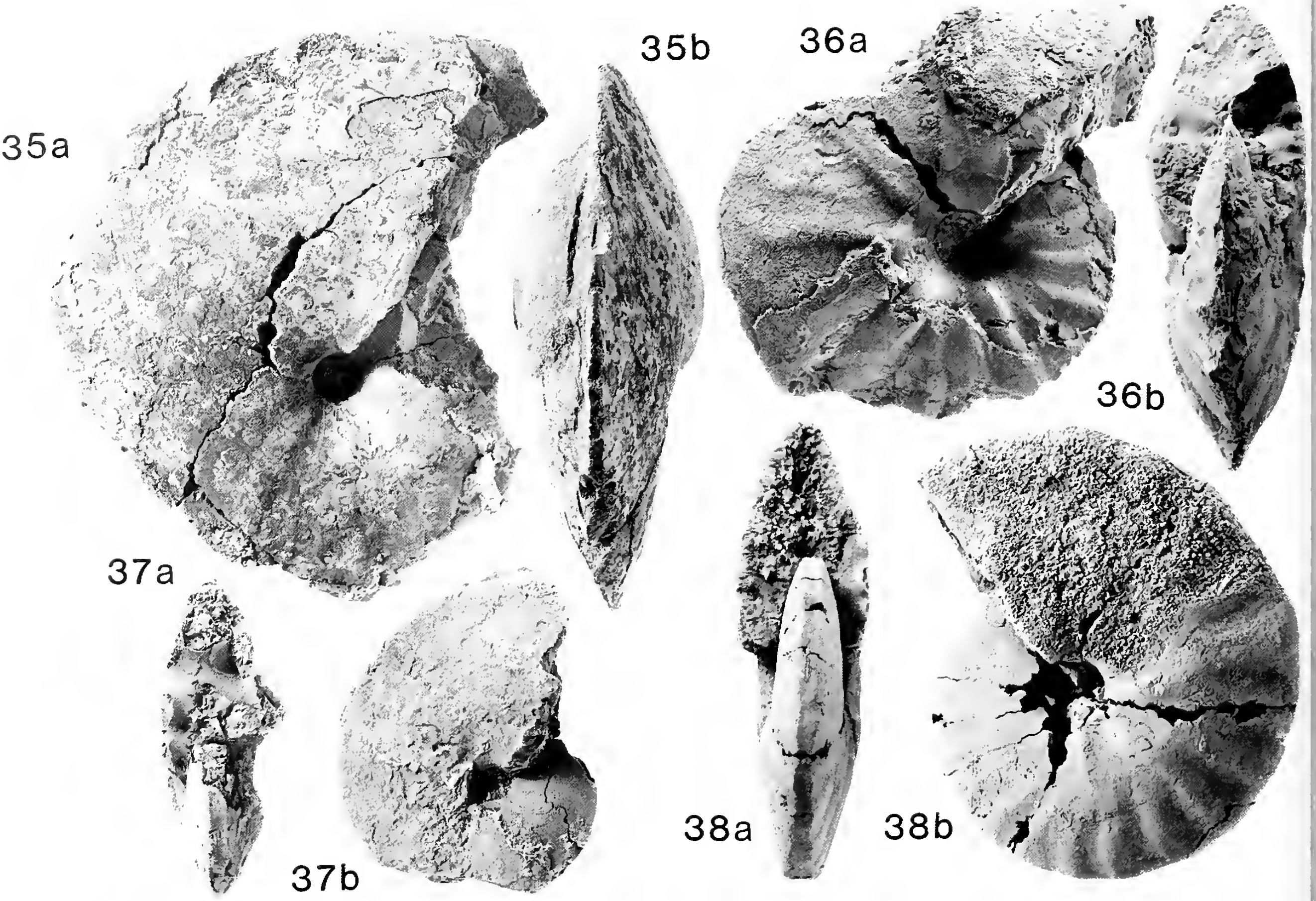
Figs 29, 30 *Wrightoceras munieri* (Pervinquière). Upper Dukul Formation, Dukul. Fig. 29, C.91236, × ¾. Figs 30a, b, C.91237, × 1.

Figs 31a, b *Neoptychites cephalotus* (Courtiller). Upper Dukul Formation, Dukul. C.91229, × ¾.

Figs 32, 33 *Fagesia* aff. *superstes* (Kossmat). Upper Dukul Formation, Dukul. Fig. 32, C.91231, × ¾. Figs 33a, b, C.91230, × 1.

Figs 34a, b *Hoplitoides ingens* (von Koenen). Upper Dukul Formation, Dukul. C.91245, × 1.

All specimens are housed in the British Museum (Natural History), London.



Figs 35, 36 *Coilopoceras discoideum* Barber. Pindiga Formation (Discoideum Zone), Bularaba. Figs 35a, b, C.91227, × ¾. Figs 36a, b, C.91226, × 1.
Figs 37a, b *Eotissotia simplex* Barber. Upper Dukul Formation, Dukul. C.91235, × 1.
Figs 38a, b *Placenticeras* aff. *cumminsi* Cragin. Pindiga Formation (Discoideum Zone), Bularaba. C.91233, × 1.
All specimens are housed in the British Museum (Natural History), London.

world, particularly Tethyan areas (see, for example, Greigert & Pougnet 1967, Freund & Raab 1969, Wiedmann 1960, Busson 1965, 1972, Kennedy & Juignet 1981, Amard *et al.* 1981, Berthou 1984).

The age of the *Pseudotissotia nigeriensis* and *Wrightoceras wallsi* Zones has been the subject of some disagreement. Barber (1957), Hancock & Kennedy (1981), Wozny & Kogbe (1983) and Kennedy *et al.* (1987) dated them Early Turonian, but Popoff *et al.* (1986) preferred a Middle Turonian age. The condensed horizon containing, amongst others, *Hoplitoides*, which occurs above the Wallsi Zone at Dukul, allows an upper age limit to be suggested for this zone. *Wrightoceras munieri* was used in Spain by Wiedmann (1960, 1979) and Wiedmann & Kauffman (1978) as an index species for the earliest Middle Turonian beds. Since *Mammites nodosoides* (Schlüter) is an associated species, however, Kennedy (1985) suggested that *W. munieri* should be assigned to the Lower Turonian in Spain. In Texas *W. munieri* occurs as low as the basal Turonian *Pseudaspidoceras flexuosum* Zone (Kennedy *et al.* 1987), while it is one of the first species to appear in the Venezuelan Turonian (Renz 1982). *Neoptychites cephalotus* is an early mid-Turonian species in the type area in France (Amédro *et al.* 1982, Robaszynski *et al.* 1983) but occurs in the lower part of the Lower Turonian in the western interior of the United States (Cobban & Scott 1972, Cobban 1984) and southern Nigeria (Zaborski 1987). *Fagesia superstes* also occurs in the Lower Turonian of the western interior (Cobban 1984) and Portugal (Berthou & Lauverjat 1979). *Eotissotia simplex* persists from the underlying Nigeriensis and Wallsi Zones at Dukul. Although *Hoplitoides latefundatus* Zaborski, 1987 occurs in the upper Lower Turonian of southern Nigeria, this genus is mainly of Middle Turonian age (Cobban & Hook 1980, Kennedy & Wright 1984). In the western interior of the United States it appears in the early Middle Turonian (Cobban 1984). In Nigeria *H. ingens* is thought to be characteristic of early Middle Turonian beds (Reyment 1978), the main occurrence of the genus being at Wadatta in the central part of the country.

This condensed fauna therefore contains elements which range from Lower to early Middle Turonian. Allix (1982) regarded the top of the Dukul Formation as basal Middle Turonian and an age very close to the Lower–Middle Turonian boundary is also suggested here. The Wallsi Zone below is almost certainly of late Early Turonian age, contrary to the opinion of Popoff *et al.* (1986). Further evidence to this effect is that *Choffaticeras barjonae*, proposed by these authors as the index species for a zone above limestones with *Wrightoceras wallsi* at Pindiga, occurs in beds assigned to the

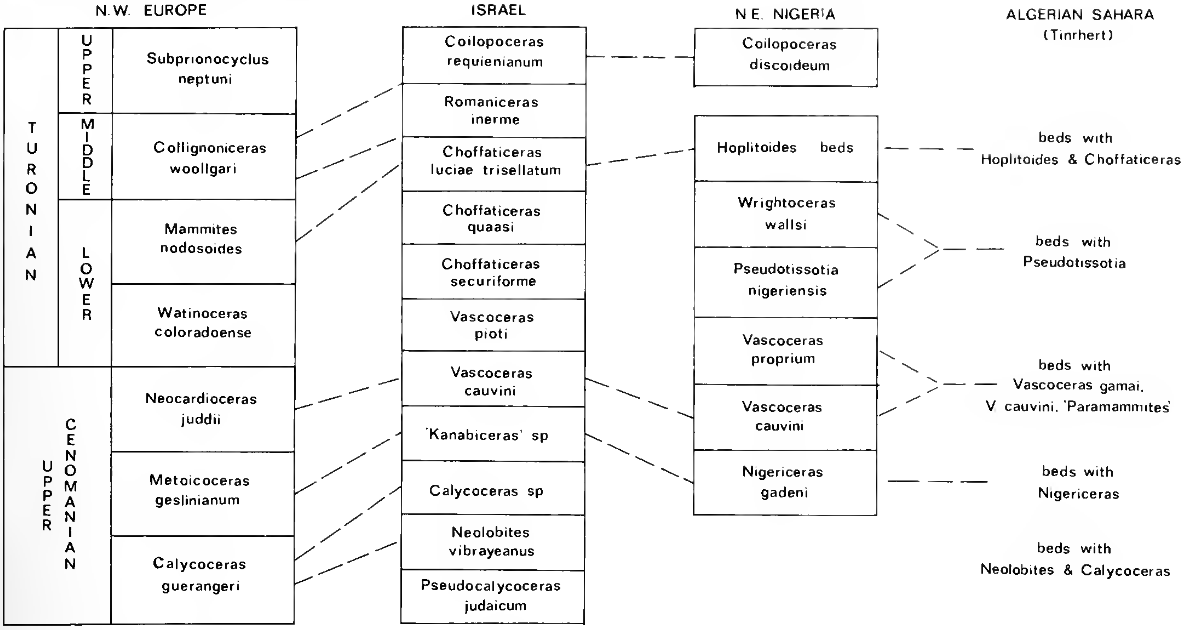


Fig. 39 Correlation of the Upper Cenomanian and Turonian in north-eastern Nigeria with the Algerian Sahara and Israel. Correlation between Israel and north-west Europe follows Lewy *et al.* (1984) and Kennedy (1985).

Lower Turonian in Portugal (Berthou 1984). Thus *Pseudotissotia* occurs considerably earlier in Nigeria than in France where the type species, *Ammonites galliennei* d'Orbigny, is of late Middle Turonian age (Kennedy *et al.* 1979, Amédro *et al.* 1982).

The Gadeni to Wallsi Zones in Nigeria therefore span an interval equivalent to the *Metoicoceras geslinianum* to *Mammites nodosoides* Zones in north-west Europe (Fig. 39). The chief remaining difficulty is the location of the Cenomanian–Turonian boundary. The Cauvini Zone in Nigeria is referrable to the Cenomanian. *Vascoceras cauvini* occurs in association with *M. geslinianum* over part of its range in Israel (Lewy *et al.* 1984). The latter species is known only from the Gadeni Zone in Nigeria, but, as noted previously, possible examples of *V. cauvini* are present in this zone. *V. cauvini* is an Upper Cenomanian species in the western interior of the United States (Cobban 1984). *Pseudaspidoceras pseudonodosoides*, common in the Cauvini Zone in Nigeria (see above, Popoff *et al.* 1986), occurs in the equivalent zone in Israel and in the uppermost Cenomanian *Neocardioceras juddii* (Barrois & Guerne) Zone of the western interior (Cobban 1984).

The overlying Proprium Zone contains, in its lower part, *Vascoceras cauvini* and *V. nigeriense*. The latter is very similar in its adult stages to *V. gamai* Choffat, 1898 (see Berthou *et al.* 1985 for a review), a species having its acme in the Upper Cenomanian. The Proprium Zone also contains the earliest examples of *Thomasites gongilensis*, a species which is known from the highest Cenomanian *Neocardioceras juddii* Zone and just below in southern England (Wright & Kennedy 1981) and in Brazil at a similar stratigraphical level (Bengtson 1983). Wozny & Kogbe (1983) also recorded *Metengonoceras dumbli*, a Cenomanian species (see Kennedy *et al.* 1981, Kennedy & Juignet 1984), from low in the Proprium Zone. In the lower part of the Nigeriensis Zone above, *Pseudaspidoceras* of *P. flexuosum* type occur at the level in which *Thomasites gongilensis* reaches its acme. The appearance of *P. flexuosum* is widely proposed as a marker for the base of the Turonian stage (Hancock 1984, Cobban 1984, Birkelund *et al.* 1984, Kennedy *et al.* 1987). As suggested by Hancock & Kennedy (1981) and Kennedy *et al.* (1987), the Cenomanian–Turonian boundary lies either within, or quite possibly at the top of, the Proprium Zone.

The stratigraphical position of *Coilopoceras discoideum* in Nigeria has previously seemed to be incongruous. It has, until now, been known only from the Mona region (Fig. 1), according to Barber (1957: 59), 'several hundred feet below the vascoceratid beds' (= Dukul Formation). This would imply a position well down in the Cenomanian. Grant (1965), on the other hand, believed it to be younger, occurring sometimes alone but in places with a typically early Turonian association of *Thomasites*, *Pseudotissotia*, *Vascoceras* and *Pseudaspidoceras*. He was, however, unable to recognize a detailed ammonite biostratigraphy. Both of these ages are at variance with current knowledge. Kennedy & Wright (1984) cast doubt on the reported occurrence of *Coilopoceras* in the Cenomanian of North Africa (see Pervinquière 1910). In the western interior of the United States the genus appears in the upper Middle Turonian but is mainly Late Turonian (Cobban & Hook 1980, Cobban 1984). In France its distribution is similar, from the *Romaniceras* (*R.*) *deverianum* (d'Orbigny) Zone (see Amédro *et al.* 1982), equivalent to the upper part of the *Collignoniceras woollgari* (Mantell) Zone of Kennedy *et al.* (1982) and Kennedy (1984) which these authors regarded as Middle Turonian, to the Upper Turonian *Subprionocyclus neptuni* (Geinitz) Zone. At Bularaba no continuous section is available but *Coilopoceras discoideum* certainly occurs some distance above the Wallsi Zone. Its only known associated ammonite is *Placenticeras* aff. *P. cumminsi*, a species found in the Lower and throughout the Middle Turonian of the western interior (Cobban 1984). At Bularaba there is no reason to believe that *Coilopoceras* appears unusually early and, as elsewhere, it can be assigned

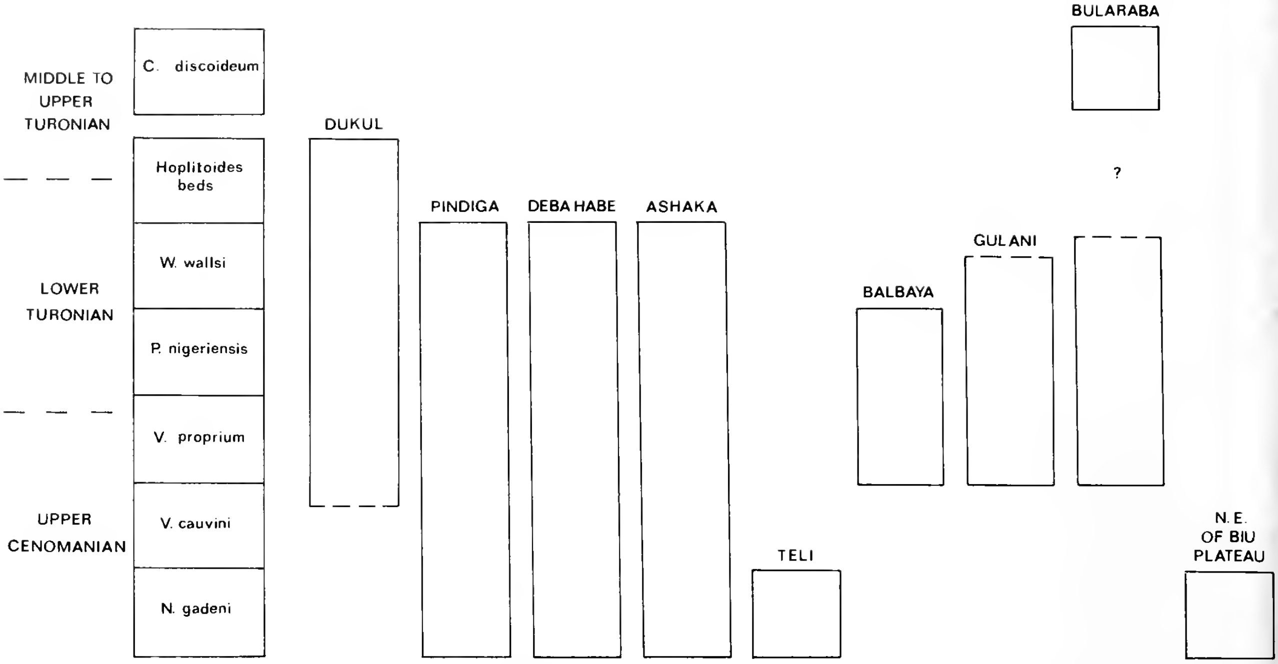


Fig. 40 Geographical distribution of ammonite biozones in north-eastern Nigeria. In most cases these biozones correspond with the limestone-bearing lithofacies.

to the upper Middle or Upper Turonian. Although the latter is more likely, a definite decision as to which is not possible in the current state of knowledge. As regards the occurrence of *C. discoideum* at Mona, it is significant that Lawal (1982) and Lawal & Moullade (1986) identified both Upper Turonian and Coniacian microfloras in the immediate area.

Whilst there are problems of provinciality involved in correlating the north-eastern Nigerian faunas with those of Boreal regions, comparison within the Tethyan province has been complicated by varying taxonomic opinions. The most straightforward correlation is probably with Israel (see Freund & Raab 1969, Lewy & Raab 1978, Lewy *et al.* 1984, and Fig. 39 herein for an ammonite biostratigraphy). There are no biostratigraphical equivalents in north-eastern Nigeria of the Israeli zones below that of '*Kanabiceras*' (properly *Euomphaloceras* Spath). The '*Kanabiceras*' Zone itself can be correlated with the Nigerian Gadeni Zone; both contain *Metoicoceras geslinianum* while *Nigericeras* of *N. gadeni* type (see Freund & Raab 1969: 19; pl. 2, fig. 1; text-fig. 40) occurs in the lower part of the Israeli zone. In the lower part of its range *Vascoceras cauvini* occurs alongside *M. geslinianum* in Israel and in Nigeria possible examples of *V. cauvini* are known from the Gadeni Zone at Pindiga. The *V. cauvini* zones in the two countries can also be correlated because of the occurrence of the index species and *Pseudaspidoceras* of *P. pseudonodosoides* type in both. The succeeding *Vascoceras pioti* (Peron & Fourtau), *Choffaticeras securiforme* (Eck) and *C. quaasi* (Peron) Zones in Israel cannot at present be directly correlated with Nigeria owing to a lack of common elements; there is only a record of *Pseudotissotia nigeriensis* from the Pioti Zone (Freund & Raab 1969: 50). The *Choffaticeras luciae trisellatum* Freund & Raab Zone in Israel, however, contains an assemblage including *Neoptychites cephalotus* and *Hoplitoides*, suggesting that it is broadly equivalent to the *Hoplitoides*-bearing bed at Dukul. The highest Turonian zone recognized in Israel is that of *Coilopoceras requienianum* (d'Orbigny) of late Middle or Late Turonian age; it can be regarded as broadly contemporaneous with the *C. discoideum* Zone in Nigeria. A noteworthy difference between the Lower Turonian of Israel and that of northern Nigeria, however, is the scarcity of *Choffaticeras* and corresponding abundance of *Pseudotissotia* and *Eotissotia* in the latter region. Interestingly, *Eotissotia simplex* is sometimes homoeomorphic with *Choffaticeras*; it may display a tricarinate venter in its middle growth stages and, more commonly, subdivision of most or all of the sutural saddles.

The Cenomanian–Turonian ammonite succession of the Algerian Sahara (see Busson 1965, 1972, Lefranc 1978, Amard *et al.* 1978, 1981; Fig. 39 here) is broadly similar to that in north-east Nigeria. There are, again, no Nigerian equivalents of the *Neolobites*-bearing beds in Algeria which include the upper parts of the ranges of *Calycoceras* Hyatt, *Eucalycoceras* Spath and *Pseudocalycoceras* Thomel and the lower part of the range of *Nigericeras* (Amard *et al.* 1978). The overlying beds in Algeria contain numerous *Nigericeras* without *Neolobites*, these horizons being equivalent to the earliest ammonite-bearing beds in northern Nigeria. The succeeding strata contain, amongst others, *Vascoceras cauvini*, *Paramammites laffittei* Collignon (1965: 186; pl. A, fig. 2) and *P. subtuberculatus* Collignon (1965: 187; pl. A, fig. 3), the last two being similar to and possibly conspecific with the various forms from Nigeria referred to *Paramammites* by Barber (1957). Next are beds with, in places, numerous *Pseudotissotia* (*Bauchioceras*) *nigeriensis* var. *egredians* Collignon (1965: 188; pl. H, fig. 1) and *P.* (*B.*) *bussoni* Collignon (1965: 190; pl. H, fig. 2), both, according to Hirano (1983), probable synonyms of *P. nigeriensis*. Collignon's figured specimens are especially close to microconchs of *P. nigeriensis* found at Deba Habe. In Algeria younger Turonian beds contain

Hoplitoides and, in the northern Tademaït region, *Coilopoceras* (Collignon & Lefranc 1974). Again *Choffaticeras* occurs in some numbers at these higher levels.

Correlation within Nigeria

In north-eastern Nigeria ammonites are almost exclusively confined to calcareous horizons and are therefore of biostratigraphical use only in formations containing such lithofacies. As shown in Fig. 40, the Cenomanian and Turonian limestones occur at various stratigraphical levels from place to place, as was pointed out by Lawal (1982) and Lawal & Moullade (1986). At Ashaka, Deba Habe and Pindiga limestone-bearing sequences ranging from the Gadeni to Wallsi Zone are present. At Dukul the Gadeni Zone has not been recognized. While the Dukul Formation includes an *Exogyra*-rich limestone at its base, the earliest ammonite present, *Pseudaspidoceras* cf. *pseudonodosoides*, occurs some 10 m higher in what is probably the upper part of the Cauvini Zone. The top of the Dukul Formation is a little younger than the highest ammonite-bearing beds at Pindiga, Deba Habe and Ashaka; no equivalent of the *Hoplitoides* fauna from Dukul is known at these localities. At Teli and north-east of the Biu plateau the Gadeni Zone alone is present. In the region between Balbaya and Bularaba the limestones of the Pindiga Formation belong to the Proprium Zone at their base. At Balbaya only ammonites typical of the overlying Nigeriensis Zone have otherwise been found but at Bularaba the main limestone body extends up into the Wallsi Zone. This species has also been reported from Gulani (Barber 1957), where the Nigeriensis Zone is also present. Apart from Mona, the Discoideum Zone is known only from Bularaba; but the strata intervening between it and the Wallsi Zone, and any ammonites they contain, are unknown.

Apart from varying in age, the limestone-bearing sequences differ markedly in thickness from place to place. In the Pindiga–Gombe–Deba Habe area variable, but consistently large, thicknesses are present. The Pindiga Formation here consists of a lower limestone-shale member and an upper shale member. The limestones, frequently marly, vary from a few cm to about 2 m in thickness. Their upper surfaces often mark minor sedimentary discontinuities. Around Pindiga village borehole records indicate thicknesses of 168 m, 294 m, and 330 m for the Pindiga Formation (Popoff *et al.* 1986). Estimates for the limestone-shale member vary: 60 m (Popoff *et al.* 1986), 80 m (Barber 1957), approximately 100 m (Wozny & Kogbe 1983). This last figure is probably closest to the true thickness. At Gombe town the limestone-shale member totalled about 65 m in one borehole (Thompson 1958, Carter *et al.* 1963: 49). To the south, at Kumo, the Pindiga Formation reaches nearly 800 m, the limestone-bearing part being in excess of 100 m in thickness (Lawal 1982, Lawal & Moullade 1986). At Deba Habe the limestone-shale member makes up the greater part of the Pindiga Formation, being about 100 m thick. At Dukul, the Dukul Formation is of comparable thickness, approximately 80 m, the formation again consisting mainly of shales, the limestones occurring as thin bands a few tens of cm in maximum thickness. At Ashaka the ammonite-bearing sequence is of intermediate thickness, approximately 20 m, the lower 9 m consisting mainly of massive limestones, the upper part shales with thinner interbedded limestones (see Wozny & Kogbe 1983, Popoff *et al.* 1986). North-east of the Biu plateau, on the other hand, the Gadeni Zone is represented by less than 1 m of hard, nodular limestone. The situation at Teli is comparable, though the Gadeni Zone may be slightly thicker. Between Balbaya and Bularaba the ammonite-bearing beds consist of condensed limestone sequences in which argillaceous and marly horizons are of subsidiary importance. At Balbaya the sequence is barely in excess of a couple of metres. It is rather thicker at Gulani and Bularaba but even here seems to be considerably less than 10 m, though no definite figures are available. In this region lithologies more closely resemble those at Ashaka than those in the Pindiga–Gombe area. Popoff *et al.* (1986: 357) found little purpose in separating the Gongila Formation and the overlying Fika Shale (see Carter *et al.* 1963) from the Pindiga Formation. This view is supported here, though Popoff *et al.* also suggested that the Dukul Formation might also be regarded as synonymous. This proposal is less tenable as the Upper Cretaceous sequence, at least in the eastern part of the Dadiya Syncline, is distinctive. In this region a sequence mainly comprising sands and silts (the Jessu Formation) separates the Dukul Formation from another major limestone-shale development of Coniacian age, the Sekule Formation (see Carter *et al.* 1963). Shales (the Numanha Shale) and sandstones (the Lamja Sandstone) complete the sequence, both being lateral equivalents of the Sekule Formation (see Petters 1978, Enu 1980, Allix 1982, Odebode 1987).

Clearly local subsidence history has had a profound effect on the lithological character and thickness of the Upper Cenomanian and Lower Turonian deposits in north-eastern Nigeria. During the Early Turonian the region between Balbaya and Bularaba seems to have been a relatively stable shelf area characterized by almost continuous limestone deposition. At Teli and north-east of the Biu plateau such conditions persisted for only a brief period during the Late Cenomanian. The Pindiga–Gombe–Deba Habe region, however, was characterized by strong subsidence virtually throughout Late Cenomanian and Early Turonian times, though the upper parts of the limestone beds here, sometimes rich in glauconite and containing reworked ammonites, often mark minor sedimentary discontinuities. Similar conditions prevailed to the south-east at Dukul where limestone deposition commenced a little later and persisted a little longer. At Ashaka limestone deposition characterized the Late Cenomanian but shales became the dominant lithology during the Early Turonian.

Allix & Popoff (1983) and Popoff *et al.* (1983) showed how, during the Early Cretaceous, sedimentation in north-eastern Nigeria was strongly influenced by faults, at first trending E–W and later NE–SW. Benkhelil (1982), Benkhelil & Robineau (1983) and Maurin *et al.* (1986) also stressed the importance of the latter structures, which they believed to be related to the South Atlantic transform fault system, during the Late Cretaceous. Sinistral strike-slip movement produced localized uplifted blocks and more extensive subsiding areas, 'pull-apart' or 'rhomb basins'. A number of such basins were identified by Maurin *et al.* (1986: fig. 12). Of these, the Pindiga and Lau Basins displayed the greatest rates of subsidence during the Late Cenomanian and Early Turonian.

Vascoceratid-dominated ammonite assemblages also occur in central and southern Nigeria. Particularly noteworthy are the Keana area with *Vascoceras nigeriense*, *V. proprium*, *Thomasites gongilensis*, *Pseudotissotia nigeriensis*, *Wrightoceras wallsi* and *Neoptychites* sp. (Offodile & Reyment 1976); and Ezillo with *Vascoceras*, *Fagesia*, *Thomasites gongilensis*, *T. koulabicus* (Kler), *Pseudotissotia nigeriensis*, *Wrightoceras* *wallsi* and *W.* cf. *munieri* (Zaborski 1987). Nowhere, however, is a detailed biostratigraphy available and the ammonite biozones applicable in the north-east cannot, as yet, be recognized outside that region. At Atom, near Makurdi, faunas including *Wrightoceras wallsi*, *Hoplitoides ingens*, *H. gibbosulus* (von Koenen) and *Mammites* spp. are present (Kogbe *et al.* 1978) but, again, the detailed stratigraphical relations of these forms are unclear. A little to the south, however, in the Icheri River near Igumale a fauna containing *Hoplitoides ingens* and *Neoptychites* (?)*cephalotus* overlies beds with *Wrightoceras wallsi* (Reyment 1955: 99), recalling the situation at Dukul. Furthermore, at Wadatta, immediately west of Makurdi, a diverse *Hoplitoides–Mammites–Benueites–Kamerunoceras* fauna (see Reyment 1955) is underlain by vascoceratid-bearing beds (Reyment 1978).

It should finally be noted that there is a marked change in both litho- and biofacies in the Lower Turonian around Lokpanta in southern Nigeria (see Zaborski 1987). Here black shales contain ammonites of boreal character. Basal Turonian beds characterized by *Watinoceras* spp. are overlain by a *Mammites nodosoides* Zone fauna containing *Hypophylloceras* sp., *Pachydesmoceras denisonianum* (Stoliczka), *Kamerunoceras puebloense* (Cobban & Scott), *Mammites nodosoides*, *Neoptychites cephalotus*, *Vascoceras venezolanum* Renz, *Paramammites polymorphus* (Pervinquière), *Fagesia catinus* (Mantell), *Hoplitoides latefundatus* Zaborski and *Herrickiceras*? sp. These black shales are, in the main, the age equivalents of the Nigeriensis and Wallsi Zones in the north-east of the country.

PALAEOBIOGEOGRAPHY

The palaeobiogeographical significance of the ammonite faunas of northern Nigeria has, in the past, often been difficult to assess as it had seemed that many of the forms present were endemic to the region. In opposition to the prevailing view (see Reyment 1980 for a review), Petters (1978) doubted that the northern Nigerian region was in direct connection with the trans-Saharan seaway during the Late Cretaceous. Popoff *et al.* (1986), however, showed that many of the Nigerian ammonite species are also known in the Saharan countries and elsewhere. Similarity is especially close in the Upper Cenomanian where *Metengonoceras*, *Nigericeras gadeni* and *Vascoceras cauvini* are important elements of the faunas in both north-eastern Nigeria and the Damergou area of Niger to the north (Chudeau 1909, Furon 1935, Schneegans 1943, Schöbel 1975). *Pseudotissotia nigeriensis* is also present at Damergou (Schneegans 1943), although in the Lower Turonian faunal similarity is reduced, *Thomasites*, *Eotissotia* and *Wrightoceras* being unknown there. *Pseudotissotia nigeriensis* is also present in the Algerian Sahara, as are *Nigericeras gadeni*, *Vascoceras cauvini* and forms probably conspecific with the Nigerian '*Paramammites*' of Barber (1957). The Late Cenomanian *Neolobites* faunas from the Saharan countries have no equivalent in Nigeria. Greigert (1966) showed that in west Africa they extend only as far south as southern Niger. Present evidence, therefore, indicates that vascoceratid ammonites first entered Nigeria from the north during *Metoicoceras geslinianum* Zone times. Microfossil evidence does indicate marine influence in the older Yolde Formation and, indeed, in the upper part of the Bima Sandstone (Doyle *et al.* 1982, Lawal 1982, Allix 1982) but environmental conditions seem to have been unsuitable for ammonites.

Marine microfossils are found virtually throughout the Upper Cretaceous in north-east Nigeria (Lawal 1982). Popoff *et al.* (1986) proposed that faunal exchange across the Sahara was continuous during the Late Cretaceous. The presence of *Hoplitoides* and *Coilopoceras* in north-east Nigeria indicates that marine conditions suitable for ammonites continued into the Middle and probably the Late Turonian here. Coniacian ammonites including *Forresteria* Reeside, *Barroisiceras* Grossouvre and *Tissotia* Douvillé occur in the limestones of the Sekule Formation in the Dadiya Syncline (see also Reyment 1954*a*, Barber 1960) and Santonian beds may exist a little further south (Reyment 1957). *Libycoceras* Hyatt has been found in Upper Campanian shales near Gombe (Reyment 1955, Zaborski 1982). Although, in ammonite terms, the major part of the Santonian and Campanian, and the whole Maastrichtian, are unknown, there is a growing body of evidence pointing to persistent marine conditions in north-eastern Nigeria during virtually the entire Late Cretaceous.

In southern and central Nigeria *Hoplitoides* is known in numbers from Wadatta and Igumale, while *Coilopoceras* (= *Glebosoceras* Reyment, 1954) occurs around Ogoja (Reyment 1954, 1957*a*) and north of Calabar (Zaborski 1985). *C. vandersluisi* Reyment (1957*a*: 62; pl. 10, figs 1a, b), indeed, is very similar to, and possibly synonymous with, *C. discoideum*. Kennedy & Wright (1984) suggested that *Glebosoceras globosum* Reyment (1954: 161; pl. 2, fig. 3; pl. 4, fig. 1; text-fig. 5) and *C. discoideum* may be a conspecific, dimorphic pair. Coniacian, Upper Campanian and Lower Maastrichtian ammonites are well known from southern Nigeria (Reyment 1954, 1954*a*, 1955, Zaborski 1982). Again, here it is Santonian to lower Upper Campanian forms that are unknown, although Klinger & Kennedy (1980: 110) speculated on the possibility of a Santonian age for *Reginaites quadrituberculatum* Reyment (1957*a*: 65; pl. 11, figs 1a, b) from near Agbani.

ADDITIONAL NOTE

After additional collecting at Ashaka, the following observations are relevant to the results of this paper and in particular to the position of the Cenomanian–Turonian boundary in north-eastern Nigeria. Firstly, weakly ribbed forms of *Thomasites gongilensis*, similar to those described from the Upper Cenomanian of Devon by Wright & Kennedy (1981), predominate in the Proprium Zone. Secondly, *Pseudaspidoceras* of *P. pseudonodosoides* type occurs in the Proprium Zone. And thirdly, *Pseudaspidoceras flexuosum* is present in the middle and upper parts of the Nigeriensis Zone (the species appears, however, at the base of this zone where large numbers of predominantly strongly ribbed *Thomasites gongilensis* occur). These further indications confirm the placement of the Cenomanian–Turonian boundary at or close to the top of the Proprium Zone, and the basal Turonian position of the Nigeriensis Zone.

Meister (1989) has recently published an extensive account of the Ashaka ammonites. It is not possible to make detailed comments on this work here but the following important points may be made concerning his proposed biozonation.

Meister's '*Nigericeras gadeni* Zone' corresponds not to that as proposed here, but to the Cauvini Zone. The forms he refers to *Nigericeras* are here regarded as *Vascoceras cauvini*. Such relatively compressed ammonites from this stratigraphical level at Ashaka, and elsewhere in north-eastern Nigeria, lack the typically acanthoceratid suture and seven rows of tubercles which characterize *Nigericeras*. True *Nigericeras* occurs below, in the Gadeni Zone as proposed here. This part of the sequence at Ashaka is not included in the section given by Meister (1989: fig. 41); its upper surface forms the floor of the quarry, but until 1987 it could be seen in vertical profile, but only in the eastern part of the quarry. It has subsequently been largely covered by dumping of overburden.

Meister (1989: 36) remarks on the astonishing diversity of morphotypes in the Proprium Zone and admits that he may have oversplit these faunas in his taxonomy. I think he does, and this explains the numerous biostratigraphical 'horizons' identified by Meister at the levels of the Proprium and lower Nigeriensis Zones as employed here.

Meister draws the base of his '*Pseudotissotia nigeriensis* Zone' at a higher level than that used here. The upper part of his '*Thomasites gongilensis* Subzone' is considered as part of the Nigeriensis Zone containing, as it does, the earliest, more tuberculated, forms of *P. nigeriensis*.

Meister employs *Wrightoceras wallsi* as a subzonal index with a further 'Subzone of *Fagesia superstes* or *Choffaticeras quaasi*–*C. pavillieri*' above. *Fagesia* of *F. superstes* type, however, extend higher than the ranges of either *W. wallsi* or *Pseudotissotia nigeriensis* at Dukul, while at Ashaka *Choffaticeras* appears not, as he suggests, at the level of his 'Superstes Zone' but considerably lower, in the middle part of the Nigeriensis Zone as proposed here.

Acknowledgements. Field work was supported by a University of Maiduguri (Nigeria) Senate Research Grant which is gratefully acknowledged. Photographs were provided by the British Museum (Natural History) photographic Unit. Thanks are due to Drs M. K. Howarth and H. G. Owen for assistance in many respects. I am grateful to Professor R. A. Reyment for information regarding central Nigerian ammonites.

REFERENCES

Allix, P. 1982. *Environnements mesozooïques de la partie nord-orientale du fossé de la Bénoué (Nigéria). Stratigraphie, sédimentologie, évolution géodynamique.* Thèse 3^{e} cycle, Univ. Aix Marseille (= *Trav. Lab. Sci. Terre St.-Jérôme, Marseille* (B) **21**). 135 pp.

——, **Grosdidier, E., Jardiné, S., Legoux, O. & Popoff, M.** 1981. Découverte d'Aptien supérieur à Albien inférieur daté par microfossiles dans la série détritique crétacée du fossé de la Bénoué (Nigéria). *C. r. hebd. Séanc. Acad. Sci. Paris*, (2) **292**: 1291–1294.

—— **& Popoff, M.** 1983. Le Crétacé inférieur de la partie nord-orientale du fossé de la Bénoué (Nigéria): un exemple du relation étroite entre tectonique et sédimentation. *Bull. Cent. Rech. Explor.-Prod. Elf-Aquitaine*, Pau, **7**: 349–359.

Amard, B., Collignon, M. & Lefavrais-Henry, M. 1978. Le Cénomanien d'El Golea (Tademaït N, Sahara Algérien): coexistence de *Calycoceras* avec *Nigericeras* et implication stratigraphique. *Cah. Micropaléont.*, Paris, **1978**: 29–46, pls 1–5.

——, **Collignon, M. & Roman, J.** 1981. Étude stratigraphique et paléontologique du Crétacé supérieure et Paléocene du Tinrhert-W et Tademaït-E (Sahara Algérien). *Docums Lab. Géol. Fac. Sci. Lyon* (H.S.) **6**: 15–173, pls 1–17.

Amédro, F., Badillet, G. & Devalque, C. 1982. Biostratigraphie et biozonation des ammonites du Turonien français. *Mém. Mus. natn. Hist. nat. Paris* (n.s.) (C) **49**: 167–173.

Barber, W. 1957. Lower Turonian ammonites from north-eastern Nigeria. *Bull. geol. Surv. Nigeria*, Kaduna, **26**: 1–86, pls 1–35.

—— 1960. Notes on Upper Cretaceous Ammonoidea from north-eastern Nigeria. *Rec. geol. Surv. Nigeria*, Kaduna, **1957**: 60–67, pls 13–14.

Bengtson, P. 1983. The Cenomanian–Coniacian of the Sergipe Basin, Brazil. *Fossils Strata*, Oslo, **12**: 1–78, 1 map.

Benkhelil, J. 1982. Benue Trough and Benue chain. *Geol. Mag.*, Cambridge, **119**: 155–168.

—— **& Robineau, B.** 1983. Le fossé de la Bénoué est-il un rift? *Bull. Cent. Rech. Explor.-Prod. Elf-Aquitaine*, Pau, **7**: 315–321.

Berthou, P.-Y. 1984. Albian–Turonian stage boundaries and subdivisions in the western Portugese Basin, with special emphasis on the Cenomanian–Turonian boundary in the ammonite facies and rudist facies. *Bull. geol. Soc. Denm.*, Copenhagen, **33**: 41–55.

——, **Chancellor, G. R. & Lauverjat, J.** 1985. Revision of the Cenomanian–Turonian ammonite *Vascoceras* Choffat, 1898, from Portugal. *Comunçoes Servs. geol. Port.*, Lisbon, **71**: 55–79, pls 1–6.

—— **& Lauverjat, J.** 1979. Essai de synthèse paléogeographique et paléobiostratigraphique du bassin occidental portugais au cours du Crétacé supérieur. *Ciências Terra Univ. nova Lisboa* **5**: 121–144.

Birkelund, T., Hancock, J. M., Hart, M. B., Rawson, P.F., Remane, J., Robaszynski, F., Schmid, F. & Surlyk, F. 1984. Cretaceous stage boundaries–proposals. *Bull. geol. Soc. Denm.*, Copenhagen, **33**: 3–20.

Busson, G. 1965. Sur les gisements de céphalopodes crétacés sahariens. *Annls Paléont.*, Paris, **51**: 151–161.

—— 1972. Principes, méthodes et résultats d'une étude stratigraphique du Mésozoïque saharien. *Mém. Mus. natn. Hist. nat. Paris* (n.s.) **26**: 1–441, pls 1–8.

Carter, J. D., Barber, W., Tait, E.A. & Jones, G. P. 1963. The geology of parts of Adamawa, Bauchi and Bornu provinces in north-eastern Nigeria. *Bull. geol. Surv. Nigeria*, Kaduna, **30**: 1–108, 6 pls, 3 maps.

Choffat, P. 1898. Recueil d'études paléontologiques sur la faune crétacique du Portugal. 1. Espèces nouvelles ou peu connus. 2, Les ammonées du Bellasien, des Couches à *Neolobites Vibrayeanus*, du Turonien et du Sénonien. *Mém. Commn géol. Port.*, Lisbon, **1898**: 41–86, pls 3–22.

Chudeau, R. 1909. Ammonites du Damergou (Sahara meridionel). *Bull. Soc. géol. Fr.*, Paris, (4) **9**: 67–71, pls 1–3.

Cobban, W. A. 1971. New and little known ammonites from the Upper Cretaceous (Cenomanian and Turonian) of the western interior of the United States. *Prof. Pap. U. S. geol. Surv.*, Washington, **699**: 1–24, pls 1–18.

—— 1984. Mid-Cretaceous ammonite zones, western interior, United States. *Bull. geol. Soc. Denm.*, Copenhagen, **33**: 71–89.

—— **& Hook, S. C.** 1980. The Upper Cretaceous ammonite family Coilopoceratidae Hyatt in the western interior of the United States. *Prof. Pap. U. S. geol. Surv.*, Washington, **1192**: 1–28, pls 1–21.

—— **& Scott, G.R.** 1972. Stratigraphy and ammonite fauna of the Graneros Shale and Greenhorn Limestone near Pueblo, Colorado. *Prof. Pap. U. S. geol. Surv.*, Washington, **645**: 1–108, pls 1–41.

Collignon, M. 1965. Nouvelles ammonites néocrétacées sahariennes. *Annls Paléont.*, Paris, **57**: 165–202, pls A–H.

—— **& Lefranc, J. P.** 1974. Découverte d'une faune du Turonien inférieur élevé à *Coilopoceras* et *Hoplitoides* dans le nord du Tademaït (Sahara algérien); son extension probable en Afrique du nord. *C. r. hebd. Séanc. Acad. Sci. Paris*, (D) **278**: 817–821.

Cooper, M. R. 1978. Uppermost Cenomanian–basal Turonian ammonites from Salinas, Angola. *Ann. S. Afr. Mus.*, Cape Town, **75**: 51–152.

Cragin, F. W. 1893. A contribution to the invertebrate paleontology of the Texas Cretaceous. *Rep. geol. Surv. Texas*, Austin, **4** (9): 139–246, pls 24–46.

Doyle, J. A., Jardiné, S. & Doerenkamp, A. 1982. *Afropollis*, a new genus of early angiosperm pollen, with notes on the Cretaceous palynostratigraphy and paleoenvironments of northern Gondwana. *Bull. Cent. Rech. Explor.-Prod. Elf-Aquitaine*, Pau, **6**: 39–117, pls 1–13.

Enu, E. I. 1980. Sukuliye (Sekule) Formation, facies equivalent of the Numanha Formation in the upper Benue Trough, Nigeria. *J. Min. Geol.*, Ibadan, **17**: 91–95.

Faraud, M. 1940. Le genre *Vascoceras* dans le Turonien du Gard. *Bull. Soc. Étud. Sci. nat. Vaucluse*, Avignon, **3**: 40–61.

Förster, R., Meyer, R. & Risch, H. 1983. Ammoniten und planktonische Foraminiferen aus den Eibrunner Mergeln (Regensburger Kreide, Nordostbayern). *Zitteliana*, Munich, **10**: 123–141, pls 1–3.

Freund, R. & Raab, M. 1969. Lower Turonian ammonites from Israel. *Spec. Pap. Palaeont.*, London, **4**: 1–83, pls 1–10.

Furon, R. 1935. Le Crétacé et le Tertiare du Sahara soudanais. *Archs Mus. natn. Hist. nat. Paris* (6) **13**: 1–96, pls 1–7.

Grant, N. K. 1965. The geology of part of the Dadiya Syncline, north-eastern Nigeria. *J. niger. Min. geol. metall. Soc.*, Ibadan, **2**: 17–28.

Greigert, J. 1966. Description des formations Crétacées et Tertiares du Bassin des Iullemmeden (Afrique occidentale). *Mém. Bur. Rech. géol. minièr.*, Paris, **36**: 1–234, map. (= *Publs Dir. Min. Géol. Niger*, Niamey, **2**).

—— & **Pougnet, R.** 1967. Essai de description des formations géologiques de la république du Niger. *Mém. Bur. Rech. géol. minièr.*, Paris, **48**: 1–238.

Hancock, J. M. 1984. Some possible boundary-stratotypes for the base of the Cenomanian and Turonian stages. *Bull. geol. Soc. Denm.*, Copenhagen, **33**: 123–128.

—— & **Kennedy, W. J.** 1981. Upper Cretaceous ammonite stratigraphy: some current problems. *In* House, M. R. & Senior, J. R. (eds), *The Ammonoidea*: 531–553. London (Academic Press, for the Systematics Association).

Hirano, H. 1983. Revision of two vascoceratid ammonites from the Upper Cretaceous of Nigeria. *Bull. Sci. Engin. Res. Lab. Waseda Univ.*, Tokyo, **105**: 44–79, pls 1–5.

Kennedy, W. J. 1984. Ammonite faunas and the 'standard zones' of the Cenomanian to Maastrichtian stages in their type areas, with some proposals for the definition of the stage boundaries by ammonites. *Bull. geol. Soc. Denm.*, Copenhagen, **33**: 147–161.

—— 1985. Integrated macrobiostratigraphy of the Albian to basal Santonian. *In* Reyment, R. A. & Bengtson, P. (comps), Mid-Cretaceous events: report on results obtained 1974–1983 by IGCP Project No. 58. *Spec. Vol. palaeont. Instn. Univ. Uppsala* **5**: 91–108.

——, **Cooper, M. R. & Wright, C. W.** 1979. On *Ammonites galliennei* d'Orbigny, 1850. *Bull. geol. Instn Univ. Uppsala*, (n.s.) **8**: 5–15.

—— & **Juignet, P.** 1973. Observations on the lithostratigraphy and ammonite succession across the Cenomanian–Turonian boundary in the environs of Le Mans (Sarthe, N.W. France). *Newsl. Stratigr.*, Leiden, **2**: 189–202.

—— —— 1977. *Ammonites diartianus* d'Orbigny, 1850, Vascoceratidae du Cénomanien supérieur de Saint-Calais (Sarthe). *Géobios*, Lyon, **10**: 583–595, pls 1, 2.

—— —— 1981. Upper Cenomanian ammonites from the environs of Saumur, and the provenance of the types of *Ammonites vibreyeanus* and *Ammonites geslinianus*. *Cret. Res.*, London, **2**: 19–49.

—— —— 1984. A revision of the ammonite faunas of the type Cenomanian. 2. The families Binneyitidae, Desmoceratidae, Engonoceratidae, Placenticeratidae, Hoplitidae, Schloenbachiidae, Lyelliceratidae and Forbesiceratidae. *Cret. Res.*, London, **5**: 93–161.

Kennedy, Juignet & Hancock, J. M. 1981. Upper Cenomanian ammonites from Anjou and the Vendée, western France. *Palaeontology*, London, **24**: 25–84, pls 3–17.

Kennedy & Wright, C. W. 1984. The Cretaceous ammonite *Ammonites requienianus* d'Orbigny, 1841. *Palaeontology*, London, **27**: 281–293, pls 35–37.

Kennedy, Wright & Hancock, J. M. 1982. Ammonite zonation and correlation of the uppermost Cenomanian and Turonian of southern England and the type areas of Sarthe and Touraine in France. *Mém. Mus. natn. Hist. nat. Paris* (n.s.) (C) **49**: 175–181.

—— —— —— 1987. Basal Turonian ammonites from West Texas. *Palaeontology*, London, **30**: 27–74, pls 1–10.

Klinger, H. C. & Kennedy, W. J. 1980. Cretaceous faunas from Zululand and Natal, South Africa. The ammonite subfamily Texanitinae Collignon, 1948. *Ann. S. Afr. Mus.*, Cape Town, **80**: 1–357.

Koenen, A. von 1897. Ueber Fossilien der unteren Kreide am Ufer des Mungo in Kamerun. *Abh. K. Ges. Wiss. Göttingen*, (N.R.) **1**: 1–48, 4 pls.

Kogbe, C. A., Tokarski, A., Osijuk, D. & Wozny, D. E. 1978. Geology of the Makurdi in the middle Benue Valley, Nigeria. *Occ. Publs Dep. Geol. Ahmadu Bello Univ.*, Zaria, **5**: 1–107, pls 1–14.

Kossmat, F. 1897. Untersuchungen über die Südindische Kreideformation. *Beitr. Paläont. Geol. Öst.-Ung.*, Vienna & Leipzig, **11**: 1–46, pls 1–8.

Lawal, O. 1982. *Biostratigraphie, palynologie et paléo-environnements des formations crétacées de la Haute-Bénoue, Nigéria nord-orientale.* 198 pp., 21 pls. Thèse 3^{e} cycle, Univ. Nice.

—— & **Moullade, M.** 1986. Palynological biostratigraphy of Cretaceous sediments in the Upper Benue Basin, N.E. Nigeria. *Revue Micropaléont.*, Paris, **29**: 61–82, pls 1–5.

Lefranc, J. P. 1978. État des connaissances actuelles sur les zonations biostratigraphiques du milieu du Crétacé (Albien à Turonien) au Sahara. *Annls Mus. Hist. nat. Nice* **4** (XIX): 1–19.

Lewy, Z., Kennedy, W. J. & Chancellor, G. R. 1984. Co-occurrence of *Metoicoceras geslinianum* (d'Orbigny) and *Vascoceras cauvini* Chudeau (Cretaceous Ammonoidea) in the southern Negev (Israel) and its stratigraphic implications. *Newsl. Stratigr.*, Leiden, **13**: 67–76.

—— & **Raab, M.** 1978. Mid-Cretaceous stratigraphy of the Middle East. *Annls Mus. Hist. nat. Nice* **4** (XXXII): 1–20, pls 1, 2.

Maurin, J. C., Benkhelil, J. & Robineau, B. 1986. Fault rocks of the Kaltungo lineament, NE Nigeria, and their relationship with Benue Trough tectonics. *J. geol. Soc.*, London, **143**: 587–599.

Meister, C. 1989. Les ammonites du Crétacé supérieur d'Ashaka (Nigéria). *Bull. Cent. Rech. Explor.-Prod. Elf-Aquitaine*, Boussens, **13** (suppl.): 1–84, pls 1–28.

Offodile, M. E. & Reyment, R. A. 1976. Stratigraphy of the Keana–Awe area of the middle Benue region of Nigeria. *Bull. geol. Instn Univ. Uppsala*, (n.s.) **7**: 37–66.

Odebode, M. O. 1987. Palynological dating of the Lamja Sandstone (Benue Basin, Nigeria) and its geological significance. *J. afr. Earth Sci.*, Oxford, **6**: 421–426.

Ojo, O. M. & Pinna, P. 1982. Palaeogeographical and structural evolution of the upper Benue Trough of Nigeria. *Cret. Res.*, London, **3**: 195–207.

Pervinquière, L. 1907. *Études de paléontologie tunisienne*, **1**. *Céphalopodes des terrains secondaires.* 438 pp., 27 pls. Paris, Carte géol. Tunis.

—— 1910. Sur quelques ammonites du Crétacé algérien. *Mém. Soc. géol. Fr. Paléont.*, Paris, **17**: 1–86, pls 1–17.

Petters, S. W. 1978. Stratigraphic evolution of the Benue Trough and its implications for the Upper Cretaceous paleogeography of west Africa. *J. Geol.*, Chicago, **86**: 311–322.

Popoff, M., Benkhelil, J., Simon, B. & Motte, J. J. 1983. Approche géodynamique du fossé de la Bénoué (N.E. Nigéria) à partir des données de terrain et de télédetection. *Bull. Cent. Rech. Explor.-Prod. Elf-Aquitaine*, Pau, **7**: 323–337.

——, **Wiedmann, J. & de Klasz, I.** 1986. The Upper Cretaceous Gongila and Pindiga Formations, northern Nigeria: subdivisions, age, stratigraphic correlations and paleogeographic implications. *Eclog. geol. Helv.*, Basel, **79**: 343–363.

Powell, J. D. 1963. Cenomanian–Turonian (Cretaceous) ammonites from Trans-Pecos Texas and north-eastern Chihuahua, Mexico. *J. Paleont.*, Tulsa, **37**: 309–332, pls 31–34.

Renz, O. 1982. *The Cretaceous ammonites of Venezuela.* 132 pp., 40 pls. Basel.

Reyment, R. A. 1954. New Turonian (Cretaceous) ammonite genera from Nigeria. *Colon. Geol. Miner. Resour.*, London, **4**: 149–164, pls 1–4.

—— 1954*a*. Some new Upper Cretaceous ammonites from Nigeria. *Colon. Geol. Miner. Resour.*, London, **4**: 248–276, pls 1–5.

—— 1955. The Cretaceous Ammonoidea of southern Nigeria and the southern Cameroons. *Bull. geol. Surv. Nigeria*, Kaduna, **25**: 1–112, pls 1–25.

—— 1956. On the stratigraphy and palaeontology of the Cretaceous of Nigeria and the Cameroons, British West Africa. *Geol. För. Stockh. Förh.* **78**: 17–96.

—— 1957. On the occurrence of Santonian in north-eastern Nigeria. *Stockh. Contr. Geol.*, (n.s.) **1**: 35–39, 1 pl.

—— 1957*a*. Über einige wirbellose Fossilien aus Nigerien und Kamerun, Westafrika. *Palaeontographica*, Stuttgart, (A) **109**: 41–70, pls 7–11.

—— 1965. *Aspects of the geology of Nigeria.* 145 pp., 18 pls. Ibadan.

—— 1978. The mid-Cretaceous of the Nigerian coastal basin. *Annls Mus. Hist. nat. Nice* 4 (XX): 1–13.

—— 1980. Biogeography of the Saharan Cretaceous and Paleocene epicontinental transgressions. *Cret. Res.*, London, **1**: 299–327.

Robaszynski, F., Alcaydé, G., Amédro, F., Badillet, G., Damotte, R., Foucher, J. C., Jardiné, S., Legoux, O., Manivit, H., Monciardini, C. & Sornay, J. 1983. Le Turonien de la region-type: Saumurois et Touraine. Stratigraphie, biozonations, sédimentologie. *Bull. Cent. Rech. Explor.-Prod. Elf-Aquitaine*, Pau, **6**: 119–225, pls 1–18.

Schöbel, J. 1975. Ammoniten der Familie Vascoceratidae aus dem Unterturon des Damergou-Gebietes, République du Niger. *Spec. Vol. palaeont. Instn. Univ. Uppsala* **3**: 1–136, pls 1–6.

Schneegans, D. 1943. Invértébres du Crétacé supérieur du Damergou (Territoire du Niger). *Bull. Dir. Mines Afr. occid. fr.*, Dakar, **7**: 87–150, pls 1–8.

Thompson, J. H. 1958. The geology and hydrology of Gombe, Bauchi Province. *Rec. geol. Surv. Nigeria*, Kaduna, **1956**: 46–65.

Wiedmann, J. 1960. Le Crétacé supérieur de l'Éspagne et du Portugal et ses céphalopodes. *In*: Colloque sur le Crétacé Supérieur Français (Dijon 1959). *C. r. Congr. Socs sav. Paris Sect. Sci.* **1959**: 709–764, 8 pls.

—— 1979. Die Ammonitiden der NW-deutschen Regensburger und Ostalpinen Oberkreide im Vergleich mit den Oberkreidefaunen des westlichen mediterrangebiets. *In* Wiedmann, J. (ed.), Aspekte der Kreide Europas. *Int. Union geol. Sci.*, Stuttgart, (A) **6**: 335–350.

—— & **Kauffman, E. G.** 1978. Mid-Cretaceous biostratigraphy of northern Spain. *Annls Mus. Hist. nat. Nice* **4** (III): 1–34, pls 1–12.

Woods, H. 1911. The palaeontology of the Upper Cretaceous deposits of Northern Nigeria. *In* Falconer, J. D., *The geology and geography of Northern Nigeria*: 273–286, pls 19–24. London.

Wozny, E. & Kogbe, C. A. 1983. Further evidence of marine Cenomanian, Lower Turonian and Maastrichtian in the Upper Benue Basin of Nigeria (west Africa). *Cret. Res.*, London, **4**: 95–99.

Wright, C. W. & Kennedy W. J. 1981. The Ammonoidea of the Plenus Marls and the Middle Chalk. 148 pp., 32 pls. *Palaeontogr. Soc. (Monogr.)*, London.

Zaborski, P. M. P. 1982. Campanian and Maastrichtian sphenodiscid ammonites from southern Nigeria. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **36** (4): 303–332, 36 figs.

—— 1985. Upper Cretaceous ammonites from the Calabar region, south-east Nigeria. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **39** (1): 1–72, 66 figs.

—— 1987. Lower Turonian (Cretaceous) ammonites from south-east Nigeria. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **41** (2): 31–66, 46 figs.

Bull. Br. Mus. nat. Hist. (Geol.) **46** (1): 19–36 Issued 31 May 1990

Two new amphisbaenians from the Lower Miocene of Kenya

ALAN J. CHARIG

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

CARL GANS

Division of Biological Sciences, The University of Michigan, Ann Arbor, Michigan 48109, U.S.A.

CONTENTS

Synopsis. Three partial skulls of two new species and genera (*Listromycter leakeyi* and *Lophocranion rusingense*) of Amphisbaenidae, from the Lower Miocene of Rusinga Island, Lake Victoria (Kenya), are described, illustrated, and compared with Recent amphisbaenians. *Listromycter leakeyi* is the largest amphisbaenian known. These new specimens extend the geographical range of the Amphisbaenidae into East–Central Africa, and they are the first fossil amphisbaenians of any age to be found in Africa.

INTRODUCTION

In 1947 the late Dr L. S. B. Leakey collected a quantity of vertebrate material from the Lower Miocene deposits on Rusinga Island, in the Kenyan waters of Lake Victoria. Three years later, in 1950, some of this material was sent to the British Museum (Natural History) in London; it included three small, very unusual skulls. All are broken and incomplete. The first, much the largest of the three, lacks the occiput and the lower jaw. The second and third lack the anterior portions and the lower jaw, each consisting of little more than the actual braincase. Yet there is just enough overlap between the first and the other two to indicate that the first is entirely distinct. The two smaller skulls, on the other hand, seem to be conspecific with each other.

The skulls were first recognized as amphisbaenian by the prominent median tooth in the first skull, the great solidity of the bones in relation to the size of the skulls, the lack of bony arcades, and the marked cranio-facial angle. However, more important as indicating that these animals could not be anything other than amphisbaenians were the extremely heavy premaxilla with its prominent facial process; the relatively few teeth and their relatively enormous size; the frontals completely surrounding the anterior end of the braincase; the peculiar interdigitating sutures between the elements comprising the braincase, resulting in a 'sandwich' construction of the latter; and, finally, the presence of a prominent processus ascendens of the supraoccipital fitting into a median notch behind the parietal. These characteristics and the general concordance between the architecture of the skulls and that of other amphisbaenians left no doubt that all three skulls had been properly assigned to that group.

The description of new genera of fossil amphisbaenians poses certain problems at present. Although the taxonomy of Recent species has now been reviewed (Broadley & Gans 1969, 1975, 1978*a*, *b*; Broadley, Gans & Visser 1976; Gans 1967*a*, *b*, 1971*a*, *b*, 1976, 1987; Gans & Alexander 1962; Gans & Broadley 1974; Gans & Kochva 1965; Gans & Kraklau 1989; Gans & Latifi 1971; Gans & Lehman 1973; Gans & Rhodes 1967), problems in the cranial osteology of the entire group have only recently been addressed (Bellairs & Gans 1983; Bellairs & Kamal 1980; Gans 1978; Jollie 1960). Numerous workers have illustrated amphisbaenian skulls (see Gans 1978 for references), but most of them have studied the same few species. Thus our knowledge of the skull in the species group *Monopeltis–Dalophia*, comprising 23 species, is based entirely upon four descriptions of *Monopeltis capensis* (Peters 1882; Zangerl 1944; Kritzinger 1946; Vanzolini 1951*a*). More extensive and detailed descriptions are being prepared.

Because of this the present paper can do little more than document the existence of the Kenyan material and describe it as fully as possible. We do include a brief discussion of the presumptive places of the new forms within the amphisbaenian radiation. Yet this analysis rests primarily upon the admittedly incomplete results of the generic review of the Amphisbaenia; it should therefore be regarded as preliminary.

ABBREVIATIONS

The following abbreviations are used in annotations of line drawings, Figs 2, 5 and 6.

bo	basioccipital
c_1	unidentified canal in premaxilla
c_2	unidentified canal in septomaxilla
ec	ectopterygoid
eo	exoccipital
f	frontal
fm	foramen magnum
f_o	foramen, presumably for the optic nerve
f_1	unidentified foramina in maxilla
f_2	
f_3	
f_4	unidentified foramen in posterolateral corner of nasal
f_5	unidentified foramen in anterior tip of vomer
f_6	unidentified foramen between palatine, pterygoid, maxilla and prefrontal
f_7	facial foramina for the VIIth nerve
g_1	unnamed groove extending forwards from the foramen for the Gasserian ganglion
m	maxilla
n	nasal
ocot	occipito-otic complex
op	opisthotic
os	orbitosphenoid
p	parietal
pbs	parabasisphenoid
pl	palatine
pls	pleurosphenoid
pm	premaxilla
pr	prootic
prf	prefrontal
pt	pterygoid
sm	septomaxilla
soc	supraoccipital
stp	stapes
v	vomer

SYSTEMATIC PALAEONTOLOGY

Suborder **AMPHISBAENIA** Gray, 1841
Family **AMPHISBAENIDAE** Gray, 1825

Genus ***LISTROMYCTER*** nov.

NAME. Greek λίστρον, spade, shovel; μυκτήρ, nose, snout. Refers to the spatulate rostrum, so well developed in the genus.

DIAGNOSIS. Large amphisbaenian with fairly short skull, dorsoventrally compressed snout and strong cranio-facial flexure; sutures well delineated; large median premaxilla with vertical process exposed in skull roof as long, broad bone extending forwards to form powerful spatulate rostrum and backwards to separate nasals entirely and frontals partly; nasal short, with concave anterior edge, extending not so far forwards as maxilla and premaxilla and thus producing embayment in dorsal view; external naris directed anteriorly, just below nasal embayment; premaxilla with one median tooth and three lateral teeth on each side; each maxilla with row of five teeth lying medial to line of premaxillary tooth row, and with stout stubby process directed anterolaterally from front end of its outer side; highly sinuous fronto-parietal suture; prefrontal partly outside and partly inside orbit; large braincase with marked sagittal crest; gap between parabasisphenoid and vomer, exposing orbitosphenoid in palatal view.

TYPE SPECIES. *Listromycter leakeyi* sp. nov.

Listromycter leakeyi sp. nov.

NAME. In honour of the collector, the late Dr L. S. B. Leakey.

DIAGNOSIS. As for the genus *Listromycter*, of which *L. leakeyi* is the only known species.

MATERIAL. Only the **holotype**, Nat. Hist. Mus. Palaeont. Dept. no. R.8292 (collector's field number 375A): skull lacking the occiput and lower jaw. Figs 1–2.

OCCURRENCE. Lower Miocene of Rusinga Island, Lake Victoria, Kenya.

Skull (general description)

The skull appears to have been larger than any other amphisbaenian skull known, fossil or Recent. It lacks the occiput and lower jaw; but the preserved portion, 29·5 mm long, extends backwards as far as a clean transverse break through the braincase (at the level of the middle of the pterygoids) and is reasonably complete. The upper surface and sides of the skull are in excellent condition, free of matrix and with well delineated sutures; most of the sutures and the surface sculpture may be distinguished without difficulty from the fracture lines, which are fairly abundant on some parts of the skull. The lower surface, on the other hand, was formerly obscured by a layer of soft buff-coloured sandstone, through which protruded the upper teeth. Careful treatment with dilute acetic acid has removed this sandstone and revealed a palate in as good a condition as the rest of the specimen. The interior of the braincase was cleaned in a similar manner.

The skull, as in all amphisbaenians, is divided into facial and cranial portions. This division is particularly marked on the dorsal surface, where the axis of the facial portion is bent down at an angle of about 50° to the axis of the cranial portion. The dorsal profile of the face, seen in lateral view, forms an absolutely straight line from the tip of the premaxilla to the fronto-parietal suture. From side to side, however, the upper surface of the face is smoothly convex, the rounding starting just above the lower margin of the skull. The ventral profile of the skull, like the dorsal profile, is bent down anteriorly at a point just behind the last tooth; the angle of the bend is rather less (about 30°).

A striking feature of the skull is the unusually large, thickened and spatulate rostral process; its magnitude is emphasized by the relative shortness, posterior position and concave anterior margin of the roof of the narial passage. The lateral limit of the facial portion of the skull is formed by the maxilla. A process projected anterolaterally just lateral to the narial passage, but now only a stump of this remains.

The orbit is not deeply recessed; the posterolateral wall of the facial region forms its anterior margin, the palato-pterygoid shelf forms its floor, and it is open behind. The posterolateral edges of the facial shelf converge backwards; they unite to form a marked sagittal crest which runs along the top of the cranial portion of the skull as far as the posterior break. The braincase is helmet-shaped in transverse section and has extraordinarily thick walls; it rests upon the posterior part of the palate (see below). The premaxillary rostral process projects well forward of the most anterior tooth.

The palatal surface is bounded by a smoothly rounded edge which forms an elliptical arc lateral and anterior to the tooth rows. The dentigerous surface of each maxilla extends medially past the tooth positions and projects like a shelf beneath the side of a wide, high central vault, roofed by the vomers and the palatines; it may be presumed that in the living animal the shelves on either side were united by a continuous floor of soft tissue, enclosing the internal choanal canals. The palatal shelf continues posteriorly beneath the orbit. Here its medial edge twists dorsally so that the shelf inclines at about 30° to the horizontal with its ventral surface facing obliquely inwards and downwards.

The cranial cavity is slightly wider than high at the site of the break; the flexure between the cranial and facial portions of the skull is also apparent within it. The cavity's diameter is least in the region of the anterior limit of the parietal. Immediately anterior to this there is a slight dorsal outpocketing just beneath the external boss which lies where the posterolateral edges of the facial shelf unite to form the sagittal crest. Farther forward still the cranial cavity increases in diameter again, though its axis now runs parallel to the face.

The skull is extremely solidly constructed. Not only are the individual bones fairly heavy, but they also show complexly interlocking sutures. The location of sutures, especially of those within the braincase, cannot be predicted from their appearance on the external surface of the skull. Elements do not meet in butt joints, but instead overlie each other in a complex manner. A lamina projecting from the edge of one element is often grasped between a pair of laminae from the adjoining one; this produces a very rigid 'sandwich' joint.

Dimensions

Length of facial plane: 23 mm. Length of cranial plane (as preserved): rather more than 10 mm. Estimated length of whole skull, measured in a straight line from tip of premaxillary rostral process to occipital condyle: about 36 mm.

Premaxilla (pm)

The unpaired premaxilla is enormous (length 12·7 mm). It consists essentially of a V-shaped tooth-bearing shelf; from the dorsal surface of this shelf rises a large, heavy vertical plate, expanded above into a transverse plate which is extended forwards to form the rostral process and backwards to form a broad complex exposure on the face.

The exposure on the facial plane consists of a more or less rectangular plate between the nasals, produced forwards into the rounded spatulate rostral process (slightly wider than the body of the bone) and produced backwards as an elliptical process which separates the frontals for half their length and is connected to the rest of the bone by an isthmus.

In lateral view the snout is sharply pointed, the angle between the facial plane and the dentigerous ventral surface being approximately 25°. Near and just dorsal to the most anterior tip of the maxilla, the premaxilla is perforated by a round, longitudinally running canal (c_1) which is open farther on the left than on the right side.

The anterior margin of the tooth-bearing portion forms a smoothly rounded but rather shallow rim (continued on either side for the whole length of the maxilla as far back as the orbit). The ventral surface of the premaxilla bears seven teeth arranged in the form of a V – one median tooth at the front, and two rows, each of three teeth, diverging backwards at an angle of 45° to each other. Only the last two teeth on the right side are preserved complete, the others being represented only by their broken bases. The elliptical median

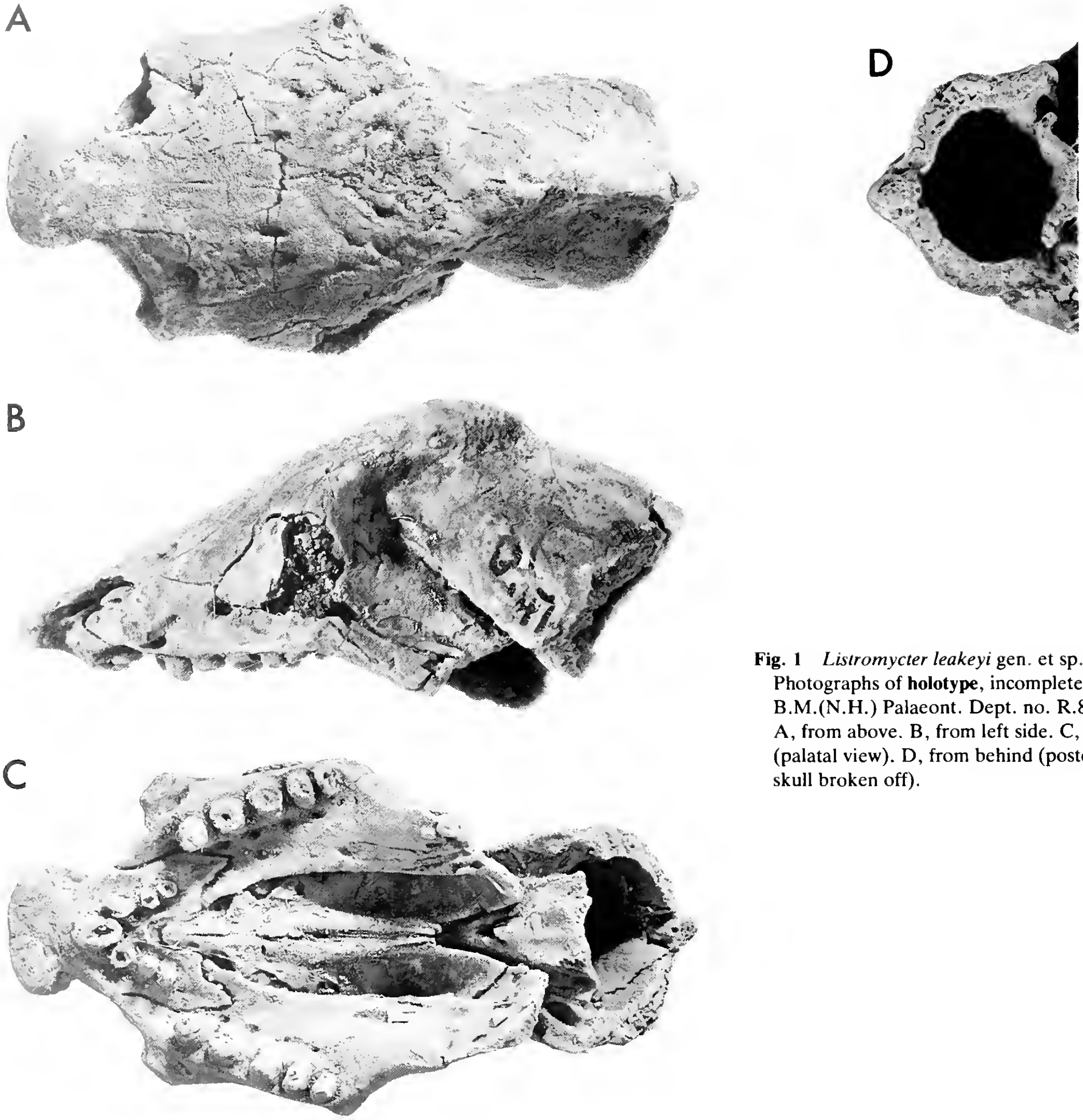


Fig. 1 *Listromycter leakeyi* gen. et sp. nov. Photographs of **holotype**, incomplete skull, B.M.(N.H.) Palaeont. Dept. no. R.8292, × 3·2. A, from above. B, from left side. C, from below (palatal view). D, from behind (posterior part of skull broken off).

tooth is by far the largest, the long diameter of the base being about twice that of the first lateral tooth. The second and third teeth are smaller still. All lateral teeth are circular rather than elliptical in section. The gap between the first and second lateral teeth is wider than the other gaps. All these teeth seem to be straight, bluntish cones with a central cavity. They are solidly anchylosed to a flat portion of the ventral surface; the method of attachment appears to be at least as much acrodont as pleurodont. A nutritive foramen lies immediately posterior to the medial side of the base of each tooth.

Maxilla (m)

The maxilla is a very heavy bone. It forms: (a) the palatal dentigerous shelf, (b) the floor, lateral wall, and part of the roof of the nasal passage (internal choanal canal), (c) a large part of the side of the face, up to the frontal suture above and the anterior rim of the orbit behind, (d) part of the palato-pterygoid shelf, and (e) a boss projecting anterolaterally. The size and importance of the maxilla may be gauged by the number (9) and the extent of its articulations with other elements, namely the premaxilla, the septomaxilla, the nasal, the frontal, the prefrontal, the pterygoid, the ectopterygoid, the palatine and the vomer.

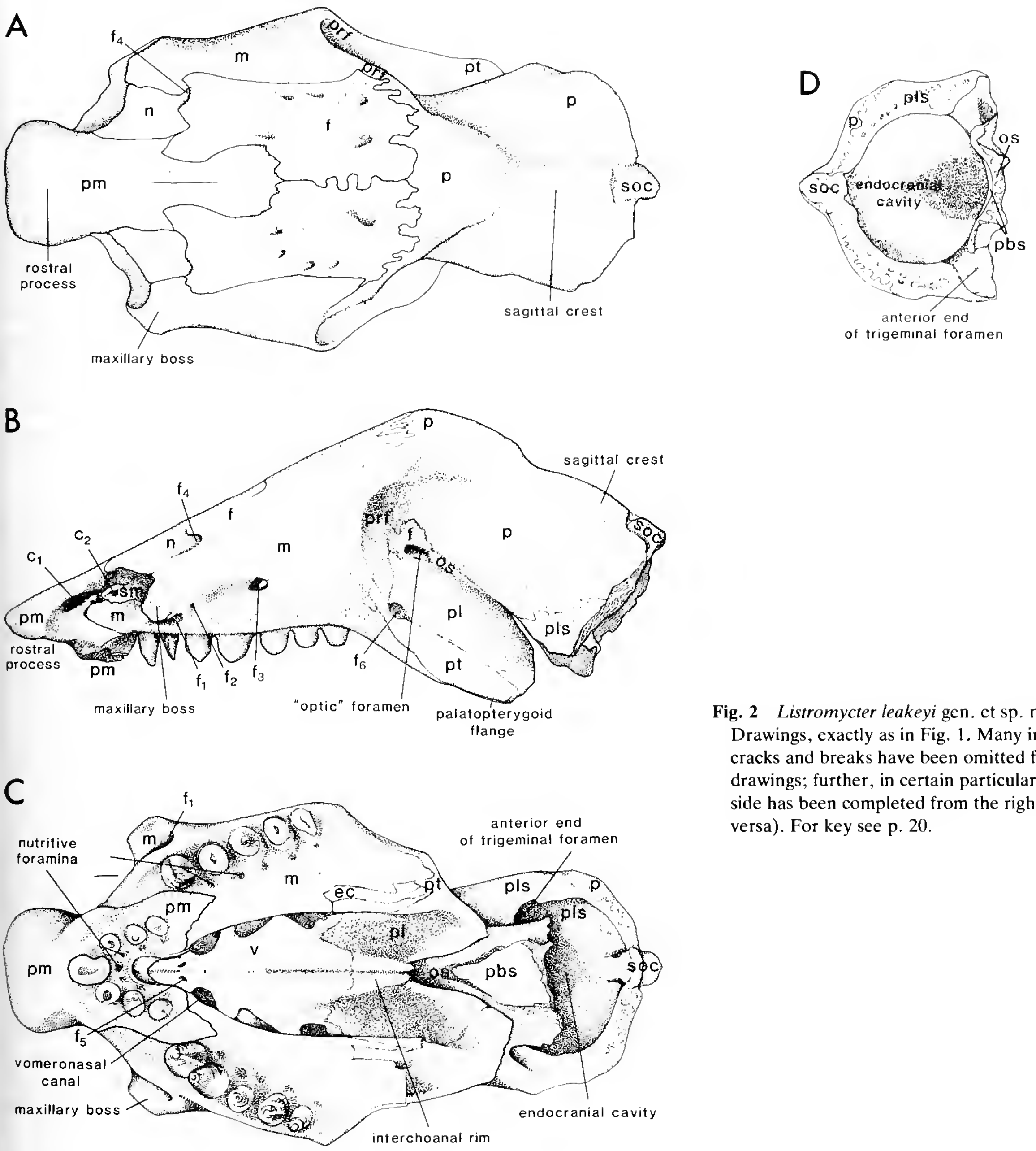


Fig. 2 *Listromycter leakeyi* gen. et sp. nov. Drawings, exactly as in Fig. 1. Many irrelevant cracks and breaks have been omitted from these drawings; further, in certain particulars, the left side has been completed from the right (and vice versa). For key see p. 20.

The curved anterior rim of the toothplate, mentioned above with reference to the premaxilla, is continued backwards by the maxilla.

In lateral aspect the maxilla has a roughly triangular appearance, the narrow apex of the triangle being directed forwards. This apex lies immediately beneath the external naris and projects into the premaxilla. Lateral to the naris lies the base of the maxillary boss; ventral to this stump is a horizontally elongate foramen (f_1) and, on the left side only, a smaller foramen (f_2) is present just posterodorsal to the first one. Yet another, even larger, foramen (f_3) may be seen dorsal to the gap between the second and third maxillary teeth, some way behind the boss. The posterodorsal horn of the triangle which the maxilla shows in this aspect just fails to reach the parietal, the two being separated by a narrow frontal–prefrontal connexion. The posteroventral horn extends down the lateral margin of the palato-pterygoid shelf to underlie the pterygoid in an oblique suture.

In palatal view the maxilla may be seen to bear a row of five teeth just medial to the rim. The line of these teeth does not continue the line of the premaxillary tooth row but, though parallel to that row, lies well outside it. Medial to the teeth the bone forms a prominent palatal shelf which projects ventral to the internal naris and the vaulted palate; anteriorly the shelf flares inwards to lie dorsal to the maxillary process of the premaxilla and to contact its median dorsal process. Another inward projection of the maxilla lies dorsal to the internal naris and palatal shelf and ventral to the lateral margins of the vomer. The broken posterior edge of the maxillary shelf shows a number of finger-like longitudinal depressions; in one of these lies the slender and elongate ectopterygoid which, anteriorly, almost reaches the last maxillary tooth. The remaining depressions contact what appear to be portions of the pterygoid, though the breaks are very irregular and the element concerned cannot be identified with certainty.

As stated above, five teeth are placed against the marginal rim of each maxilla. The second tooth is the largest, with the first, third, fourth and fifth in descending order of size. The cusps of all except the first left and last right tooth are broken at various levels. The spaces between the teeth are more or less equal. The teeth are elliptical in outline near their bases and are firmly fused to the maxilla in subpleurodont fashion (Gans 1957). The long axes of the ellipses are directed posteromedially. Shallow nutritive foramina lie medial and slightly posterior to the teeth at the point where the extension of the long tooth axis crosses the shallow lingual groove.

Nasal (n)
Each flatly oval nostril is roofed by a small nasal; its anterior edge forms a gentle concave curve. [After the writing of this description an attempt was made to remove more matrix from the cavity of the right external naris. Unfortunately this resulted in damage to the anterior edge of the nasal on that side. We both affirm, however, that this edge was previously a smooth concave curve, complete and apparently natural, as is confirmed by photographs and by the condition on the other side.] The dorsal exposure is roughly quadrilateral, small because the nasal is overlapped by the three adjacent bones. The posterolateral corner of the nasal is depressed into a foramen (f_4) that passes horizontally beneath the anterior process of the frontal and the wall of which also includes a small portion of the maxilla. Erosion of the nasals does not seem to be responsible for the peculiar shovel-shaped appearance of the snout. Certainly the survival of the delicate rostral tips of the septomaxillae argues for a minimum of erosion in this area and suggests that the embayment is natural.

Septomaxilla (sm)
The medioventral wall of the cavity of each external naris is formed by the shell-like septomaxilla, applied to the surfaces of the premaxilla above and the maxilla below. The slender anterior tip projects just beyond the front edge of the nasal; a little behind this tip is the aperture for a canal (c_2) which runs longitudinally back into the bone. The posterior part of the septomaxilla is still encased in the matrix filling the back of the nostril.

Vomer (v)
The vomers lie next to each other along the midline of the palate. Each has a slender anterior projection adjacent to the midline and a blunter posterior projection, and laterally each extends into a flat horizontal plate. The median edges of the vomers appear not simply to end in two straight edges abutting against each other, but to curve sharply dorsad into two parallel plates of unknown extent. In ventral exposure the vomers occupy an arrow-shaped area between the medial edges of the maxillae. The anterior tips lie ventral to the premaxilla, fitting into a median depression on the underside of that bone and extending as far forwards as the front of the last premaxillary tooth; each tip is perforated by a small foramen (f_5). The lateral edge of each vomer passes directly backwards, turns in towards the midline, and then, at the level of the second maxillary tooth, curves sharply outwards and disappears dorsal to the maxilla; the oval aperture left between the vomer and the maxilla at this point is the opening of the vomeronasal canal (Jacobson's organ). Posterior to this point the roof of the internal choanal canal is formed by the lateral portions of the vomers and, farther back, by the palatines. The lateral edge of the vomer appears once more, however, the bone being embayed to accommodate the supporting process which runs from the medial lamina of the maxilla to the palatal shelf. The straight, slender posterior projection that extends medial to the medial edge of the corresponding palatine forms the interchoanal rim.

Palatine (pl)
The palatine, as seen from below, is a semicylindrical bone forming the roof and sides of the choanal canal. Its lateral edge lies in close contact with, and dorsal to, the medial edge of the palato-pterygoid shelf. From here the bone curves outwards, first swinging laterad, then dorsad and mediad, and finally ventrad to complete the vault. The anterior portion of the medial edge of the palatine lies adjacent to the protruding posterior tip of the vomer and in fact forms the lateral portion of the posterior end of the interchoanal rim. The central portion of the bone is deeply concave. The anterior edge of the palatine lies ventral to the posterior edge of the vomer, projecting forwards so that the suture has a marked angulation of about 90°.

The palatine is broadly exposed in a lateral view of the skull, in which it may be seen to close the orbit ventrally. It extends dorsad from the pterygoid to articulate anteriorly in a complex series of sutures with the prefrontal and frontal, and dorsally with the orbitosphenoid. There is a deep foramen (f_6) close to the point of contact between the anterior tip of the palatine, the pterygoid, the maxilla and the prefrontal (clockwise in that order when viewed from the left).

Ectopterygoid (ec)
A slender rod-shaped ectopterygoid lies smoothly inserted in a furrow on the ventral surface of the posterior end of the maxilla. It extends into and possibly under the pterygoid. The anterior tip of the right ectopterygoid is broken off.

Pterygoid (pt)
The pterygoid forms the posterior portion of the palato-pterygoid shelf. Its anterior tip lies dorsal to the posterior part of the maxilla, with which it is in close and interdigitating contact. The shelf extends medially to the edge of the palatine vault, where both pterygoid and palatine are in contact with the base of the braincase.

Frontal (f)
The frontal is perhaps the most characteristically amphisbaenian element of the skull. Not only is there the usual extensive exposure on the dorsal surface of the skull (i.e. the 'face') and a minor exposure on the lateral wall of the orbit, but, with its fellow, the frontal forms also a complex and reinforced ring around the front part of the brain. It articulates complexly with the parietal and orbitosphenoid behind and

above and with the premaxilla, nasal, maxilla and prefrontal before and below. The following description is based on the external exposures of all these elements and also upon their internal exposures within the braincase.

The smoothly margined anterior wing of the frontal on the facial plane is separated from its fellow by the posterior process of the median premaxilla. The suture between the two frontals and the suture that they make with the parietal across the posterior apex of the 'face' are digitiform and interlock in a complex manner. The exposure of the frontal on the facial surface is markedly rugose; numerous foramina enter the bone, often from the end points of shallow canals.

Within the braincase the articulations of the frontal and the orbitosphenoid are again relatively simple. It may be seen by looking into the braincase from behind that the frontals form the roof, sides and floor of its anterior portion.

The exposure of the frontal on the anteromedial wall of the orbit is also complexly bent, and its margins show evidence of digitiform sutures with the palatine, the prefrontal and the parietal. A large foramen passes between the ventral margin of this exposure of the frontal and the orbitosphenoid; the foramen may be seen to run anteriorly and then curve medially.

Prefrontal (prf)
A short but relatively tall prefrontal forms the anterior wall of the orbit. It articulates laterally with the maxilla; dorsally with the facial exposures of the frontal and parietal; and medially with the parietal, the orbital exposure of the frontal and the palatine. Whether or not there was contact with the anterior tip of the pterygoid is not clear because of the broken condition of the specimen. All the sutures are digitiform.

Orbitosphenoid (os)
The amphisbaenian orbitosphenoid is a median bone that is apparently formed in membrane and may not be homologous with the element thus named in lizards (Bellairs & Gans 1983). It forms all that may be seen of the floor of the braincase in ventral view, except for the forwardly directed triangle in the midline which is the broken-off anterior part of the parabasisphenoid and underlies the orbitosphenoid; on either side lies part of the pleurosphenoid, also broken off behind. Anteriorly the orbitosphenoid is hidden by the palato-pterygoid flanges. It appears also in the lateral view of the skull between the lateral wall of the braincase (formed by the parietal) and the palato-pterygoid flange, extending forwards, between the parietal above and the palatine below, as far as the 'optic' foramen.

Within the braincase it may be seen that its floor is formed by the orbitosphenoid, immediately posterior to the ventral juncture of the two frontals and anterior to the tip of the basisphenoid. The bone is shortest in the ventral midline, where it appears to be faintly grooved as if composed of fused paired elements, though there is no suture line and the grooving appears to be restricted to the internal surface of the bone. The orbitosphenoid is produced anteriorly into a small, square-ended median process, which is clasped on either side by a small, backwardly projecting horn of the frontal. The anterior wings of the orbitosphenoid extend dorsad and anteriorly inwards to the fronto-parietal suture in the lateral wall of the braincase, overlapping that suture medially. Posteriorly the orbitosphenoid extends around the trigeminal foramen on either side, near the anterior edge of which the specimen is broken off. A single small foramen penetrates each side of the orbitosphenoid in the floor of the braincase.

Parabasisphenoid (pbs)
Only the anterior part of the parabasisphenoid is preserved. It appears as a narrow, forwardly directed triangle in the floor of the braincase, seemingly inserted into the back of the orbitosphenoid both internally and externally. In fact, however, the relations are more complex than they seem. The internal exposure obviously consists of a very thin sheet of bone fitting into a shallow, triangular depression on the upper surface of the orbitosphenoid. The external exposure consists mainly of a narrower, thicker, triangular sheet of bone projecting a little farther forwards and fitting into a correspondingly deeper depression, within which it has slipped back a little *post mortem* from its proper position; on either side of this median plate is a very much thinner lateral wing, projecting forwards but not so far. Just how far the orbitosphenoid extended back between these two sheets of parabasisphenoid, rather like the filling in a sandwich, is a matter for conjecture.

The inner suture seems to be radially digitiform on the right side but much straighter on the left; it is difficult to determine which is the natural condition. The cross section provided by the break through the skull indicates that the bone consists of a lamina forming the floor of the braincase, reinforced by a central thickening; the thickening bears three longitudinal external ridges below—a median ridge and, on either side, a lateral ridge which forms the margin of the central triangular plate. The thickened region corresponds to the centre of the interpterygoid vacuity.

Parietal (p)
The unpaired parietal forms much of the roof and sides of the braincase. It is shaped like a squat inverted trough, an inverted U; dorsally it is thickened by the sagittal crest, the anterior termination of which may be detected internally. The nature of the limits of the parietal and of its articulations with the frontals, prefrontals and orbitosphenoid has already been indicated in the appropriate sections above; the complex articulation with the pleurosphenoid and the contact with the supraoccipital are described immediately below.

Pleurosphenoid (laterosphenoid) (pls)
The pleurosphenoid (considered part of the prootic by Rieppel, 1981) appears on either side as a bone that forms a considerable part of the lateral wall of the braincase. Its union with the parietal is highly complex; the external and internal exposure patterns differ greatly, and once again it is obvious that in some places the elements overlap to a considerable extent. The external exposure of the pleurosphenoid on the preserved part of the skull is restricted to the posterolateral corner of the preserved portion of the braincase. Internally, however, the pleurosphenoid exposure extends up the wall of the braincase as far as the dorsal midline, where it makes contact with the supraoccipital. Thus, at the level of the fracture, the lower part of the lateral wall of the braincase consists entirely of pleurosphenoid, but in the upper two-thirds of the wall the thick pleurosphenoid is covered externally by the thin parietal. The cross section shows the pleurosphenoid itself to consist of two layers of dense bone with a central spongy layer and to be separated from the parietal by an undulating suture.

It may also be seen within the braincase that the parietal extends back towards the fracture line and overlaps the pleurosphenoid posteriorly. Thus it is evident that the pleurosphenoid extends farther forwards, hidden between two layers of parietal. On the dorsal side of the brain cavity the overlapping parietal is produced backwards into a pair of little horns, lying on either side of the supraoccipital and just reaching the level of the fracture posteriorly.

Supraoccipital (soc)
The hindmost tip of the preserved part of the sagittal crest is occupied by a separate bone, the anterior portion of the supraoccipital. Its suture with the parietal, as seen in the section of the skull afforded by the break, does not run straight through the thickness of the bone but forms an S-shape. Just anterior to the supraoccipital there is a wedge-shaped gap which may originally have been filled with cartilage, as in many Recent forms.

Phylogenetic position
Vanzolini (1951*b*) proposed a new subfamily of the family Amphisbaenidae, the Rhineurinae, characterized by a strong cranio-facial angle, a horizontally flattened face and a shovel-like snout. This classification was accepted in such standard works of reference as those of Hoffstetter (1955) and Romer (1956). Gans, however, suggested (1967*a*, 1974) that the various members of the 'Rhineurinae' had developed those same structural features in common because they all shared a style of burrowing called 'shovel-snouted digging' (Gans 1968, 1969) and that, in consequence, the assemblage was almost certainly polyphyletic. Berman (1973) raised the Rhineurinae to family status but separated some of Vanzolini's fossil rhineurines from North America into further distinct families. Gans (1978) accepted the Rhineuridae as a family but, unlike Berman, retained within it all the fossils from North America as well as the single Recent species from that continent; on the other hand, he left all the 'rhineurine' genera from other continents within the Amphisbaenidae.

Gans (1978) recognized also two other families: the Bipedidae (characterized by the retention of hypertrophied forelimbs and other derived characters) and the Trogonophidae (characterized by an acrodont dentition). No 'cladistic analysis' of the Lepidosauria as a whole had at that time been carried out. Gans' classification, however, was based upon a properly conducted character distribution analysis (essentially the same thing) of the genera concerned, and it is now supported further by the results of a wider, as yet unpublished generic/familial analysis.

Listromycter cannot be placed in the Trogonophidae, for its dentition is subpleurodont instead of acrodont. Its skull is very different in other respects; in particular, the cranial suture pattern of *Listromycter* does not accord with the oscillating style of locomotion peculiar to trogonophids. The new genus must therefore be compared with other 'shovel-snouted' extant amphisbaenians, of which there are four genera of Amphisbaenidae (*Monopeltis* and *Dalophia* from Africa; *Leposternon* and *Aulura* from South America) and one single species of the family Rhineuridae (*Rhineura floridana* from North America). *Monopeltis* has 16 species and *Dalophia* 7 (Broadley *et al.* 1976); the present range of neither genus comes closer than 500 km to Rusinga. *Leposternon* has approximately 7 species (Gans 1971*a*) and *Aulura* has but one (Gans 1971*b*).

Aulura is rare and its skull has never been described. The skull of *Dalophia* is also undescribed; in the points mentioned here, however, it is known to resemble that of *Monopeltis*. Indeed, there are only three Recent 'shovel-snouted' species of which the skull has been described: *Monopeltis capensis* from Africa (see p. 20), *Rhineura floridana* from North America (cf. Gans 1967*b*) and *Leposternon microcephalum* from South America (cf. Gans 1971*a*).

The adaptations for shovel-snouted digging in those three species may be arranged under four headings, the first two of which are to some degree related to each other and likewise the last two.

1. *Flattening of the skull*. In all three genera under discussion there is a very marked dorsoventral flattening of the skull, as contrasted with that of the generalized *Blanus* or *Amphisbaena* and even more with the 'spade-snouted' *Anopsibaena* (Gans & Kochva 1965). The dorsal surface, however, remains gently convex from side to side.
2. *Development of rostral shield*. In all three genera the anterior and lateral margins of the upper jaw are extended well beyond the tooth row so as to produce a wide, effective, digging (penetrating) spade with an arc-shaped cutting edge. This extension consists of outgrowths variously formed of the premaxilla and maxillae. A secondary result is the roofing over of the external nares which thus face downwards rather than anterolaterally; this protects them during both the penetrating and the tunnel-widening movements. Yet another effect of the shield development is that the skull appears even flatter than it otherwise would. (Again, contrast this with the conditions in *Blanus* and *Amphisbaena*.)
3. *Flexure of the skull*. The anterior portion of the skull is bent strongly downwards from a point on the cranial roof just behind the fronto-parietal suture. This produces a sharp angulation in the dorsal profile of the skull of between 45° and 70° and a somewhat lesser angulation in the ventral profile, and it results in the ventral deflection of the tooth row from the long axis of the body: in other amphisbaenians the anterior part of the skull is bent down through a much smaller angle (not more than 25°) and the flexure is a gentle curve rather than an abrupt angulation. A marked effect of this is to shorten the ventral perimeter of the skull between the rostral tip and the occipital condyle and, coincidentally, the length of the mandible (see also 4 below).
4. *Shortening of the skull*. In shovel-snouted digging a mechanical advantage is conferred by shortening the distance between the fulcrum and the point of force exertion (thus increasing the forces that may be exerted for whatever moment is generated by the musculature). This may explain the reduction, apparent in all three genera, in the relative length of the entire skull. Since any reduction of the occipital region must be limited by the spatial requirements of the braincase and of the auditory capsule, and since any reduction of the rostral region (the effective digging organ) is also disadvantageous, it is mainly in the anterior part of the cranial region that this shortening takes place.

The combined effect of adaptations 3 and 4 is to shorten the ventral surface of the skull to such an extent that the gap between the parabasisphenoid and the vomer closes entirely. In none of these three genera is the orbitosphenoid exposed in palatal view, and the tip of the cultriform process (the anterior rostrum of the parabasisphenoid) always fits between the posterior processes of the vomers.

Although *Listromycter* possesses all four of these adaptations, it is interesting to note that two of them (nos 2 & 4) are developed to a significantly lesser degree than in any of the three Recent genera:

1. The skull is flattened to much the same degree.

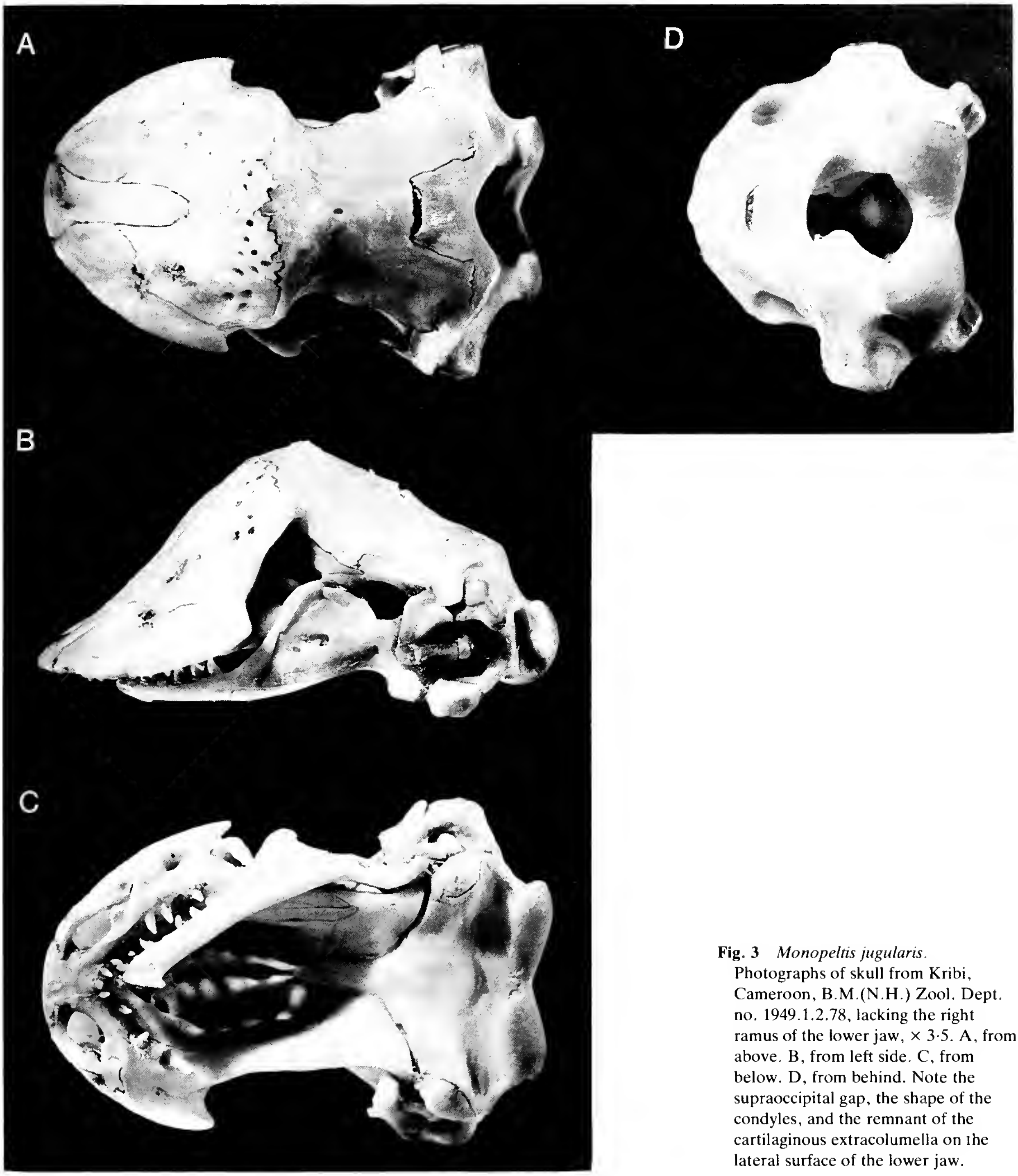


Fig. 3 *Monopeltis jugularis.* Photographs of skull from Kribi, Cameroon, B.M.(N.H.) Zool. Dept. no. 1949.1.2.78, lacking the right ramus of the lower jaw, × 3·5. A, from above. B, from left side. C, from below. D, from behind. Note the supraoccipital gap, the shape of the condyles, and the remnant of the cartilaginous extracolumella on the lateral surface of the lower jaw.

2. There is no complete bony rostral shield; but there is a very large anterior extension of the premaxilla, and each maxilla bears an anterolateral protuberance of unknown size (maxillary boss). On the other hand, the maxilla is not extended laterally beyond the tooth row as it is in *Monopeltis*. The external naris, in consequence, is not directed ventrally; it still faces anteriorly, a little dorsally and a little laterally, much as in *Blanus*. However, it is possible that the maxillary bosses in *Listromycter* were connected by a horny plate, which would have produced an arc-shaped cutting edge and a downwardly directed external naris much as in Recent forms.
3. There is a sharp cranio-facial flexure of the skull, measuring 50° in the dorsal profile. This is less than in *Monopeltis*

jugularis (70°), *Rhineura* (65°) and *Leposternon* (60°); but no particular significance can be attached to the size of the angle because it is only 45° in the small *M. capensis*.

4. The skull is shorter than in amphisbaenians which are not shovel-snouted, though not as short as in any of the three Recent shovel-snouted genera listed above.

The figures in Table I should not be taken as exact indicators; the parameters chosen have been selected for convenience rather than for their biological significance, and the ratios, which would doubtless vary considerably within a species (especially during ontogeny) are in each case cited for a single specimen rather than given as a mean for a series. Nevertheless they do indicate a trend. In *Listromycter* the gap between parabasisphenoid and vomer is open, *not* closed, and the orbitosphenoid is exposed in the palatal view of the skull.

Table 1 Recent and fossil amphisbaenians. A, ratios of length of facial region to maximum width of facial region. B, ratios of length of whole skull to maximum width of facial region.

Museum and number	Species	A	B
K.M.	*Amphisbaena alba*	1·18	2·79
B.M.(N.H.) R.8292	*Listromycter leakeyi*	1·48	2·40*
C.G. 3722	*Leposternon microcephalum*	1·33	2·30
C.G. 0150	*Rhineura floridana*	1·37	2·10
C.G. 3567	*Monopeltis capensis*	1·16	2·00
B.M.(N.H.) 1949.1.2.78	*Monopeltis jugularis*	1·08	1·69

* length estimated

There is another character in which *Listromycter* appears to be intermediate between 'round-headed' forms on the one hand and the 'shovel-snouted' *Monopeltis* and *Leposternon* on the other. In *M. jugularis* (the largest Recent African amphisbaenid with a spade-snout) [undescribed skull: B.M.(N.H.) Zool. Dept. no. 1949.1.2.78: Fig. 3] the posterolateral corners of the palatal exposure of the premaxilla extend back to beyond the last (4th) maxillary tooth and there contact the ectopterygoid. In *L. microcephalum* the same corners reach back only as far as the middle of the 2nd maxillary tooth and again contact the ectopterygoid. In *Listromycter* and *Rhineura* they extend back as far as the middle of the 2nd maxillary tooth but do *not* contact the ectopterygoid. In forms not shovel-snouted, the posterolateral corners of the palatal exposure of the premaxilla are not extended in this fashion; in *Blanus*, for example, they terminate at the level of the 1st maxillary tooth. We do not understand the significance of this character.

The 'shovel-snouted' *Listromycter, Rhineura, Monopeltis* and *Leposternon* show remarkably similar modifications of the skull, perhaps as adaptations to a presumably similar mode of life. (As might be expected, those adaptations are less well expressed in the Miocene form than in the three Recent genera.) However, several important differences between the four genera suggest that there is no close phylogenetic relationship uniting them all into one monophyletic group. Can we deduce anything about the more distant phylogenetic relationships that must exist between these shovel-snouted reptiles?

The most striking anatomical differences between their skulls relate to the formation of the rostral process, more specifically the arrangement of the premaxilla, maxilla, nasal, frontal and external naris. *Rhineura* is unique in that its nasals are in median contact, each of them extending from the anterodorsal border of the external naris to the midline; they are not separated from each other by the backward extension of the premaxilla, as they are in most other Recent amphisbaenians (Gans & Alexander 1962). It is important to note that all the fossil amphisbaenian skulls hitherto described (all of which date from the Lower Eocene or Middle Oligocene of the U.S.A. and have hitherto been referred to the Rhineuridae; references in Gans 1978, Estes 1983) agree with *Rhineura* in this respect. [Other alleged fossil amphisbaenians are *Crythiosaurus mongoliensis* Gilmore, 1943 from the Oligocene of Inner Mongolia and *Changlosaurus wutuensis* Young, 1961 from China. But it seems to us that the former is a primitive boid snake and that the latter is a true lizard.] In *Listromycter*, however, as in *Monopeltis* and *Leposternon*, the nasals are separated by the premaxilla, which, in all three genera, extends so far back as also to effect a partial separation of the paired frontals. In all three genera too the maxilla meets the premaxilla below the external naris. But *Leposternon* differs from *Listromycter* and *Monopeltis* in that its maxilla extends also to meet the premaxilla *above* the naris and thus excludes the nasal from the border of that aperture.

Other characters do not help very much in our present state of knowledge, seeming to be distributed in a somewhat random manner. For example, the fact that a canal enters the posterolateral corner of the nasal in all these forms except *Rhineura* might appear to have some significance, until it is observed that it is present also in *Amphisbaena alba* but absent in *Blanus cinereus*. On the other hand, the frontals are distinctly pitted in all the shovel-snouted forms except *Leposternon*, and again this character is present in *Amphisbaena alba* but absent in *Blanus*. The frontoparietal suture is straight in both *Rhineura* and *Leposternon*, almost straight in *Monopeltis capensis*, wavy in *M. jugularis*, and moderately digitate in *Listromycter*—as it is in both *A. alba* and *Blanus*. One character that is clearly of no taxonomic importance at this level is the tooth count (Vanzolini 1951*a*, *b*); in *Monopeltis capensis* there is but one premaxillary tooth and two in each maxilla (a total of five), and in *M. jugularis* there are seven premaxillary teeth and four in each maxilla (a total of fifteen). *Listromycter leakeyi* retains the maximum (and presumably primitive) tooth count of seven and five—seventeen altogether.

The phylogenetic placement of the Kenyan fossil obviously depends upon the generic arrangement of the shovel-snouted amphisbaenians, a revision of which is now under way. Meanwhile the only reasonable inference that may be drawn is that *Listromycter* is neither a rhineurid, trogonophid nor bipedid but is a member of the Amphisbaenidae; within that family it appears to be on or near the line of ancestry of *Monopeltis* (*Dalophia*) but not of *Leposternon* (*Aulura*). However, it may also be that *Listromycter* represents a separate evolutionary line; we need to examine more species of the *Monopeltis* radiation.

An interesting additional point is that one of the oldest fossil amphisbaenians known, *Jepsibaena minor* (Gilmore & Jepsen, 1945) from the Lower Eocene of Wyoming, has two anterolateral protuberances of the maxilla which are in much the same position as the maxillary bosses of *Listromycter*. In other respects, however, *Jepsibaena* appears to belong to the Rhineuridae, which suggests that the presence of similar structures in *Jepsibaena* and *Listromycter* is due to adaptive convergence.

Genus *LOPHOCRANION* nov.

NAME. Greek λόφος, the crest of a helmet; κρᾱνίον, skull. Refers to the sagittal crest on the skull roof, so well developed in the genus.

DIAGNOSIS. A medium-sized amphisbaenian with weak cranio-facial flexure; slender elongate braincase with pronounced sagittal crest widened just anterior to tip of supraoccipital; transverse crest on supraoccipital; marked lateral expansion of temporal lobe beyond braincase.

TYPE SPECIES. *Lophocranion rusingense* sp. nov.

Lophocranion rusingense sp. nov.

NAME. From Rusinga Island, the only place where the species has been found.

DIAGNOSIS. As for the genus *Lophocranion*, of which *L. rusingense* is the only known species.

MATERIAL. Two incomplete skulls in the Brit. Mus. (Nat. Hist.) Palaeont. Dept. **Holotype**, no. R.8293 (collector's field number not known). Paratype, no. R.8294 (collector's field number 33A). Figs 4–6.

OCCURRENCE. Lower Miocene of Rusinga Island, Lake Victoria, Kenya.

General

Both these fossil skulls were evidently much smaller (see Table 2 for dimensions) than that of *Listromycter*. All that remains of each is the posterior part of an amphisbaenian skull (with occiput and ear region) broken through transversely in front. Amphisbaenian skulls, of course, do not possess bony arcades; both these specimens also lack palatopterygoid flanges, quadrates and lower jaw, so that each consists of little more than a portion of the braincase itself. As far as can be determined, the two specimens are identical except in that the holotype R.8293 represents a smaller individual than the paratype R.8294 and has better delineated sutures; it is therefore likely to be ontogenetically younger. The skull of the larger individual (paratype) is broken off anteriorly not far forward of the anterior tip of the parabasisphenoid; rather more is preserved of the smaller skull (holotype), in which the transverse break runs across the top of the face, just anterior to the highly digitate fronto-parietal suture. Both specimens have been rounded off at the fractures by subsequent rolling.

Despite their incompleteness, however, sufficient of these skulls is preserved—namely, the anterior part of the braincase—to permit a comparison with the corresponding region of *Listromycter*. It is immediately evident that they are quite unlike that genus. In particular, the braincase itself is far more slender and elongate, especially the part between the hindmost processes of the frontals and the anterior tip of the supraoccipital.

The following description is based on the holotype. Any relevant differences observed on the paratype are noted (between parentheses) at the appropriate place; it may otherwise be assumed that the two fossils are alike or that the relevant part of the paratype is missing.

Skull (general description)

The cranial region of the skull, just behind the cranio-facial flexure, is transversely narrow. Enough is preserved of the apex of the face to indicate that the cranio-facial angle was approximately 20°. The lateral margins of the braincase pass backwards, at first parasagittally and almost straight and then curving outwards at an angle of about 20° to the midline. Just before they reach the back of the skull they sweep out almost laterally to the strongly projecting otic capsules. The much abraded posterior margin of the skull is very roughly convex, the otic capsules lying farther forwards than the occipital condyle. (In the paratype the posterior margin is only slightly convex, but the remaining lateral portions of the occipital condyle project posteriorly beyond this.)

Table 2 *Lophocranion rusingense*: dimensions (in mm).

	R.8293	R.8294
Length of entire specimen as preserved	11·2	9·1
Length of cranial plane	9·6	–
Transverse width at anterior end of cranial region, i.e. at fronto-parietal suture	3·0	–
Transverse width in middle of cranial region, at widest part of sagittal crest	3·6	5·5
Transverse width across otic capsules	8·4	9·2
Median height of occiput	4·4	5·5
Length of parabasisphenoid	5·3	6·5

In lateral view the skull as preserved tapers forwards. (The paratype is too short to show this.) The ventral margin is more or less straight, except for its anterior tip which inclines ventrad at some 10°. The dorsal margin slopes gradually downwards as it passes forwards in a smooth convex curve. In this aspect the posterior margin appears as a distorted L (on the right side). The vertical, shorter arm of the L is represented by a backwardly-facing surface; the near-horizontal, longer arm is represented by a surface that faces obliquely backwards and downwards. The obtuse angle of the L would have been formed by the occipital condyle, which is here broken off (but present in the paratype).

There are only two pairs of large apertures and one single one (together with some smaller foramina) in the preserved part of the skull, other than the opening of the braincase at the broken front end. Just beneath the otic capsule, on either side, lies the fenestra ovalis; the latter is closed by the stapedial footplate in these specimens, for the stapes remain in place. Farther forward and directed ventrolaterally is the large, anteroposteriorly elongate foramen for the Gasserian ganglion. The fifth, unpaired aperture is the foramen magnum (fm), in the midline of the dorsal part of the occipital surface and extending right up to its dorsal margin; as far as can be seen, this is a more or less straight-sided quadrilateral, wider above than below. (The remaining fragments of the condyles of the paratype suggest that these originally blocked the ventral third of the aperture as preserved.) On either side of the foramen magnum, at the same height as the lower margin of the aperture as preserved and lateral to the occipital condyle, is a round, much smaller canal, the jugular foramen—actually a compound foramen (see under 'Exoccipital', p. 34). Other smaller, less noticeable foramina will be described below.

The only other prominent feature of the skull is the sagittal crest. This is fairly thick from side to side in the middle part of the cranial region and becomes narrower anteriorly and posteriorly. Although pronounced, the crest is not very high. Midway along its length it bears a triradiate boss which

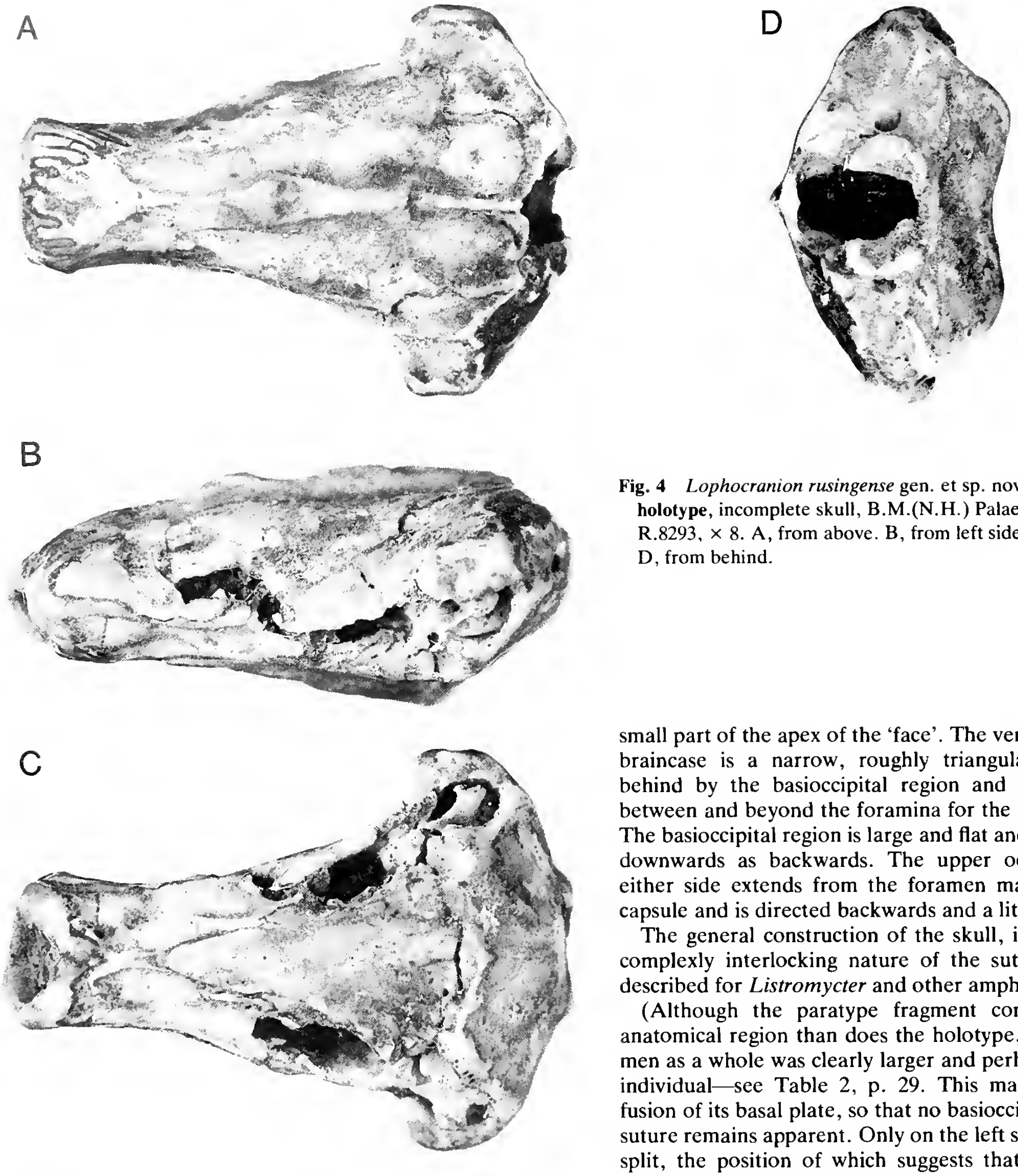


Fig. 4 *Lophocranion rusingense* gen. et sp. nov. Photographs of **holotype**, incomplete skull, B.M.(N.H.) Palaeont. Dept. no. R.8293, × 8. A, from above. B, from left side. C, from below. D, from behind.

presumably served for the usual tendinous attachments; immediately posterior to this the crest is flattened and then rises again to reach its highest point just anterior to the notch for the supraoccipital. A distinct edge at the posterior margin of the cranial roof separates it from the occiput.

The skull as preserved has therefore seven major surfaces. On either side is the outer surface of the braincase; posteriorly these two surfaces may together be regarded as a cranial roof, extending out more or less horizontally from the sagittal crest and running onto the otic capsule. Farther forwards each descends laterally in a convex curve towards the foramen for the Gasserian ganglion (the paratype is broken here); and farther forwards still, where the braincase is very slender, it descends quite steeply towards its lower rim and might justifiably be regarded more as a lateral wall than as a roof. At the very anterior tip of the specimen as preserved is a small part of the apex of the 'face'. The ventral surface of the braincase is a narrow, roughly triangular area, bounded behind by the basioccipital region and tapering forwards between and beyond the foramina for the Gasserian ganglia. The basioccipital region is large and flat and directed as much downwards as backwards. The upper occipital region on either side extends from the foramen magnum to the otic capsule and is directed backwards and a little outwards.

The general construction of the skull, its solidity and the complexly interlocking nature of the sutures are much as described for *Listromycter* and other amphisbaenians.

(Although the paratype fragment comprises a smaller anatomical region than does the holotype, the former specimen as a whole was clearly larger and perhaps from an older individual—see Table 2, p. 29. This may account for the fusion of its basal plate, so that no basioccipital-basisphenoid suture remains apparent. Only on the left side is there a small split, the position of which suggests that it represents the remnant of a former suture between two bones.)

Parabasisphenoid (pbs) and *'element X'*

The median parabasisphenoid forms the greater part of the floor of the braincase. It consists essentially of a narrow triangle with its apex directed forwards, between and beyond the foramina for the Gasserian ganglia; the apex, which makes an angle of about 30°, is rounded off, although it may have extended farther forwards as a sharp cultriform process, the rounding off being due to postmortem rolling. The base of the triangle is the suture of the parabasisphenoid with the basioccipital; this runs more or less transversely except that on either side it makes one short, sharp zigzag halfway along its length and, in consequence, the triangle looks rather like a stylized drawing of a Christmas tree standing on a very short, wide pedestal. The external, ventral surface of the triangle is

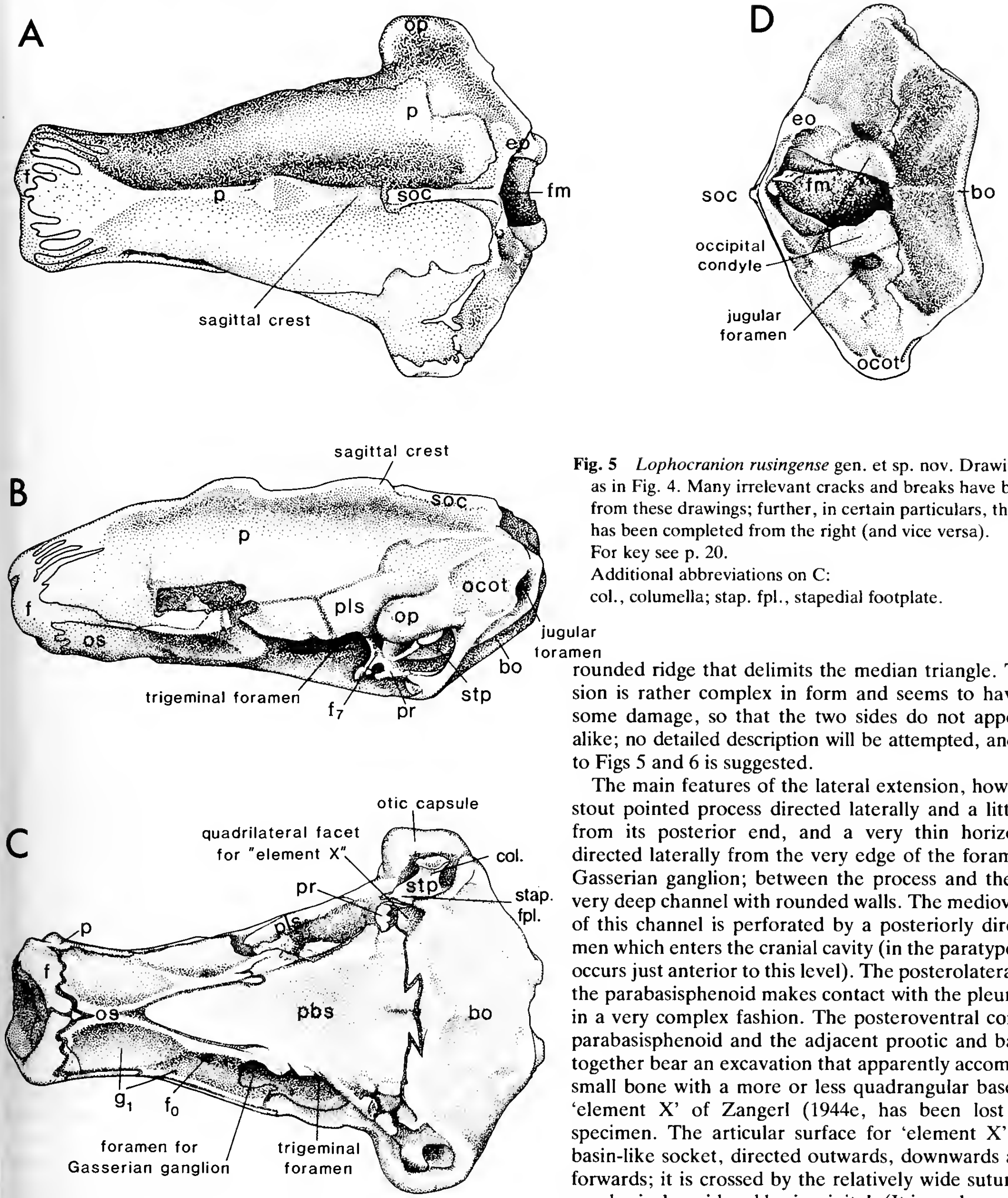
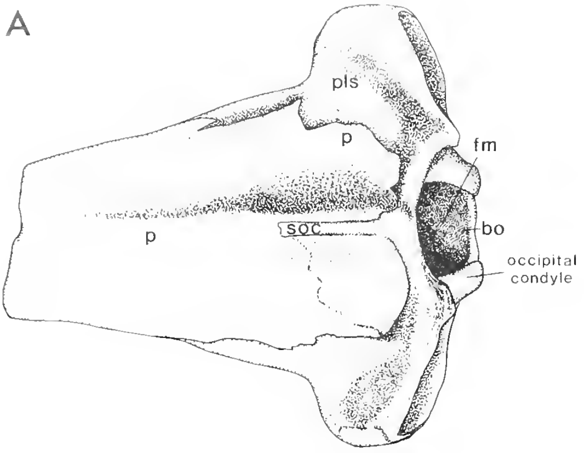


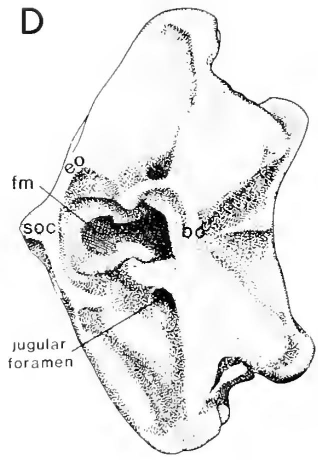
Fig. 5 *Lophocranion rusingense* gen. et sp. nov. Drawings, exactly as in Fig. 4. Many irrelevant cracks and breaks have been omitted from these drawings; further, in certain particulars, the left side has been completed from the right (and vice versa).
For key see p. 20.
Additional abbreviations on C:
col., columella; stap. fpl., stapedial footplate.

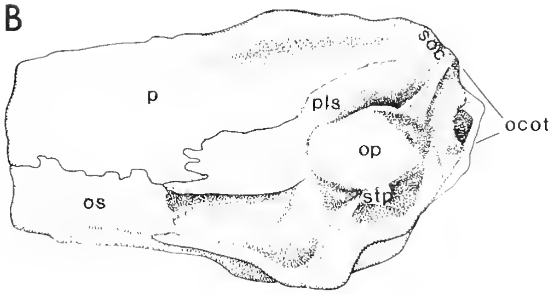
gently concave, the concavity being more transverse than anteroposterior.

The anterior third of the lateral margin of the parabasisphenoid sutures in a more or less straight line with the orbitosphenoid. At the level of the front end of the foramen for the Gasserian ganglion, however, the parabasisphenoid sends out a small lateral wing; at that point the suture between the parabasisphenoid and the orbitosphenoid becomes digitiform, terminating at the medial edge of the foramen a little way behind its anterior end. Posterior to this the parabasisphenoid forms the medial edge of the foramen; it extends dorsally and laterally on either side of the straight rounded ridge that delimits the median triangle. This extension is rather complex in form and seems to have suffered some damage, so that the two sides do not appear exactly alike; no detailed description will be attempted, and reference to Figs 5 and 6 is suggested.

The main features of the lateral extension, however, are a stout pointed process directed laterally and a little dorsally from its posterior end, and a very thin horizontal shelf directed laterally from the very edge of the foramen for the Gasserian ganglion; between the process and the shelf is a very deep channel with rounded walls. The medioventral wall of this channel is perforated by a posteriorly directed foramen which enters the cranial cavity (in the paratype the break occurs just anterior to this level). The posterolateral corner of the parabasisphenoid makes contact with the pleurosphenoid in a very complex fashion. The posteroventral corner of the parabasisphenoid and the adjacent prootic and basioccipital together bear an excavation that apparently accommodated a small bone with a more or less quadrangular base; this, the 'element X' of Zangerl (1944e, has been lost from this specimen. The articular surface for 'element X' is a deep basin-like socket, directed outwards, downwards and a little forwards; it is crossed by the relatively wide suture between parabasisphenoid and basioccipital. (It is unclear whether the element has indeed been lost from the paratype, or whether it fused to the posterior corners of the basisphenoid and abraded with these. Certainly there is no sharply defined facet and no trace of the triradial fossa.) It is also crossed by a canal, the foramen of which opens immediately anteroventral to the footplate of the stapes; the upper surface of the lost 'element X' formed the floor of the canal. (None of these canals is visible in the paratype and the entire area is solid. If the differences between the specimens are due to ontogenetic changes, one would then suspect that the absence of canals reflects either that the canals have closed, or that the fossil is broken within the 'element X' so that the canals are not exposed.)







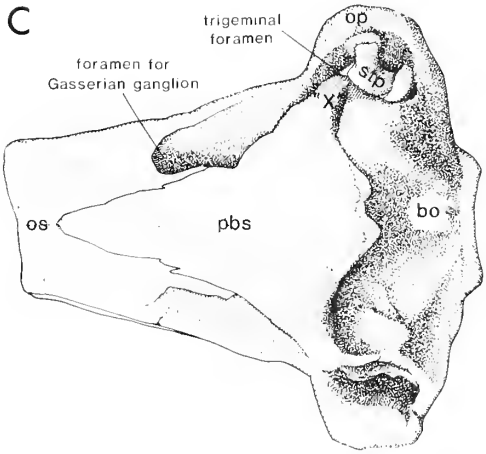


Fig. 6 *Lophocranion rusingense* gen. et sp. nov. Drawings of **paratype**, incomplete skull, B.M.(N.H.) Palaeont. Dept. no. R.8294, × 7·25. A, from above. B, from left side. C, from below. D, from behind. Many irrelevant cracks and breaks have been omitted from these drawings; further, in certain particulars, the left side has been completed from the right (and vice versa). For key see p. 20.

Orbitosphenoid (os)
The orbitosphenoid forms the ventral surface of the braincase between the region of the cranio-facial flexure and the anterior end of the foramen for the Gasserian ganglion. Its median part is underlain—and therefore covered in ventral, i.e. external view—by the parabasisphenoid triangle just described. In the midline there is a low flat-topped ridge, separating the orbitosphenoid into two halves (although there is no trace of a median suture). Anteriorly the orbitosphenoid is bounded by the frontals meeting each other in the floor of the braincase; the suture is more or less transverse but rather irregular. The lateral surface on either side is simple and externally concave; its anterior third is with a backwardly directed process of the frontal, the rest is with the parietal. Posteriorly the orbitosphenoid extends a short way along both lateral and medial edges of the foramen for the Gasserian ganglion on either side; its posterior termination on the lateral edge abuts against the anterior termination of the pleurosphenoid. Although the elongated foramen for the Gasserian ganglion ends a little anterior to this point, it continues farther forwards as a broad, shallow groove (g_1) in the ventral surface of the orbitosphenoid which curves gently outwards and tapers forwards to end near the point where frontal, parietal and orbitosphenoid meet. On the inner edge of this groove, about a quarter of the way from the foramen for the Gasserian ganglion to the frontal-orbitosphenoid suture, a small foramen (f_0)—presumably for the optic nerve—enters the bone; it is directed posteromedially.

Frontal (f)
Only the extreme posterior ends of the frontals remain; these together form a ring around the front end of the cranial region of the skull. (The frontals are missing entirely in the paratype.) They are separated from each other only by a convoluted median suture above and below the cranial cavity. Posteriorly they suture with the orbitosphenoid below, by a more or less transverse but rather irregular suture, and elsewhere with the parietal. The fronto-parietal suture is rather complex. Beginning in the dorsal midline, just below the apex of the 'face', it proceeds laterally by a series of four or five narrow interdigitations of progressively increasing length; the front ends of the interdigitations lie at about the same transverse level as the starting point, but their back ends

lie progressively more posteriorly. The first two or three are on the 'face', the last and most lateral two interdigitations are on the side of the skull. The last interdigitation of the frontal, seen in lateral view, appears to be directed backwards and upwards. From its base another process of the frontal, about as long as the last interdigitation but directed backwards and downwards, runs down between the parietal above and the lateral margin of the orbitosphenoid below. The most anterior part of the parietal, between the last interdigitation of the frontal above and this posteroventral process below, is broken off on the right side of the holotype. This break reveals that the frontal is more extensive internally and is merely overlapped by the parietal in this region; the parietal lies in a deep trough of the frontal, the bottom of which bears shallow longitudinal grooves.

Parietal (p)
The greater part of the external surface of the roof and sides of the braincase is formed by the unpaired parietal, which forms also the extreme posterior apex of the 'face'. Except in the anterior region, however, the roof and sides of the braincase are also formed in part by the fused pleurosphenoid, occipital and otic bones, henceforth to be referred to here as the occipito-otic complex (ocot). The parietal overlaps this complex posteriorly, but in the holotype described here parts of the parietal have been broken off and the resulting 'suture lines' are rather misleading; the true extent of the parietal is indicated by a depression in the occipito-otic complex which is bounded by a distinct rim. The irregular surface of the depression and the broken edges of the parietal indicate very clearly the complex interdigitating nature of the suture.

Posteriorly the parietal has a deep, very distinct median slot running forwards for about a quarter of its length; this accommodates the supraoccipital process, which thus forms the median portion of the sagittal crest in this region. The parietal-supraoccipital suture passes backwards down the side of this bar, parallel to the midline and very close to it. Just before reaching the back of the skull it curves outwards to run more or less parallel to the posterior margin of the skull roof in the region lateral to the foramen magnum. More laterally still it curves forwards again, passes medial to the otic capsule, and then continues forwards and a little downwards along the side of the braincase as the parietal-pleurosphenoid suture (in the paratype the edges are variably broken in this region); this is only very slightly irregular except in that, at its extreme anterior end, a short 'finger' of parietal points backwards and downwards towards the middle of the trigeminal foramen (the break is near the posterior third in the paratype). Forward of this point the ventral edge of the parietal reaches the lower rim of the braincase and sutures with the orbitosphenoid.

Anteriorly the parietal sutures with the frontal (missing in the paratype); this too has been described above. The sagittal crest on the parietal has already been dealt with in the general description of the skull.

Occipito-otic complex (ocot)
The posterior part of the skull is represented in this specimen by a single co-ossification, lacking apparent sutures but presumably of compound origin. Comparisons with descriptions of the skulls of lizards (Jollie 1960) and particularly of amphisbaenians (Zangerl 1944, Kritzinger 1946, Bellairs & Kamal 1980, Rieppel 1981) suggest that the complex includes the pleurosphenoid, supra- and exoccipital, pro- and opisthotic bones; except for the supraoccipital all those bones are paired. They are here described in sequence without discussion of the position of the presumed lines of suture. While we thus follow other authors, we do so with some reservations since the true nature of the complex has yet to be studied—preferably on embryological material.

Pleurosphenoid (laterosphenoid) (pls)
The pleurosphenoid region of the occipito-otic complex (cf. Rieppel 1981) seems to form a considerable part of the roof and sides of the posterior region of the braincase; but, except for the posteroventral part of the lateral wall, immediately above the trigeminal foramen, it seems likely that it was generally overlain by the parietal. In the holotype the external exposures of the pleurosphenoid-supraoccipital appear to be rather greater than this because parts of the overlying parietal—at the back end of the skull, dorsomedial to the otic capsules—seem to have been lost. (Relatively more has been lost in the paratype, where the square lateral edges of the parietal confirm that these have been broken.) The anterior termination of the pleurosphenoid (missing in the paratype) is on the lateral edge of the trigeminal foramen, a short way behind the anterior end of the latter; here it abuts against the posterior termination of the orbitosphenoid. The pleurosphenoid is delimited above by the parietal, as already described; the suture is only very slightly irregular except in that, at its extreme anterior end, a short 'finger' of parietal points backwards and downwards towards the trigeminal foramen. Ventrally the pleurosphenoid forms the more or less straight lateral edge of the trigeminal foramen and then contacts the prootic, opisthotic and supraoccipital without apparent suture.

Supraoccipital (soc)
The unpaired supraoccipital adjoins the parietal anteriorly, the pleurosphenoids anteroventrally, the opisthotics laterally and the exoccipitals below. The only suture that can be discerned, however, is the suture with the parietal, described above. The external exposure of the supraoccipital consists essentially of four regions. Most distinct is the exposure of the supraoccipital process in the skull roof, which appears as a narrow, keeled, straight-sided bar fitting into the median slot in the parietal mentioned above; its anterior end, the processus ascendens, is not tapered but ends bluntly in a straight transverse line. There is a semicircular gap around its anterior end which was presumably filled with cartilage in the living animal (as in *Dalophia* and *Monopeltis*; Kritzinger 1946, Gans personal observation) and beyond this the ridge of the sagittal crest is continued forwards by the parietal as already described. The supraoccipital itself begins to widen backwards before the parietal sutures on either side begin to diverge, i.e. the parietal overlies it laterally towards the back of the skull.

Despite the lack of sutures, it may also be presumed that the supraoccipital forms:

1. A narrow strip along the posterior edge of the skull, the roof of which is not quite covered by the parietal.
2. That part of the skull roof that is posteromedial to the otic capsule.
3. The uppermost strip of the occipital surface of the skull.

Prootic (pr)
The element that we consider to be the prootic lies behind the trigeminal foramen, of which it forms the concave posterior

border; it contacts the parabasisphenoid medially and the pleurosphenoid (without suture) laterally. Posterolaterally it contacts the otic capsule, of which it may also form a part. From this region a short, stout process descends to the socket for the articulation of the 'element X' of Zangerl (1944; see below), of which it forms the anterolateral portion (and to which it is fused in the paratype). The anteromedial portion of 'element X' is formed by the parabasisphenoid and the posterior portion by the basioccipital (all of which are fused in the paratype). The suture with the basioccipital is presumed to be represented by the canal that runs across the articulation—as described in the section on the parabasisphenoid, p. 31—although the two elements seem to be continuous at the base of the canal (fused in the paratype). Posterolaterally this element is overlain by the anterior part of the stapedial footplate. Just anterior to its contact with the stapes two small foramina, one above the other, penetrate the bone; on the left side (f_7) they are very closely adjacent, on the right they are much farther apart. (A single large oval foramen lies in an equivalent position on each side of the paratype. It is uncertain whether a second foramen is covered by the stapes, yet these do not seem to be displaced.) These, from their spatial relations to the stapes, are presumed to be the facial foramina for the VIIth nerve.

As all the elements in this region are fused together, we must give our reasons for believing this particular part to be the prootic:

1. The element forms the posterior wall of the trigeminal foramen (Romer 1956: 28).
2. It is perforated by the two small foramina that carry the VIIth nerve; these lie just anterior to the extent of the stapes.
3. It forms the anterior part of the rim of the fenestra ovalis and supports the wide anterior flange of the stapedial footplate.
4. It lies immediately anteroventral to the otic capsule.
5. It lies lateral to the lateral termination of the basisphenoid-basioccipital suture (obliterated in the paratype).

Opisthotic (op)

The opisthotic forms the greater part of the otic capsule; it is a large, solid, rounded swelling that projects laterally from the posterolateral corner of the skull roof and overlies the fenestra ovalis. No sutures are visible, either on it or around it, but it is possible that the capsule includes also a contribution from the prootic. The rounded anterior face of this process apparently formed the articular surface for the cup-shaped head of the quadrate, a bone that is missing in all these specimens. The texture of the head is rougher than that of the cranial roof; in particular, the dorsolateral half is penetrated by numerous small pits as well as by one fairly large foramen (not apparent on either side of the paratype) placed along the dorsal edge of what is here interpreted as being the articular surface.

Exoccipital (eo)

Most of the upper part of the occipital surface of the skull, facing upwards and backwards on either side of the foramen magnum, is presumably formed by the exoccipitals. As mentioned above, the uppermost strip of this surface is probably formed by the supraoccipital, but no suture can be seen. On each side a slightly irregular suture (fused in the paratype) runs from beneath the otic capsule and passes below the exoccipital to reach the bottom of the foramen magnum; beneath this is the basioccipital. The large oval occipital condyle, the back of which is strongly abraded (mostly missing in the paratype) is thus formed jointly by the basioccipital and the exoccipitals. On either side of the occipital condyle, within the exoccipital, is the jugular foramen (for the IXth, Xth, XIth and XIIth cranial nerves); while it appears as a single opening, it is actually a somewhat convoluted cup-shaped depression containing one lateral, two ventral and at least two anterior foramina penetrating deeply (these are not clear in the paratype). The exoccipital is in contact with the otic capsule, more specifically (one presumes) with the opisthotic, but again the suture is obliterated.

Basioccipital (bo)

This element forms essentially the lower part of the occipital surface (partially broken out in the paratype), a large flat area directed as much downwards as backwards. Its upper suture with the exoccipitals and its lower suture with the parabasisphenoid have already been dealt with in the respective descriptions of those bones. (All are fused in the paratype.) As also mentioned above, it contributes towards the formation of the occipital condyle. Laterally it contacts the otic capsule above and the fenestra ovalis below; indeed, it forms the posterior and ventral margins of that aperture. More ventrally still, between the fenestra ovalis and the parabasisphenoid, it contacts the prootic; together with the latter two elements it forms the socket-like articulation for the 'element X' of Zangerl (1944).

Stapes (stp)

The large fenestra ovalis is closed by the more or less oval footplate of the stapes, which seems to extend forwards beyond the margins of the fenestra. From this, directed not only outwards but also a little upwards and backwards, projects the short, laminar columella (missing on the right side of the paratype). The columella is supported by a buttress running anteroventrally.

Phylogenetic position

The phylogenetic position of *Lophocranion* is especially difficult to determine; the remains of the animal consist of little more than the braincase, which is very constant in structure throughout the Amphisbaenia. It is easier to determine what *Lophocranion* is not than what it is.

Rusinga, where the *Lophocranion* material was found, is not far outside the somewhat restricted geographical range of the Recent Trogonophidae (north-west Africa; the 'horn of Africa' and Socotra; and southern Arabia and the lands around the Persian Gulf). But the Trogonophidae may at once be excluded from consideration. *Lophocranion* has a triradiate boss on the sagittal crest which may have served for the attachment of tendons from the axial musculature; none of the trogonophids possesses that character, although it is found in several other amphisbaenians (Amphisbaenidae *sensu* Gans 1967*a*). The form of the processus ascendens of the supraoccipital is also characteristically amphisbaenid in *Lophocranion*; in the trogonophids its structure is typified by that of *Trogonophis* itself, of which Gans wrote (1960: 151) 'The processus ascendens must not be considered to be an actual process here. Because the cranial plates overlap widely rather than join by suture, the processus is actually that portion of the supraoccipital exposed between the two posterior lobes of the parietal. There is no cartilaginous plug or foramen apparent at the very tip of the processus.'

Lophocranion is therefore likely to be an amphisbaenid. But it cannot be placed among the horizontally flattened, shovel-snouted forms (a) because the anterior part of the cranial region is not shortened (it is relatively much longer even than in *Listromycter*, where the shortening is less marked than in Recent shovel-snouts), and (b) because the cranio-facial angle is only about 20°. Nor can it be placed with or near any genera with vertically compressed skulls, such as *Ancylocranium* or *Geocalamus*; in those genera the braincase is definitely oval in section, higher than wide. It is therefore probable, more specifically, that the new form is one of the more generalized, round-headed amphisbaenids.

The Recent amphisbaenids of Africa include four such genera: *Chirindia, Cynisca, Loveridgea* and *Zygaspis*. All are much smaller than *Lophocranion* (and also smaller than most of the species from South America: see Gans 1968, 1974). Indeed, none of those four African genera has a skull longer than 13 mm, whereas the total length of the skull of the *Lophocranion* holotype is estimated to have been about 17 mm (and that individual is considered to have been a juvenile, the paratype being much larger still). The braincase of *Lophocranion* appears to be altogether more slender and elongated, the distance between the fenestra ovalis and the fronto-parietal suture being greater than the distance between the fenestra ovalis and the occiput. None of the four African genera mentioned above has a processus ascendens that projects relatively as far forwards into the back of the parietal, none has a sagittal crest, and none has a braincase of the same outline (in particular, the otic capsules of *Lophocranion* seem to project more laterally, those of the Recent forms more anterolaterally). In addition, *Loveridgea* differs from *Lophocranion* in that its fronto-parietal suture is not nearly as digitiform as that of the Miocene genus, whilst that of *Chirindia* is almost straight.

On the other hand, in every one of the features mentioned above *Lophocranion* is much more like the larger South American amphisbaenids or the Cuban *Cadea*. In particular, there is little to distinguish *Lophocranion* from the South American genus *Amphisbaena*, especially from the larger species (e.g. *A. alba*) of that complex and possibly polygeneric assemblage. Resemblances lie in the pronounced sagittal crest, the widening of that crest just anterior to the supraoccipital tip, the transverse crest of the supraoccipital, and the marked lateral expansion of the temporal lobes on so slender a braincase. Indeed, we cannot yet establish any characteristics in which the preserved portions of the braincases of *Lophocranion* differ from those of *Amphisbaena*.

It must be pointed out that little is known of the variability within the genus *Amphisbaena*. Such characters as the proportions quoted above and the development of a sagittal crest may well be dependent upon absolute size or stage of ontogeny. It is also possible that the characters in question may eventually turn out to be those of large, generalized amphisbaenians, rather than autapomorphies of a derived group.

The zoogeographical importance of *Lophocranion* may not be as great as would superficially appear. It is faintly possible that we might be dealing with a 'South American' form in Africa, but much more likely that (a) the characteristics of the posterior portion of the skull are much less diagnostic at the amphisbaenian species level than are those of the anterior portion, and (b) the aspects shown here represent an earlier grade of specialization still demonstrated in the fossil and retained in South American species but lost in the present-day African forms. Similarly, some early North American rhineurids show an amphisbaenid pattern (Estes 1975). In any case, it must be remembered that the comparison is between a Miocene member of an African lineage and extant members of the South American group. In this case we had three options:

1. To leave the Rusinga form unnamed, merely describing it as 'amphisbaenid gen. et sp. indet.' This has the disadvantage of complicating citation.
2. To assign the Rusinga form to the genus *Amphisbaena*, hitherto restricted to South America. This course of action might lead to the basing of important zoogeographical conclusions upon nothing more than the posterior parts of braincases, lacking all those elements that are generally used in diagnosing amphisbaenians.
3. To give a new generic name to the Rusinga form, even though it may later prove that the species is congeneric with certain South American species of *Amphisbaena* (or with Miocene populations ancestral to them or to modern African genera).

We have chosen the third option as being the least of three evils.

On the information now at our disposal we cannot go further than this. Additional studies, and perhaps the acquisition of new material, may lead to taxonomic conclusions that are less vague; and those, in turn, may prove to have interesting zoogeographical implications.

ACKNOWLEDGEMENTS. We thank Professors A. d'A. Bellairs, C. B. Cox and R. Estes, and Miss A. G. C. Grandison, for their comments on the manuscript; the late Mr A. E. Rixon and Mr P. J. Whybrow for preparing the specimens; Miss M. L. Holloway for making the drawings; Mrs A. S. Gaunt and Mrs S. D. Gillespie for technical assistance; Dr M. J. Charig and Miss K. Vernon for typing some of the many earlier versions of the manuscript; and Mrs J. R. Crane for reading the proofs.

Comparative Recent skeletal material came from the British Museum (Natural History) [B.M.(N.H.)] by courtesy of Miss A. G. C. Grandison, from the Universitetets Zoologiske Museum in Copenhagen [K.M.] by courtesy of Dr F. W. Braestrup, and from the private collection of Carl Gans [C.G.]. The work of Gans is supported by the U.S. National Science Foundation, most recently by Grant DEB-8121229.

REFERENCES

Bellairs, A. d'A. & Gans, C. 1983. The reinterpretation of the amphisbaenian orbitosphenoid. *Nature, Lond.* **302** (5905): 243–244.

—— **& Kamal, A. M.** 1980. The chondrocranium and the development of the skull in Recent reptiles. *In* Gans, C. & Parsons, T. S. (eds), *Biology of the Reptilia* **11** (1): 1–263. London.

Berman, D. 1973. *Spathorhynchus fossorium*, a Middle Eocene amphisbaenian (Reptilia) from Wyoming. *Copeia*, New York, **1973** (4): 704–721.

Broadley, D. G. & Gans, C. 1969. A new species of *Zygaspis* (Amphisbaenia: Reptilia) from Zambia and Angola. *Arnoldia (Rhodesia)*, Bulawayo, **4** (25): 1–4.

—— —— 1975. Additional records for *Zygaspis niger* and *Z. quadrifrons*. *Herpet. Rev.*, Cincinnati, Ohio, **6** (1): 21.

—— —— 1978*a*. Southern forms of *Chirindia* (Amphisbaenia, Reptilia). *Ann. Carneg. Mus.*, Pittsburgh, **47** (3): 29–51.

—— —— 1978*b*. Distribution, variation, and systematic status of *Zygaspis violacea* (Peters) (Amphisbaenia Reptilia), endemic to southeastern Africa. *Ann. Carneg. Mus.*, Pittsburgh, **47** (14): 319–334.

—— , —— **& Visser, J.** 1976. Studies on amphisbaenians (Amphisbaenia, Reptilia). 6. The genera *Monopeltis* and *Dalophia* in southern Africa. *Bull. Am. Mus. nat. Hist.*, New York, **157** (5): 311–486.

Estes, R. 1975. Lower vertebrates from the Fort Union Formation, Late

Paleocene, Big Horn Basin, Wyoming. *Herpetologica*, Chicago, **31** (4): 365–385.

—— 1983. Sauria terrestria, Amphisbaenia. *In* Wellnhofer, P. (ed.), *Handbuch der Paläoherpetologie* **10A**. xxii + 249 pp. Stuttgart & New York.

Gans, C. 1957. 'Anguimorph' tooth replacement in *Amphisbaena alba* Linnaeus, 1758 (Reptilia: Amphisbaenidae). *Breviora*, Cambridge, Mass., **70**: 1–12.

—— 1960. Studies on amphisbaenids (Amphisbaenia: Reptilia), 1. A taxonomic revision of the Trogonophinae and a functional interpretation of the amphisbaenid adaptive pattern. *Bull. Am. Mus. nat. Hist.*, New York, **119** (3): 129–204.

—— 1967*a*. A check list of Recent amphisbaenians (Amphisbaenia, Reptilia). *Bull. Am. Mus. nat. Hist.*, New York, **135** (2): 61–106.

—— 1967*b*. *Rhineura*. *In* Dowling, H. G. & McCoy, C. J. (eds), *Catalogue of American amphibians and reptiles*: 42.1–42.2. Gainesville, Am. Soc. Ichthyol. Herpet.

—— 1968. Relative success of divergent pathways in amphisbaenian specialization. *Am. Nat.*, Chicago, Ill., **102** (926): 345–362.

—— 1969. Amphisbaenians—reptiles specialized for a burrowing existence. *Endeavour*, London, **28** (105): 146–151.

—— 1971*a*. Studies on amphisbaenians (Amphisbaenia, Reptilia), 4. A review of the amphisbaenid genus *Leposternon*. *Bull. Am. Mus. nat. Hist.*, New York, **144** (6): 379–464.

—— 1971*b*. Redescription of three monotypic genera of amphisbaenians from South America: *Aulura* Barbour, *Bronia* Gray and *Mesobaena* Mertens. *Am. Mus. Novit.*, New York, **2475**: 1–32.

—— 1974. *Biomechanics: approach to vertebrate biology*. x + 261 pp. Philadelphia. [Reissued 1980, Ann Arbor.]

—— 1976. Three new spade-snouted amphisbaenians from Angola (Amphisbaenia, Reptilia). *Am. Mus. Novit.*, New York, **2590**: 1–11.

—— 1978. The characteristics and affinities of the Amphisbaenia. *Trans. zool. Soc. Lond.* **34**: 347–416.

—— 1987. Studies on amphisbaenians (Reptilia), 7. The small round-headed species (genus *Cynisca*) from western Africa. *Am. Mus. Novit.*, New York, **2896**: 1–84.

—— **& Alexander, A. A.** 1962. Studies on amphisbaenids (Amphisbaenia, Reptilia), 2. On the amphisbaenids of the Antilles. *Bull. Mus. comp. Zool. Harv.*, Cambridge, Mass., **128** (3): 65–158.

—— **& Broadley, D. G.** 1974. A new dwarfed species of *Monopeltis* from the Middle Zambesi Valley (Reptilia: Amphisbaenia). *Arnoldia* (*Rhodesia*), Bulawayo, **6** (35): 1–5.

—— **& Kochva, E.** 1965 (1966). A systematic review of *Ancylocranium* Parker (Amphisbaenia, Reptilia). Notes on amphisbaenids 22. *Israel J. Zool.*, Jerusalem, **14**: 87–121.

—— **& Kraklau, D.** 1989. Studies on amphisbaenians (Reptilia), 8. Two genera of small species from East Africa (*Geocalamus* and *Loveridgea*). *Am. Mus. Novit.*, New York, **2944**: 1–28, 20 figs.

—— **& Latifi, M.** 1971. Redescription and geographical variation of *Monopeltis guentheri* Boulenger (Amphisbaenia, Reptilia). *Am. Mus. Novit.*, New York, **2464**: 1–21. [Reprinted 1972, *Archs Inst. Razi*, Tehran, **24**: 63–82.]

—— **& Lehman, G. C.** 1973. Studies on amphisbaenians (Amphisbaenia: Reptilia), 5. The species of *Monopeltis* from north of the river Zaire. *Occ. Pap. Mus. Zool. Univ. Mich.*, Ann Arbor, **669**: 1–34.

—— **& Rhodes, C.** 1967. *Chirindia* from Tanganyika (Amphisbaenia, Reptilia) [Notes on amphisbaenids no. 19]. *Ann. Carneg. Mus.*, Pittsburgh, **39** (1): 1–32.

Gilmore, C. W. 1943. Fossil lizards of Mongolia. *Bull. Am. Mus. nat. Hist.*, New York, **81** (4): 361–384.

—— **& Jepsen, G. L.** 1945. A new Eocene lizard from Wyoming. *J. Paleont.*, Tulsa, Okla., **19** (1): 30–34.

Hoffstetter, R. 1955. Squamates de type moderne. *In* Piveteau, J. (ed.), *Traité de paléontologie* **5**: 606–662. Paris.

Jollie, M. T. 1960. The head skeleton of the lizard. *Acta zool., Stockh.*, **41** (1–2): 1–64.

Kritzinger, C. C. 1946. The cranial anatomy and kinesis of the South African amphisbaenid *Monopeltis capensis* Smith. *S. Afr. J. Sci.*, Cape Town, **42**: 175–204.

Peters, W. C. H. 1882. *Naturwissenschaftliche Reise nach Mossambique auf Befehl Seiner Majestät des Königs Friedrich Wilhelm IV in den Jahren 1842 bis 1848 ausgeführt. Zoologie III, Amphibien*. xv + 196 pp. Berlin.

Rieppel, O. 1981. The skull and the jaw adductor musculature in some burrowing scincomorph lizards of the genera *Acontias, Typhlosaurus* and *Feylinia*. *J. Zool., Lond.*, **195**: 493–528.

Romer, A. S. 1956. *Osteology of the reptiles*. xxi + 772 pp. Chicago.

Vanzolini, P. E. [1951*a*]. *Evolution, adaptation and distribution of the amphisbaenid lizards (Sauria: Amphisbaenidae)*. 148 pp. Thesis, Harvard Univ., Cambridge, Mass. (unpublished).

—— 1951*b*. A systematic arrangement of the family Amphisbaenidae (Sauria). *Herpetologica*, Chicago, **7** (3): 113–123.

Young, C.-C. 1961. On two new fossil lizards of China. *Vertebr. palasiat.*, Peking, **5** (2): 118–121.

Zangerl, R. 1944. Contributions to the osteology of the skull of the Amphisbaenidae. *Am. Midl. Nat.*, Notre Dame, Ind., **31** (2): 417–454.

Bull. Br. Mus. Nat. Hist. (Geol). **46** (1): 37–60 Issued 31 May 1990

A revision of the English Wealden Flora, II. Equisetales

JOAN WATSON

Departments of Environmental Biology and Geology, The University, Manchester, M13 9PL

DAVID J. BATTEN

Institute of Earth Studies, UCW–Aberystwyth, University of Wales, Aberystwyth, SY23 3DB

CONTENTS

SYNOPSIS. The three known equisetalean species from the English Wealden are revised and type specimens selected. Their geological occurrence and stratigraphical range are discussed.

Equisetum burchardtii Dunker is known only from *in situ* rhizomes and tubers in the English Wealden, but in the German Wealden also from subterranean parts of aerial shoots. An emended diagnosis is given, a neotype chosen and a reconstruction suggested. The poorly characterized tuberous species *Equisetites yokoyamae* Seward is discussed, compared with other tuberous material and the lectotype selected. Both species were probably deciduous. *Equisetites lyellii* (Mantell) Seward, which occurs extensively *in situ* in the soil beds of the Wealden in Sussex, is known also from dispersed aerial parts in fragment partings above the soil beds. The diagnosis is emended to include cuticular and anatomical details and the lectotype is chosen. *E. lyellii* was probably winter-green. The subgeneric affinities of the fossil species are discussed in relation to comparable extant species.

Pilasporites allenii Batten, the probable spore of *E. lyellii* which is now known from dispersed sporangiophore heads, is discussed and compared to other putative equisetalean spores. Palaeoenvironments are considered and probable habitats suggested.

INTRODUCTION

Many beds in the Wealden succession of south-east England contain plant roots in positions of growth. Usually the tops of the plants have been eroded away and it is normally impossible to suggest affinities for such isolated roots, although occasionally it is reasonable to guess that they belonged to *Equisetum* or *Equisetites*. However, sometimes they are connected to excellently preserved equisetalean rhizomes, tubers and underground parts of aerial shoots, and can then be identified with confidence. Three members of the Equisetales have been described from the English Wealden: *Equisetum burchardtii* Dunker, *Equisetites yokoyamae* Seward and *Equisetites lyellii* (Mantell) Seward. From England *E. burchardtii* is known only as lengths of thin rhizomes bearing tubers, but since aerial shoots are known from the Wealden of Germany these are described and figured here. *E. yokoyamae* is very poorly characterized and may even represent only a different preservational state of *E. burchardtii*. *E. lyellii* is by far the best represented of the three species, known from an abundance of excellent material found in positions of growth and is one of the few Wealden plant species which can still reliably be found in the field. It is widely preserved *in situ* in the 'soil beds' (fossil aquatic soils of Allen, 1976) in the Wealden succession of south-east England and the bulk of this paper is devoted to the taxonomy and geological significance of this species.

The material studied belongs to several collections made by a number of people over a period of about 150 years, starting with Mantell (1833) and later Rufford (Seward 1894), but notably in this century by Allen (1941, 1947, 1976) and most recently by Batten. The collections are mainly housed in the British Museum (Natural History) (B.M.(N.H.)) with numbers prefixed V.; the Sedgwick Museum, Cambridge with numbers prefixed K.; the Museum für Naturkunde, Humboldt University, East Berlin, numbers without a prefix. The Appendix lists all the specimens figured here together with their locality, stratigraphical horizon and present location, as well as details of other interesting specimens which have not been figured.

GEOLOGICAL OCCURRENCE

Of the several Wealden formations the Wadhurst Clay, which is thought to be of Valanginian age, has yielded the most numerous *Equisetum* and *Equisetites* finds both in positions of growth and as dispersed fragments. Most of the 'soil beds' are in the Wadhurst Clay and the majority of the specimens in them are referable to *E. lyellii* without reservation. Conveniently referred to as 'soil beds' for descriptive purposes, they were undoubtedly aquatic (Allen 1976) and are discussed in more detail below. Allen (1976, Appendix I) has given a comprehensive check-list of soil horizons and their localities in the Wealden of the Weald. Details of the upper parts of the aerial shoots of the species have been obtained entirely from macroscopic stem fragments which are common in thin debris partings associated with the soil beds. Older and younger occurrences of the species are scarce, but dispersed remains of aerial stems have been found in Berriasian and Valanginian–?Hauterivian strata in the Weald. Some of the *in situ Equisetum* which has been recorded from these rocks may differ from *E. lyellii*. In particular some rhizomes are very slender; not so slender, however, as the tuber-bearing rhizomes of *E. burchardtii*. Tuberous forms of *Equisetum*, including *E. burchardtii*, are rare and, by contrast with *E. lyellii*, have not been found in the Wadhurst Clay Formation. Records so far are limited to isolated occurrences in arenaceous facies of the Ashdown Beds Formation and Weald Clay Group (Allen 1959, 1962, 1976; Kennedy & MacDougall 1969). It is clear that *E. lyellii* can have rather thin rhizomes, such as those shown in Fig. 17 from Poundsford (top Purbeck) and in Fig. 23 from the Brede Soil Bed (Wadhurst Clay). They could represent a response to less suitable environmental conditions such as an increase in salinity or more arenaceous deposition. Similar specimens from Philpots Quarry (lower Grinstead Clay) and the Hackenden Soil Bed (possibly the same horizon) are less well preserved, but can be identified with confidence as *E. lyellii* on the basis of their characteristically very short internodes. However, the possible presence of one or more completely different and as yet unrecognized species should not be ruled out because preservation is often so poor as to preclude specific identification.

Many other beds contain roots in position of growth but the plants to which they belonged are usually missing because an erosion surface supervenes. It is normally impossible therefore to suggest affinities for them, although when interbedded with deposits in which rhizomes of *Equisetum* or *Equisetites* occur, it is reasonable to guess that they too are equisetalean.

All the equisetalean material described from the Wealden of Germany by Dunker (1846) and Schenk (1871, 1876) is from localities regarded as Berriasian in age. Unfortunately all but one of their original specimens are missing.

SYSTEMATIC DESCRIPTIONS

Class **SPHENOPSIDA**
Order **EQUISETALES**
Family **EQUISETACEAE**

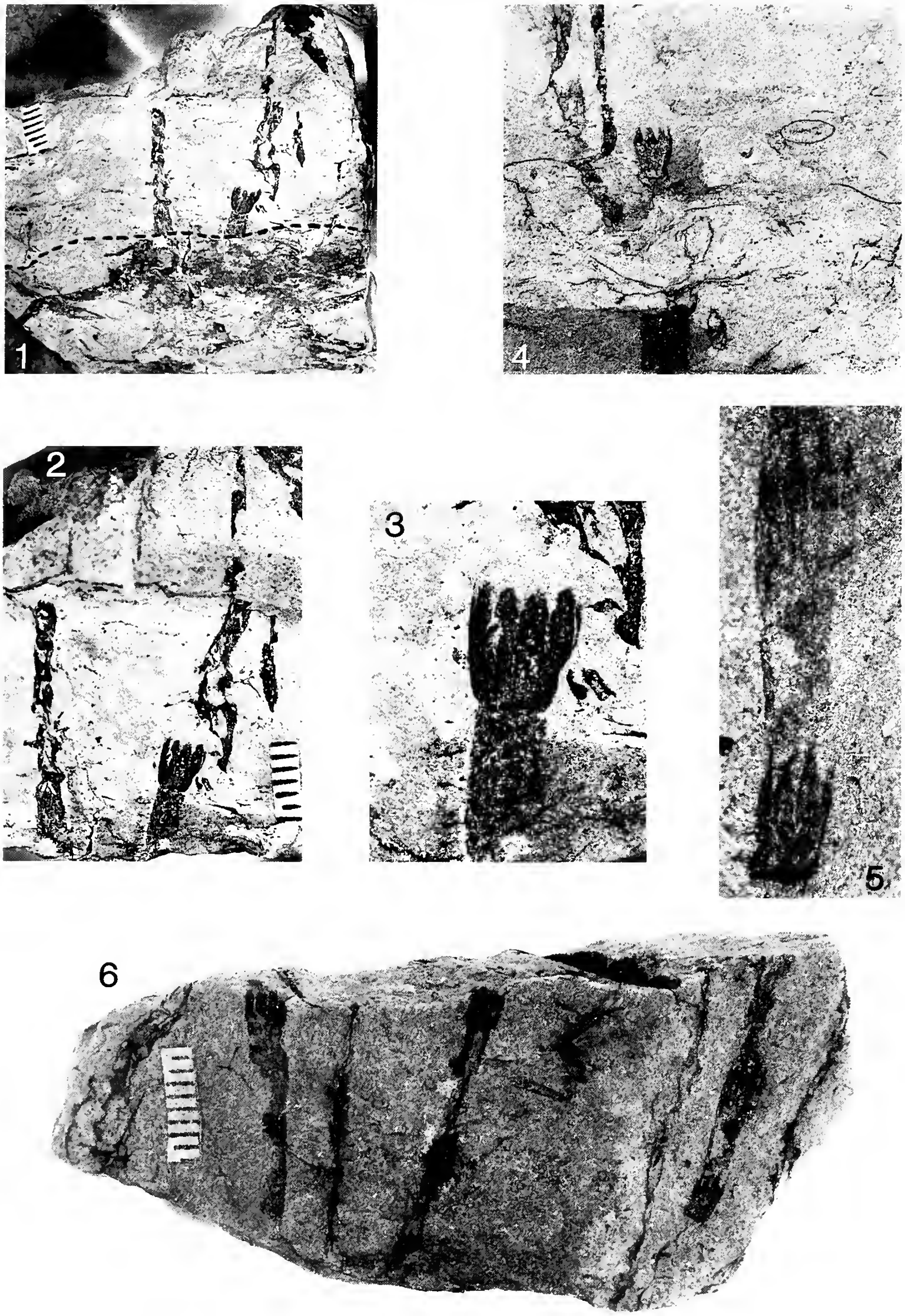
Genus ***EQUISETUM*** Linnaeus

Opinions and conventions concerning the use of the Recent genus *Equisetum* L. for fossil species have swung back and forth over the past 150 years, as the synonymies of *E. burchardtii* and *E. lyellii* show. There is a strong argument for retaining *Equisetites* Sternberg for all extinct species, however closely they resemble modern forms, and in many ways we prefer this usage. However, there has been an increasing tendency in recent years (Harris 1961, Gould 1968) to include a species, whatever its geological age, in the living genus when differences cannot be demonstrated. This is of course common practice with Tertiary plants. Although anatomical details of *Equisetum burchardtii* Dunker are not available it is so similar to living species of the genus *Equisetum* (subgenus *Equisetum*) that it is difficult to imagine that any generic differences could exist. We have therefore decided to include it in *Equisetum* L., as indeed did Dunker and Schenk.

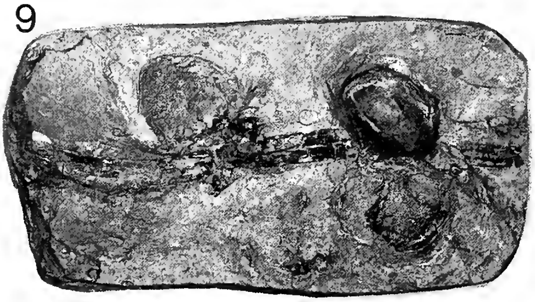
Equisetum burchardtii Dunker Figs 1–12, 14

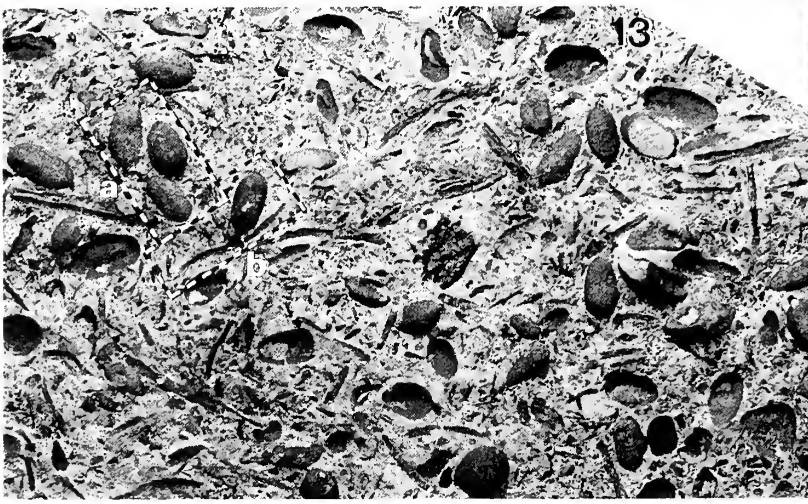
?1824 *Carpolithus Mantellii* Stokes & Webb: 425; pl. 46, figs 3, 4; pl. 47, fig. 1. (Tubers only).
?1827 *Carpolithus mantellii* Stokes & Webb; Mantell: 56; pl. 3, figs 3, 4; pl. 3*, fig. 1. (Repeat of Stokes & Webb figures).
?1833 *Carpolithus Mantelli* Stokes & Webb; Mantell: 245; text-fig. on p. 246.
1846 *Equisetites (Equisetum) Burchardti* Dunker: 2; pl. 5, fig. 7.
1846 *Carpolithus Lindleyanus* Dunker: 22; pl. 2, fig. 7 in part.
1846 *Carpolithus cordatus* Dunker: 22; pl. 2, figs 7 (in part), 10.
1846 *Carpolithus Huttoni* Dunker: 22; pl. 2, fig. 8.
1846 *Carpolithus certum* Dunker: 22; pl. 7, fig. 3.
1852 *Equisetum Burchardti* Dunker; Ettingshausen: 10; pl. 1, figs 3, 4.
1871 *Equisetum Burchardti* Dunker; Schenk: 205; pl. 22, figs 1–5; pl. 30, fig. 1 (see Fig. 10).
1876 *Equisetum Burchardti* Dunker; Schenk: 157; pl. 26, fig. 1.
1894 *Equisetites Burchardti* Dunker; Seward: 27; pl. 1, figs 5, 6.
1983 *Equisetum burchardtii* Dunker; Watson: 266; pl. 13, figs 1–3.

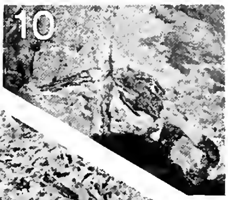
EMENDED DIAGNOSIS. Underground rhizomes 2–4 mm wide, internodes at least 3 cm long, each node bearing 2 or more ellipsoidal tubers up to 1·5 cm long. Vertical aerial shoots 2–3 mm wide arising at intervals from rhizome; internodes up to at least 3 cm long. Whorl of 8 leaves at each node on aerial



Figs 1–6 *Equisetum burchardtii* Dunker. 1, small block of sediment with plants in growth position. The dotted line marks the junction between the bedding plane (below) with rhizomes and tubers and the vertical face (above) with lower parts of aerial shoots; **neotype** (here selected), Dunker Catalogue 57, × 1. 2, vertical face of same specimen showing underground parts of aerial shoots *in situ*, × 2. 3, single shoot showing whorl of leaves with blunt tips at node; part of same specimen, × 5. 4, vertical face with various ramifying shoots, some of which may be vertically ascending rhizomes; Dunker Cat. 6, × 2. 5, aerial shoot showing sharply pointed leaves in successive whorls; Dunker Cat. 7, × 5. 6, vertical face of whole block as last, with closely spaced, well preserved underground parts of aerial shoots; see Figs 7, 8 for top surface of this block, Dunker Cat. 7, × 2.







Figs 7–12 *Equisetum burchardtii* Dunker. 7, 8, top horizontal surface of block shown in Fig. 6, showing hollow stems in transverse section (compare Fig. 48, p. 52); Dunker Cat. 7; 7 × 2, 8 × 5. 9, *in situ* tubers attached to length of rhizome; V.1070, × 1. 10, Schenk's (1871: pl. 30, fig. 1) original specimen showing tubers attached to rhizome; Dunker Cat. 88, × 1. 11, *in situ* tubers from German Wealden; Dunker Cat. 87, × 2. 12, typical isolated tuber from Germany, very closely similar to numerous English specimens in B.M. (N.H.) collections; Dunker Cat. 85, × 2.

Fig. 13 *Equisetites yokoyamae* Seward. Surface of block showing portions of rhizomes and numerous tubers, may not be in growth position; see text for discussion. The dotted lines mark the areas figured by Seward (1894): a, Seward's fig. 3; b, Seward's fig. 3*. [N.B. Seward attributed the wrong specimen number to the former]. V.2335, × 1.

shoot, fused laterally to form adpressed or somewhat inflated sheath up to 5 mm long. Acutely pointed leaf tips free for more than 1 mm; well-defined commissures between leaves reaching almost to node. [Internal anatomy unknown; microscopic details unknown].

NEOTYPE. Specimen 57 in the old Dunker Catalogue, Museum für Naturkunde der Humboldt Universität, East Berlin, here selected. Figs 1–3.

TYPE LOCALITY AND HORIZON. Harrel bei Bückeburg, northwest Germany. Berriasian.

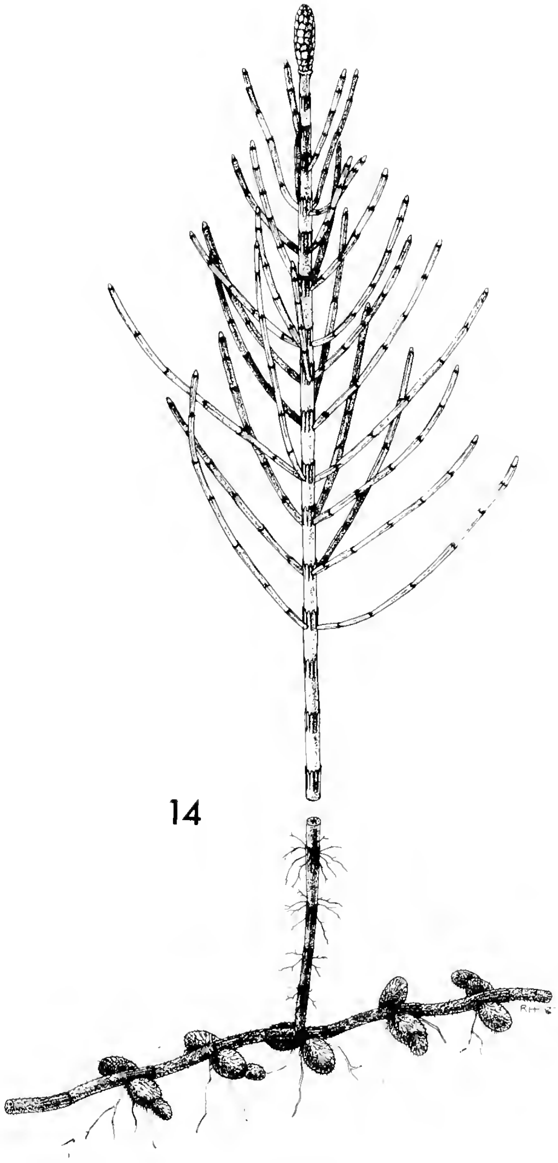
ENGLISH MATERIAL. The only English specimens so far reliably identified as *E. burchardtii* are those in the B.M.(N.H.)

collected by Rufford. They are merely recorded as being from Ecclesbourne, near Hastings, and therefore their exact horizon is in doubt. They could have come from either the Ashdown Beds Formation or the Wadhurst Clay Formation and thus may be either Berriasian or Valanginian in age. It seems most likely that they are from the Ashdown Beds as there are no other records of tuberous rhizomes from the Wadhurst Clay (Allen 1976: 428).

DESCRIPTION. The true identity of the specimens described as fruits by Stokes & Webb (1824) and likened to palm kernels by Mantell (1827, 1833) is not known, but they were almost certainly isolated *Equisetum* tubers of which there are many in the B.M.(N.H.) collections (Fig. 12). Such tubers attached to *Equisetum* rhizomes (Fig. 9) were not described from the English Wealden until much later (Seward 1894), when they were identified with *Equisetum burchardtii* Dunker (1846) from the Wealden of Germany, where they are known also from aerial shoots. There is no doubt about the specific identity of the material described by Seward (1894), but in the absence of the Stokes & Webb specimens we retain Dunker's specific epithet. Dunker (1846) at the same time erected a number of *Carpolithus* species, also probably isolated *Equisetum* tubers. Unfortunately none of Dunker's figured specimens have been recognized in any of the German collections, but the old Dunker collection in the Museum für Naturkunde, East Berlin, still has several excellent small blocks showing *in situ* rhizomes, tubers and aerial shoots. One of these (Figs 1–3) is here selected as the neotype for *Equisetum burchardtii*. This block has rhizomes, fine roots and tubers on the bottom horizontal face (Fig. 1, below the dotted line) and portions of aerial shoot on one of the vertical faces (above the dotted line). One of the aerial shoots (Figs 2, 3) clearly shows the details of a leaf sheath, with a whorl of probably eight leaves. This particular specimen has eroded leaf tips but other specimens (Figs 4–6) show acute, sharply pointed, intact tips. The shoots shown in Figs 5 and 6 have several successive nodes intact and therefore the internodal length has been taken from here, though of course these specimens must represent only the extreme basal portions of aerial shoots.

No microscopic details of *E. burchardtii* have been obtained. All attempts at making cuticle preparations were unsuccessful. As with *E. lyellii* the cuticle is rendered featureless by oxidative maceration. Our best hope is to obtain newly collected, naturally oxidized fragments now that several of the old German Wealden localities have been reopened (Riegel *et al.* 1986).

DISCUSSION. The specimen of *E. burchardtii* in Fig. 9 with thin rhizomes, long internodes and bearing tubers at the nodes is strikingly like the living species *Equisetum palustre*. The known parts of the aerial shoots may also be compared to such a species with few facets (leaves); typically five in *E. palustre* (Hyde *et al.* 1969: fig. 26) and eight in *E. burchardtii*. All the known features of *E. burchardtii* point very strongly to it being a typical species of the genus *Equisetum* subgenus *Equisetum*. All extant members of this subgenus are deciduous, with soft, easily broken aerial shoots which decay at the end of each growing season, whilst bearing food storage tubers on the rhizomes which, in all but one species, lack a central canal. The presence of tubers therefore indicates that the fossilization process began during the winter after the deciduous aerial stems had died down. Thus it is clear that the *in situ* shoots attached to tuberous rhizomes were the underground parts and of course a seasonal climate is strongly indicated, supporting the conclusions of Batten (1975) and Harris (1981) from other palaeobotanical evidence, and Allen (1976) on sedimentological grounds. It seems probable that *E. burchardtii* displayed other features typical of its subgenus. In the suggested reconstruction in Fig. 14 we have incorporated some of these likely features, such as solid, strongly angular branches distinct from the main axis and cones with rounded tops. The choice of monomorphic habit with cones borne at the apices of the green shoots is purely arbitrary.



14

Fig. 14 Suggested reconstruction of *Equisetum burchardtii* Dunker. Approximately × ½. © Joan Watson, 1990.

COMPARISON. For comparison with other tuberous rhizomes from the English Wealden see below under *Equisetites yokoyamae*, p. 42.

Equisetum burchardtii has been listed in several floras from different parts of the world but it is impossible to assess the reliability of the identifications. Most similar are some of the specimens, including tuberous rhizomes, which Fontaine (1889, 1905) described from the Lower Cretaceous Potomac Group of the U.S.A., ascribing them to various species. Berry (1911) redescribed this material and transferred some of it to *E. burchardtii*, but unfortunately the whereabouts of the specimens is now unknown.

E. burchardtii is distinct at the subgeneric level from the Wealden species *Equisetites lyellii*, which shows significant differences from all the living species and is discussed in detail below. From what we know about *E. burchardtii* it is more similar to living members of the group than to any of the other Mesozoic species which are known in comparable detail.

Genus *EQUISETITES* Sternberg

1833 *Equisetites* Sternberg: 43.
1894 *Equisetites* Sternberg; Seward: 23.
1961 *Equisetum* Linnaeus; Harris: 14.
1968 *Equisetum* Linnaeus; Gould: 155.

The genus *Equisetites* Sternberg was put into synonymy with *Equisetum* Linnaeus by Harris (1961), who considered that morphologically none of the fossil forms assigned to *Equisetites* could be separated at the generic level from extant *Equisetum*. This is probably true for most of the species hitherto described, but that is not to say that *Equisetites* should not be retained for use as it was originally intended, that is for plants which cannot positively be assigned to the living genus. We therefore propose its reinstatement and are retaining within it two of the Wealden species.

Equisetites yokoyamae Seward is so poorly characterized that it really does not warrant a name change on the basis of the information available, and *Equisetites* seems a perfect repository for it. *Equisetites lyellii* (Mantell), on the other hand, is now known in considerable detail including its anatomy. The evidence shows that the anatomical features of *E. lyellii* are rather further removed from modern *Equisetum* than the external morphology suggests, and in the light of this we prefer to retain it within *Equisetites* Sternberg.

Equisetites yokoyamae Seward — Fig. 13

1894 *Equisetites Yokoyamae* Seward: 33, text-figs 2, 3.

HOLOTYPE. V.2335, B.M.(N.H.)

TYPE LOCALITY AND HORIZON. Ecclesbourne near Hastings. Berriasian or early Valanginian; see comments above about the age of *E. burchardtii* and the Ecclesbourne locality.

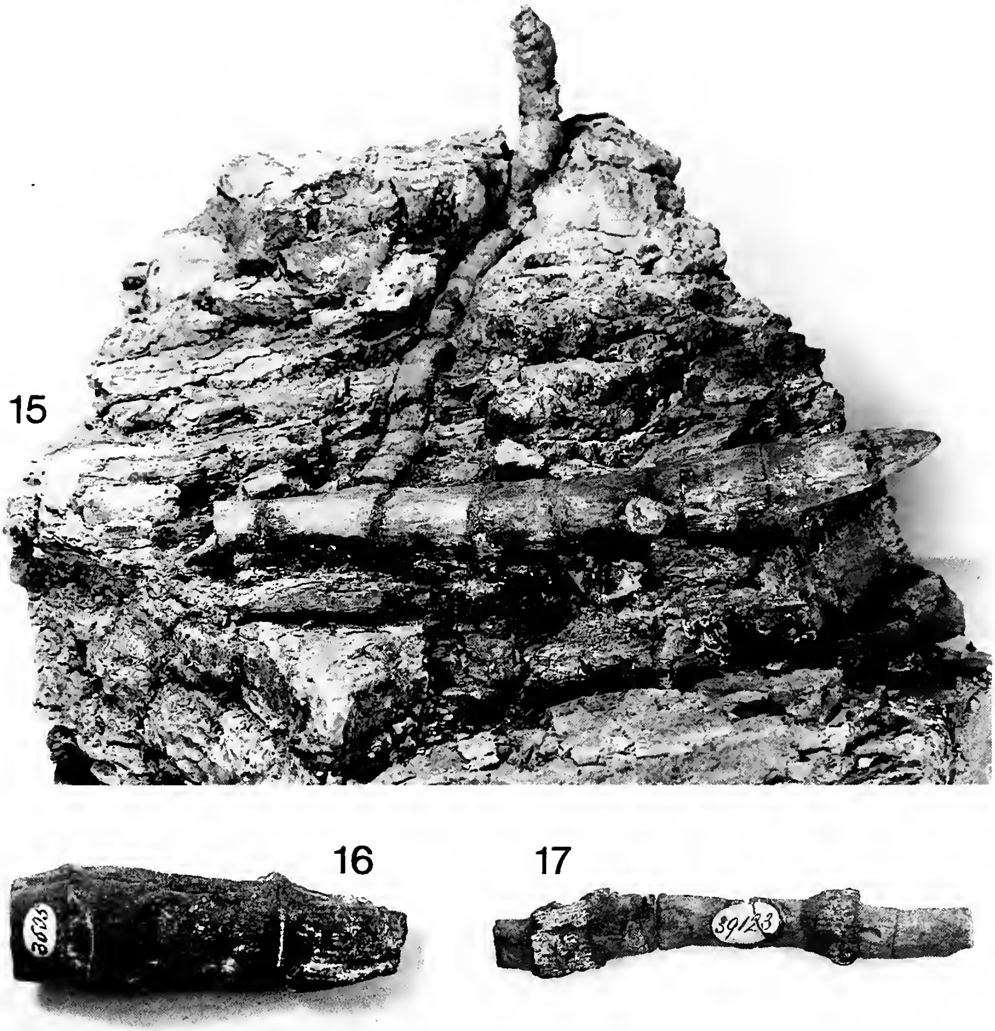
DESCRIPTION AND DISCUSSION. Fig. 13 shows part of the block of red-stained fine white sandstone covered with tubers and lengths of very thin rhizome, on the basis of which Seward (1894) erected the species *Equisetites yokoyamae*. The dotted lines on Fig. 13 indicate the areas figured by Seward (1894: figs 3, 3*). Almost all the material attributed to *E. yokoyamae* by Seward is in this same matrix and could represent a single occurrence found by P. Rufford and subsequently distributed to various museums. The tubers are much smaller and narrower than most of those of *E. burchardtii* (Fig. 9) from the English Wealden but the German material (Figs 10–12) shows a wide range in variation of tuber size. Fig. 10 illustrates the sole remaining German figured specimen (Schenk 1871: pl. 30, fig. 1), which is very close in shape and size to *E. yokoyamae* and could represent the same species in a different preservational state. However there are a few other specimens in the B.M.(N.H.), tentatively attributed by Seward to *E. yokoyamae*, which have extremely small tubers and thin rhizomes (see Appendix). The extreme difference in size between these and the largest *E. burchardtii* tubers must indicate the presence of more than one species. But, in the absence of cellular detail and without information from aerial parts, the exact nature of *E. yokoyamae* remains uncertain.

Other tuberous rhizomes recorded by Allen (1976: 427) from the Weald Clay are unlikely to be either *E. burchardtii* or *E. yokoyamae*. Those from the Slinfold Soil Bed have rhizomes about 1 cm in diameter, whereas the fattest rhizomes of *E. burchardtii* barely reach 4 mm. Specimens from the Vann Lane Sand have rhizomes 1·5 cm across and the tubers are rounded rather than elongate (Allen, personal communication). It seems likely that several herbaceous, tuberous species of *Equisetum* were present in the Wealden flora.

Equisetites lyellii (Mantell) Seward — Figs 15–42, 45–51, 53–55, 57–63, 67

1833 *Equisetum Lyellii* Mantell: 245, figs 1–3. (Rhizomes figured as aerial shoots).
1846 *Equisetites Phillipsii* Dunker: 2; pl. 1, fig. 2. (Poor figure of fat rhizome).
1871 *Equisetum Phillipsii* Dunker: Schenk (*pro parte*): 206; pl. 22, figs 6–8; *non* pl. 22, fig. 9. (Rhizomes in their fattest form).
1871 *Equisetum Lyelli* Mantell; Schenk: 207; pl. 22, figs 10–12. (Rhizomes of medium size).
1894 *Equisetites Lyelli* (Mantell) Seward: 24; pl. 1, fig. 4. (Mainly list of material in B.M.(N.H.) collections).
1913 *Equisetites lyelli* (Mantell); Seward: 85; pl. 11, figs 1a, 1b.
1941 *Equisetites lyelli* (Mantell); Allen: 362, text-figs 54–56; pl. 24. (*In situ* material with new diagnosis and full synonymy including doubtful identifications).
1947 *Equisetites lyelli* (Mantell); Allen: 303, text-fig. 57. (Soil beds and rhizomes showing vascular strands).
1983 *Equisetum lyellii* Mantell; Watson: 265; pl. 13, figs 5–8; pl. 14, figs 1–7, 9–12. (Including preliminary description of stomata and sporangiophore).

DIAGNOSIS (emended after Allen, 1941). Underground rhizomes horizontal, thick, usually unbranched, with large central canal, having internodes of variable length and width, internode length 5 mm to 3 cm or more, width less than 1 cm to over 2 cm. Hollow erect stems arising singly or in pairs with internodes typically 7 mm long and 7 mm wide in the lower subterranean part, tapering to 3 mm long and 2·5 mm wide in the upper aerial part; some nodes of aerial shoots bearing whorls of narrow branches. Central canal of aerial shoot large, surrounded by a ring of vascular bundles with crescent-shaped metaxylem, tracheid thickenings probably annular. Cortex with ring of vallecular canals, oval in section [vascular bundles and vallecular canals presumed to equal leaves in number]. Leaf sheath varying from half as long to nearly as long as internode, composed of slender tapering leaves united to near their toothed apices by commissures with strongly sculptured surface; commissures extending backwards from node. Whorls of up to 46 leaves on rhizome, 26 on the lower



Figs 15–17 *Equisetites lyellii* (Mantell). 15, Allen's (1941) specimen of a rhizome with growing tip and aerial shoot preserved in growth position; specimen now broken, printed from original negative; K.2221, × 1. 16, 17, the two remaining original specimens figured by Mantell (1833). 16, **lectotype** (here selected), 3605, × 1. 17, 39123, × 1.

and 18 on the upper parts of the erect stems. Tubers not formed.

Ordinary epidermal cells of internode in longitudinal files, rectangular with sinuous walls marked with tranverse ridges; features less apparent in longer, narrower cells of leaf sheath. Broad longitudinal band of scattered stomata in lower part of each segment of leaf sheath on aerial shoot; stoma oval, typically 40 µm long and 20 µm wide; outer stomatal cells level with surrounding surface, ornamented with beaded sculpture along slit-like aperture and around distal margin.

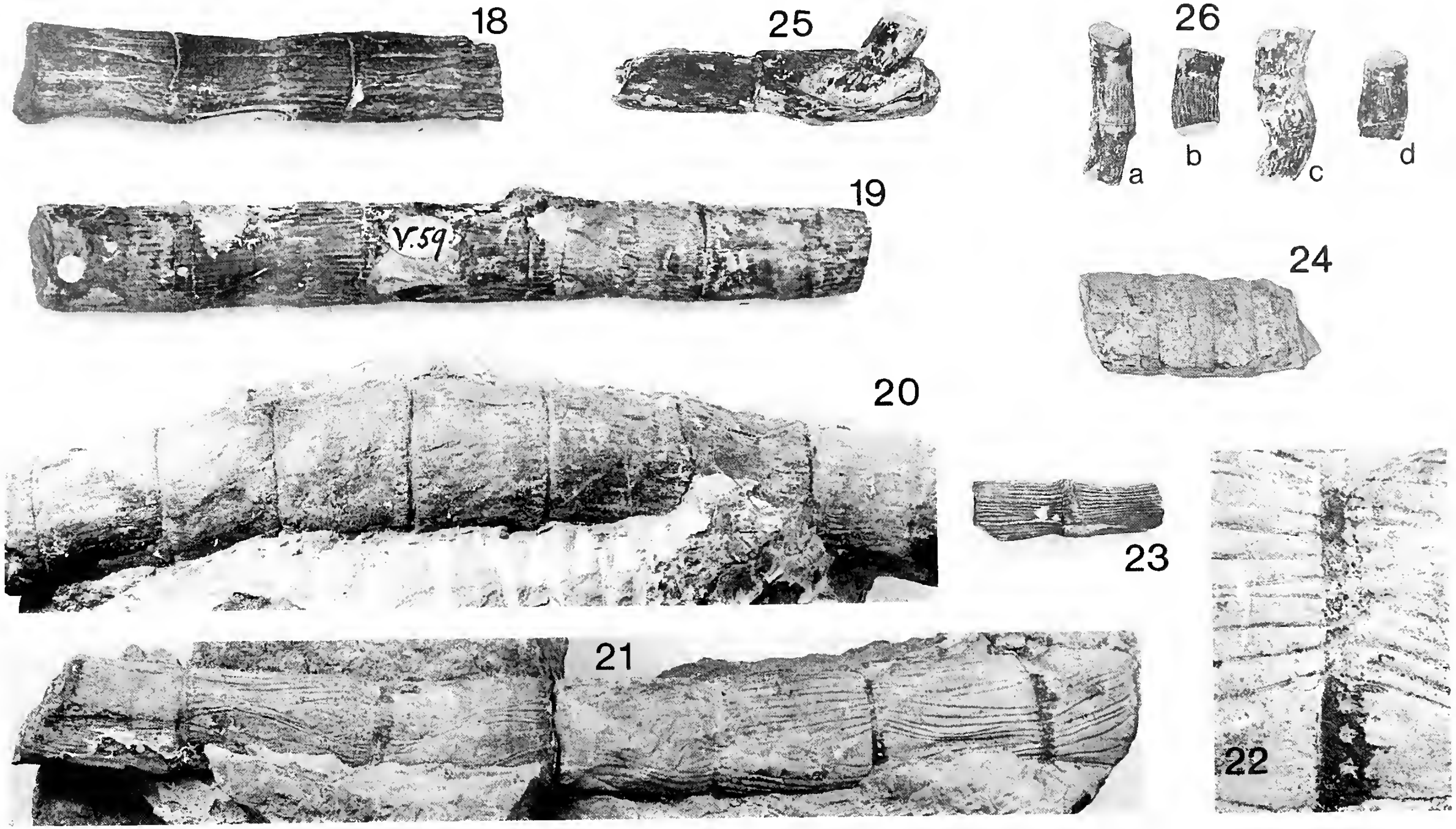
Sporangiophore peltate, head circular with about 24 surface ribs radiating from centre; epidermal cells rectangular with sinuous walls parallel to ribs. Sporangia rounded [number unknown], containing spores of *Pilasporites allenii* Batten.

LECTOTYPE. Specimen 3605 in the B.M. (N.H.), here selected. Figured by Mantell (1833: 245, fig. 3). Fig. 16.

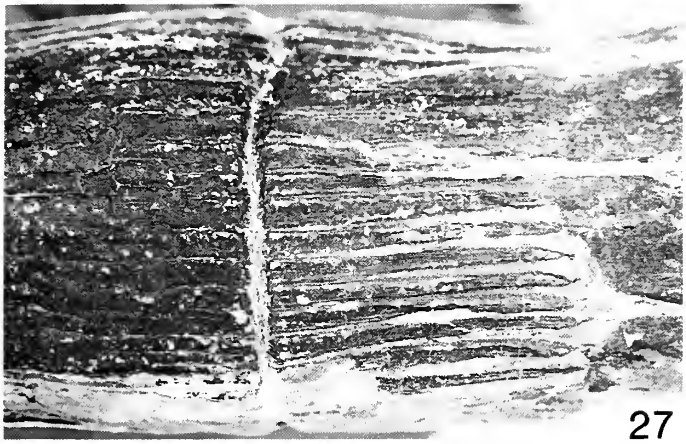
TYPE LOCALITY AND HORIZON. The locality given by Mantell (1833) as Pounceford was later confirmed by Hunter (1835) and Topley (1875: 498) as being Poundsford, south of Burwash Common, E. Sussex (TQ 637225). Poundsford lies athwart the Purbeck–Ashdown boundary and the quarries from which the specimens apparently came were in the top Purbeck (Topley 1875: 37–41, 408), of presumed Berriasian age.

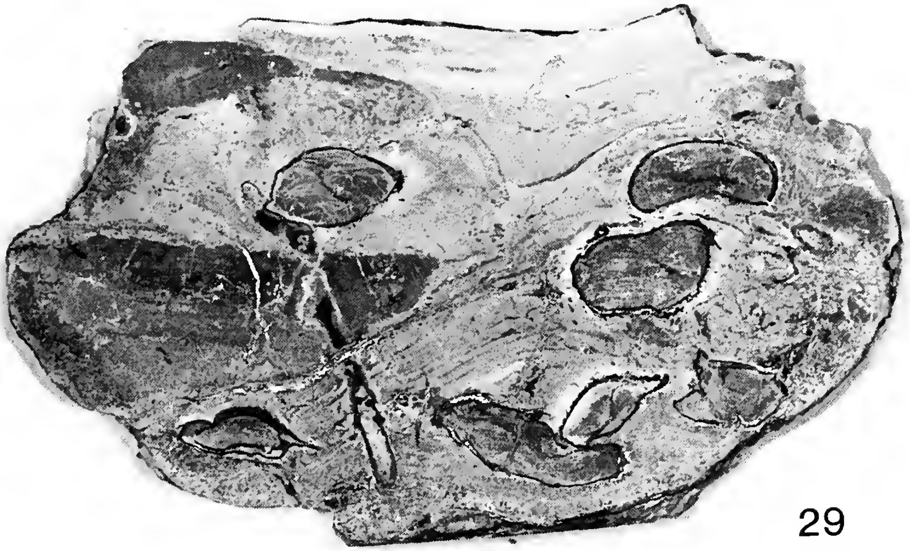
STRATIGRAPHICAL RANGE. The material from the type locality is the oldest recorded occurrence of *E. lyellii*. The youngest stratigraphically are specimens from the Hackenden Soil Bed within the Grinstead Clay Member of the Tunbridge Wells Sandstone Formation, in the upper part of the Hastings Bed Group.

MATERIAL. The material studied comes from numerous localities (see Appendix) and horizons and consists of the following parts of the plant: a large number of lengths of underground rhizome found *in situ* in various states of compression or as internal moulds; short lengths of underground parts of aerial shoots, also *in situ* and often attached to the rhizome; two separate but related finds of petrified underground parts in a carbonate matrix; presumed erect axes from above ground



Figs 18–26 *Equisetites lyellii* (Mantell). All except Fig. 22 × 1. 18–25, rhizomes showing different preservation states and typical variation in width and internode length. 18, 19, rhizomes with well preserved leaf-sheaths and the longest internodes; 18, V.710; 19, V.59. 20, the fattest rhizome known, V.45457. 21, internal mould of hollow rhizome showing impressions of vascular strands along internodes, V.51137. 22, single node of same specimen showing apparent leaf-gaps, × 4. 23, narrow rhizome of similar preservation showing vascular bundles as ferruginous grooves (see Allen 1947: fig. 57A), K.2139. 24, shortest internodes known, probably close behind growing tip missing from right, V.63058. 25, rhizome with aerial shoot apparently emerging below node, V.28642. 26, portions of aerial shoots with well preserved leaf-sheaths and typically retaining circular section; a, V.63070; b, V.28643; c, V.63071; d, V.63072.





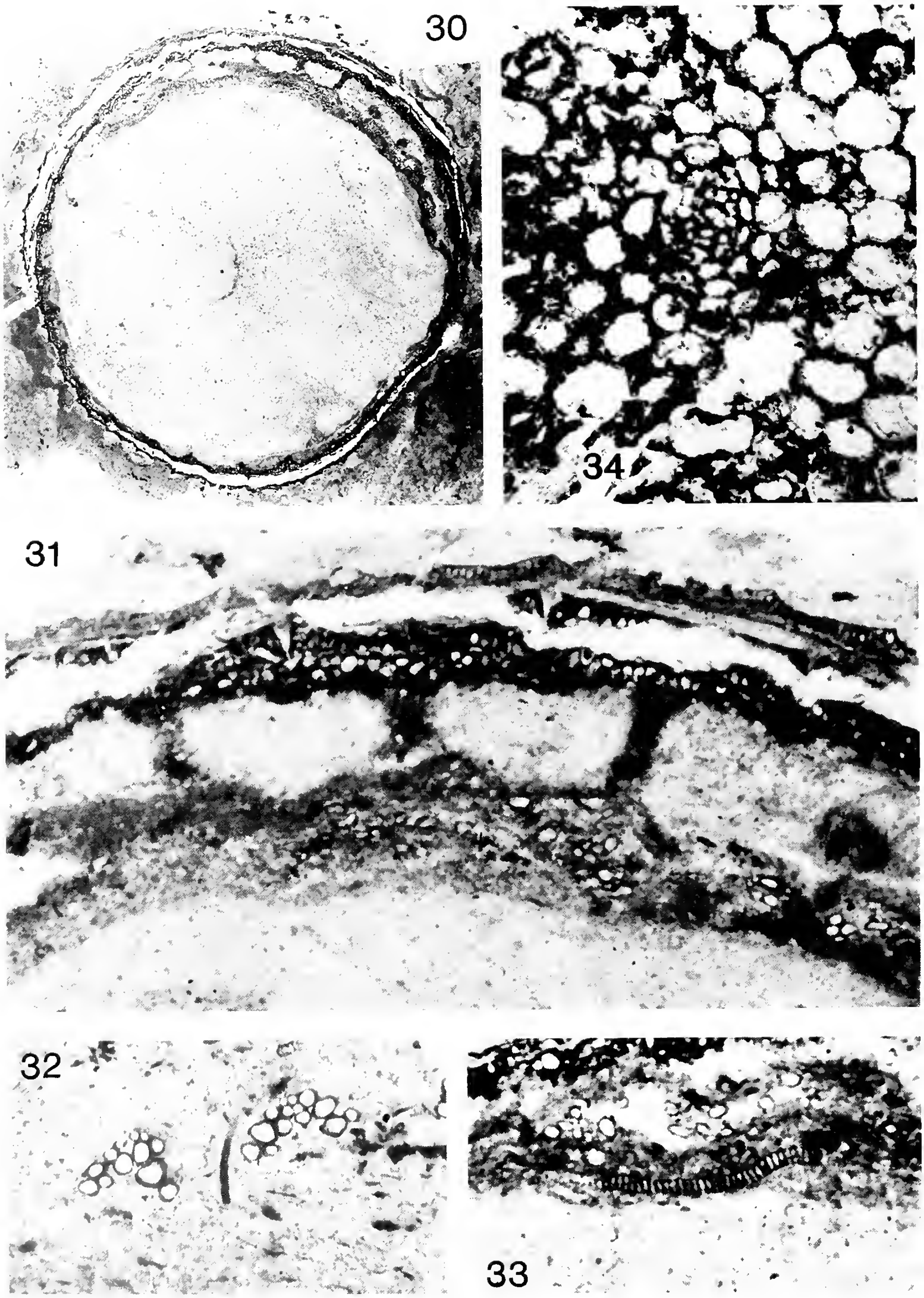
Figs 27–29 *Equisetites lyellii* (Mantell). 27, portion of rhizome showing large number of leaves in whorl with pointed tips intact; V.710, × 4. 28, portion of aerial shoot with eroded tips of leaves; V.28643, × 4. 29, vertical cut face of carbonate nodule containing rhizomes with well preserved cellular structure; V.63059, × 1

level which are known only from fragment partings in compression form; the probable spores both dispersed and from sporangiophores. Unfortunately the aerial parts are those about which we know least and organic connection has not strictly been proved. The dispersed spores are also identified only on evidence of abundant association.

All the material is from the English Wealden. *E. lyellii* is present but uncommon in the German flora.

DESCRIPTION. Figures 15–28 illustrate the easily recognizable and most characteristic features of *E. lyellii*: the thick horizontal rhizomes with a large central canal and a large number of leaves, up to 46 per node; the narrower upright stems also with a large number of leaves; the very short internode length of both rhizome and aerial shoot. The absence of tubers must also be regarded as diagnostic.

When Mantell (1833) first described *Equisetites lyellii* he failed to distinguish between rhizomes and aerial parts and did not recognize that the specimens were in growth position. This was first recognized by Allen (1941). Two of Mantell's original specimens are shown in Figs 16 and 17. The former, which has been selected as the lectotype, is a clearly recognizable portion of rhizome with one whole and two half internodes, elliptical in cross section. The tip of the specimen (Fig. 16, right side) which Mantell (1833: fig. 2) figured vertically as the 'cryptogamous head' is a broken, squashed, hollow internode. Specimen 39123 (Fig. 17) is more problematical, being very poorly preserved with incrustations of heavy mineralization. On the basis of the internode length we are inclined to think that this is also a piece of rhizome, although it is at the lower limit of recorded rhizome width. However, the specimen in Fig. 23 (collected and figured by Allen, 1947: fig. 57), which is very little wider, is without doubt a portion of rhizome, though with much shorter internodes. A third specimen (3579) in the B.M.(N.H.), which has the same poor preservation, is possibly the original of Mantell's figure 1



Figs 30–34 *Equisetites lyellii* (Mantell). All sections prepared from carbonate nodules. 30, transverse section of aerial shoot indicating large central canal and vallecular canals; V.44953, × 10. 31, portion of same section showing ridged stem surface, cells of cortex, vallecular canals and vascular bundles out of place; × 50. 32, t.s., vascular bundles showing more extensive xylem than in living species; phloem was probably present between the arms of the V-shaped xylem; V.44951, × 50. 33, displaced tracheid seen longitudinally, showing thickenings; V.44953, × 50. 34, part of cortex shown in Fig. 35, with small subsidiary trace of uncertain nature, discussed on p. 49; V.44949, × 400.

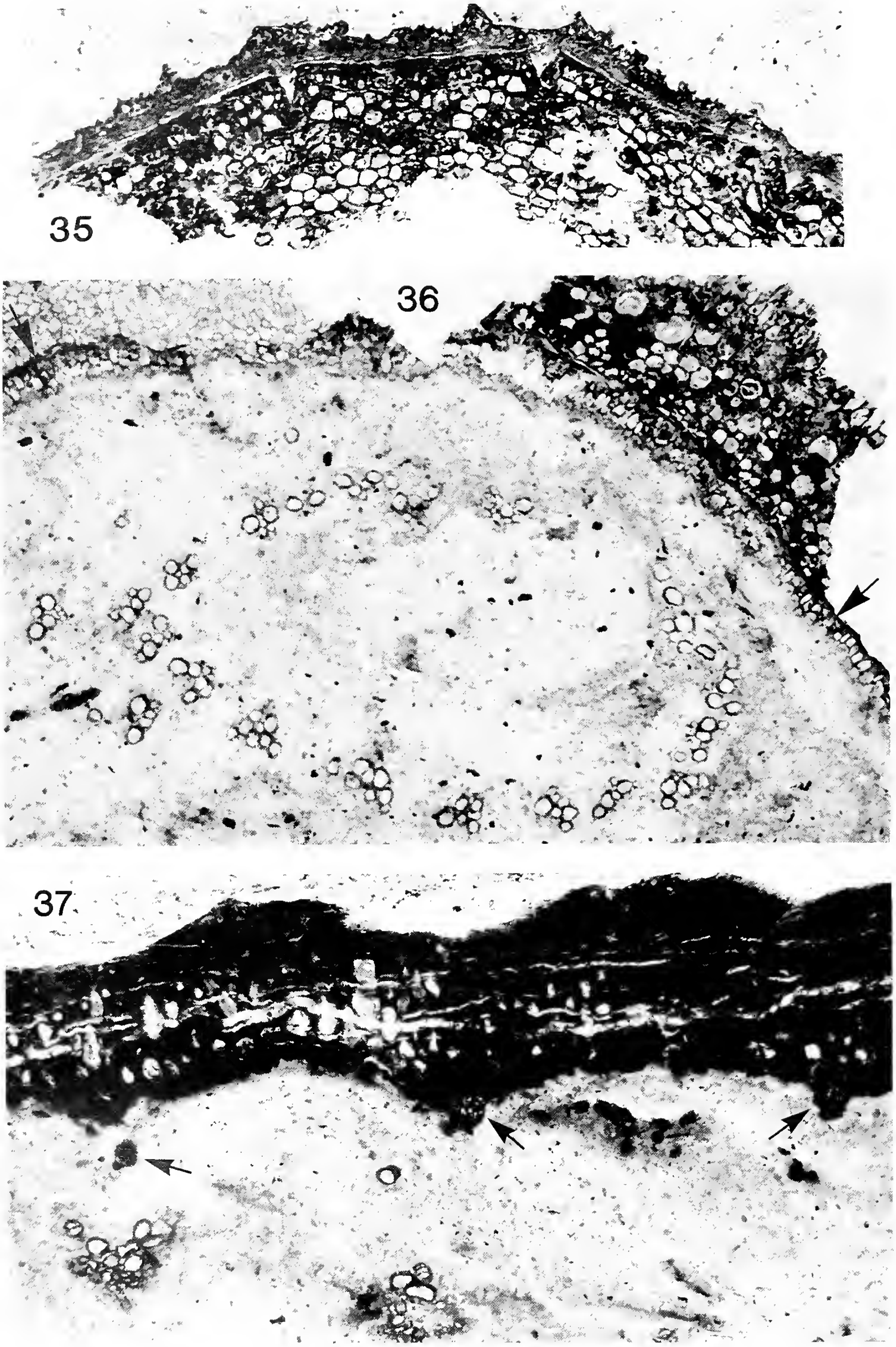
(1833), but is less easily recognizable than the other two. About a dozen other rhizomes with this same preservation survive; probably all were collected by Mantell at Poundsford. Four of them (see Appendix for details) are of particular interest in that they retain their original circular cross section. The hard, blue-grey calcareous matrix with a metallic ring which fills the rhizomes is probably one of the 'Blue limestones' of Topley (1875: 37). It seems likely that early lithification by calcium carbonate forming locally in the mud before compression produced incompressible patches. One of the four rhizomes is circular for half its length but shows considerable compression in the other half without lateral spreading (see Allen, 1947). Allen (personal communication) has observed similar partially uncompressed rhizomes in the field, associated with various lateral changes of lithology.

Since Mantell's time *E. lyellii* in growth position has been collected extensively by Allen, Batten and others in the numerous soil beds in the Wealden of Sussex. Material collected and studied by Allen (1941, 1947) included the splendid specimen from the Brede Soil Bed (Wadhurst Clay) illustrated in Fig. 15, which shows the rhizome complete with growing tip and an extensive length of the subterranean part of an upright stem. Unfortunately the growing tip and most of the aerial shoot are now missing from this specimen (Sedgwick Museum, K2221) and Fig. 15 has been printed from one of Allen's original glass plate negatives. Allen's description of *E. lyellii* (1941) based on the *in situ* soil bed material is very comprehensive, and apart from SEM studies of the cuticle can be little improved upon. The new information presented here comes largely from two other sources; compressions of aerial parts dispersed in the fragment beds and anatomically preserved material in carbonate nodules (Fig. 29) found by P. J. Whybrow and C. H. Shute of the B.M.(N.H.) in the Balcombe (= High Brooms) Soil Bed in the upper Wadhurst Clay near East Grinstead.

The epidermal details of the subterranean parts, which of course lack stomata, were figured by Allen (1941). Indeed cuticle preparations are easy to obtain, although they very rapidly deteriorate in acid, becoming so featureless that no cell outlines can be seen. The cells and their bars of thickening (Figs 45–49) are best seen in naturally oxidized fragments. Some of the best dispersed fragments, from the Cuckfield No. 1 borehole (Lake & Thurrell 1974), have yielded details of the stomata which were hitherto unknown. The stomata are scattered in a wide band (Fig. 40) in the flat areas of the leaf sheath between the commissures (Fig. 39). Fig. 39 shows part of a well-preserved leaf sheath from the borehole. This specimen has well-preserved stomata, two of which are shown in Figs 41 and 42. The outer stomatal cells are seen to be level with the surface and have beaded ornamentation around the perimeter and along the stomatal slit. Amongst living species we found strikingly similar stomata (Figs 43, 44) in *Equisetum sylvaticum*. It seems reasonable to suppose, therefore, that the stomata of *E. lyellii* have the same unusual construction as in living *Equisetum* (Hauke 1957, Chatterjee 1964, Page 1972*a*), the guard cells being completely covered and hidden by the two subsidiary cells which are seen at the surface. These are usually referred to as the 'stomatal cells'. Both the distribution and form of the stomata are features of taxonomic significance which will be further discussed below.

Figure 53 shows the freshly split surface of a block of fragment bed photographed under paraffin. Surfaces such as this have provided valuable new information about the subaerial parts of *E. lyellii* but have also posed problems to which we have as yet no answers. Most prominent amongst the various dispersed remains on these blocks are the so-called nodal diaphragms (Figs 53, 55). These wheel-like bodies are familiar from almost all fossil equisetalean species (Harris 1961, Gould 1968) although no such structure is known in living species. Watson (1983) has already indicated that we have reason to call into doubt their real nature, and to suggest that they may often, if not always, be a preservational effect. During the course of this study several specimens of *Equisetum telmateia* obtained for epidermal preparations were kept in a polythene bag in a dry, centrally heated room for several months. Apart from obvious changes in colour and dryness the plants remained ostensibly intact. However, upon removal from the bag and subsequent handling, they all fell apart into single internodes with a leaf sheath at the top node and a 'nodal diaphragm' at the bottom node as shown in Fig. 56. Clearly the drying and shrinking of the hollow stem had caused it to shrivel inwards a few mm above the node whilst the node itself remained as a firm ring. This has had the effect of making the vascular bundles between the vallecular canals appear as spokes radiating from the centre, presenting an unmistakable similarity to the nodal diaphragms so well known in fossil *Equisetum*. It is easy to see that during preservational degradation this resistant structure could readily become detached and rotate through 90°, the position in which the diaphragms are commonly preserved (Harris 1961: figs 4D, 5C). The nodal diaphragms found associated with *E. lyellii* are all 2 mm or less in diameter, and are almost certainly from slender branches which are one of the least known features of this plant. Allen (1941) reported seeing only one branch, about 2 mm across, but further evidence of extensive branching in some shoots comes from the specimen shown in Fig. 50 and from a number of specimens such as that in Fig. 48. The specimen in Fig. 50 on the surface of the fragment parting appears to be an unexpanded shoot with unexpanded whorls of branches at each node. Fig. 48 is one of many branch-like fragments about 2 mm wide which are cylindrical and have epidermal cells with bars of thickening (Fig. 49) closely matching those of *E. lyellii* epidermis from elsewhere on the plant.

Other circular bodies with radiating striations (Figs 57–60) are quite different from the nodal diaphragms in having a complete covering of cuticle, and are without doubt the sporangiophores of *E. lyellii*. Some have been removed whole from the matrix using HF and then either macerated or mounted for the SEM. The outer surface seen in Fig. 61 shows that the epidermal cells are of the usual rectangular wavy-walled type and Fig. 60 shows the radiating striations as strong surface ridges. The macerated specimens yielded compact clumps of spores such as that in Fig. 62, presumably representing the contents and shape of a single sporangium. Similar spore masses are common in the fragment partings in association with isolated dispersed spores and occur in many palynological preparations. They are sometimes attached to tissues that suggest the remains of sporangiophores. We have been completely unable to ascertain or even estimate the number of sporangia borne on the under surface of the sporangiophore, which we assume had a central stalk as usual. The fairly featureless spores (Fig. 63) lacking elaters match the probable dispersed spore *Pilasporites allenii* Batten. Attempts have been made to find elaters amongst the spore masses by mounting broken, unmacerated pieces of the sporangiophores but this has so far proved unsuccessful. However, the amount of fragment bed material studied in this



Figs 35–37 *Equisetites lyellii* (Mantell). All × 50. 35, transverse section of cortex showing outer layer with ridged surface, and parenchymatous inner layer with notches into which outer cortex protrudes; V.44949; see also Fig. 34. 36, t.s. showing solid cortex, dark endodermis (arrows) and ring of metaxylem; V.44948. 37, t.s. of specimen showing remains of vallecular canals and small subsidiary traces (arrowed); V.44951.

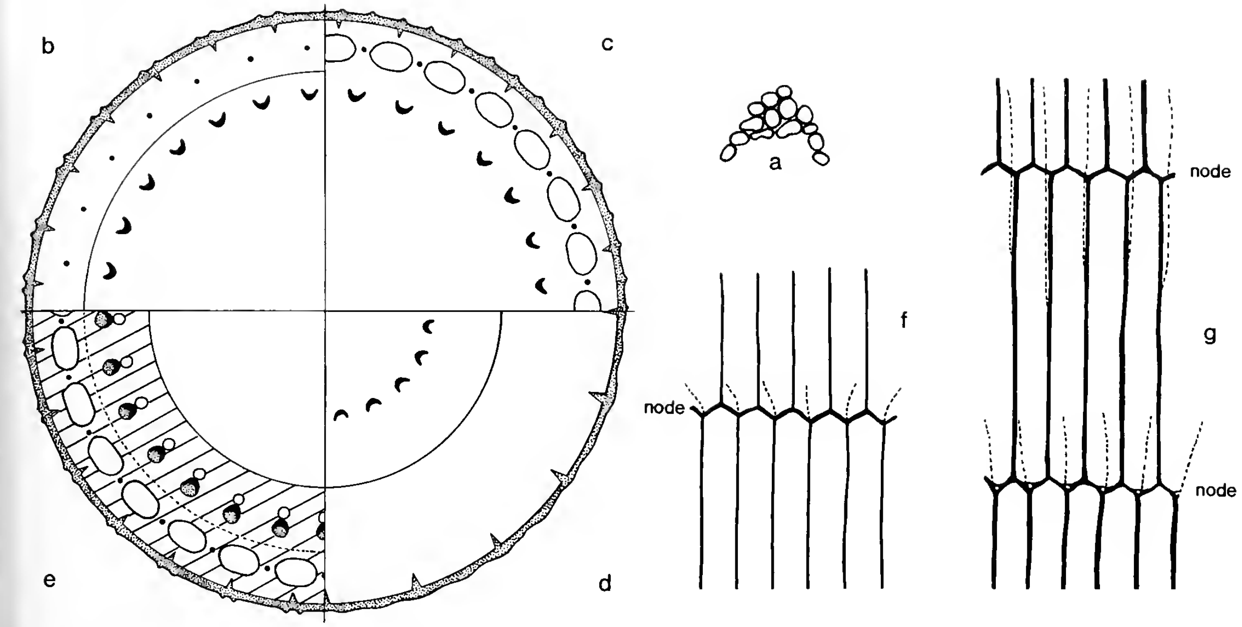


Fig. 38a–e, g *Equisetites lyellii* (Mantell). a, crescent-shaped xylem of a single well-preserved internodal bundle; protoxylem appears intact; V.44951, × 50. b, c, d, diagrammatic transverse sections: b, V.44949; c, V.44953; d, V.44948; e, reconstructed transverse section; all × 15. g, diagram to show suggested form of stele in *E. lyellii*; f, diagram to show form of stele in extant *Equisetum*; both × 10.

way has been relatively limited and extensive searching of newly collected blocks might prove fruitful.

A further type of circular body (Figs 53, 54), with an even, all-over pattern of small perforations in a layer of coalified material, continues to mystify us. The diameter of these spotted bodies is about 2 mm. It seems highly likely that they originate from *E. lyellii* and any suggestions as to their nature would be welcome.

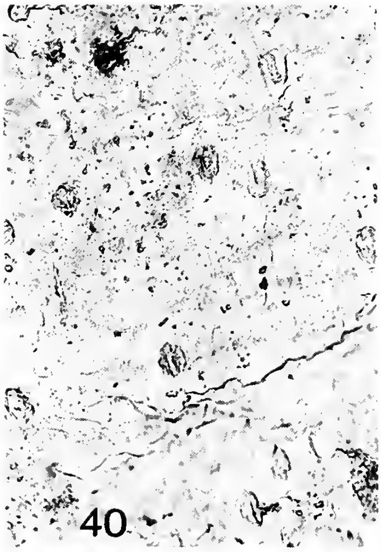
The carbonate nodule with petrified material consists of two separate finds. The first was a single nodule of calcareous mudstone, the whole of which was used to produce, by grinding, a number of longitudinal and transverse sections which were then made into permanent slide mounts. The preservation is imperfect but adds some information about the internal anatomy of *E. lyellii*. The second find of nodular material included the specimen shown in Fig. 29. This is a vertical cut-face showing transverse sections across the hollow rhizomes in growth position. Several such faces have been used to prepare cellulose acetate peels but the preservation of the plant material is less good than that in the permanent mounts. Some of the slides show little or no detail, particularly the longitudinal sections, and the information presented below has been obtained only from the transverse sections. It is certainly possible that the nodule V.63059 (Fig. 29) and others found with it would yield considerably more details of the internal anatomy with further study, but the specimens would have to be sacrificed to further cutting and extensive peeling.

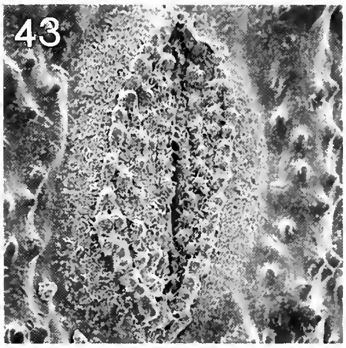
Figure 30 shows the best of the transverse sections, which is obviously from an aerial shoot with a diameter of 7 mm and circular cross section. There is some doubt about whether the other sections represent rhizome or aerial shoot but certain features, such as the ridged and grooved surface (Figs 35, 38) and the number of vascular bundles, point to the latter. The rhizome surface of a living *Equisetum* undulates rather than having a sharply and evenly ridged surface like the aerial shoot of most *Equisetum* species.

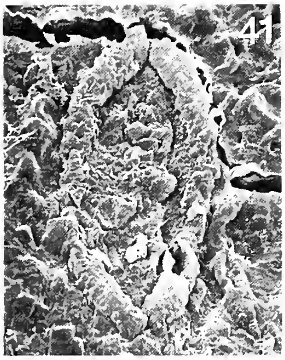
The cortex is composed of two distinct layers; an outer dark, fibrous layer (Figs 31, 35) in which thickened cells are sometimes seen, and a deep inner cortex (Figs 35, 36) of large isodiametric cells with fairly thin walls. The outer cortex is approximately 0·1 mm deep except at a point opposite the vallecular canal where it protrudes into the inner cortex in a wedge shape (Figs 35, 38c). In some slides the inner cortex is solid (Figs 35, 36, 38b) whereas in others the vallecular canals are present in it (Figs 30, 31, 37, 38c). The former are taken to indicate that a parenchymatous diaphragm was present in the nodal region; the latter are internodal sections. In the sections from both regions occur what appear to be small, circular vascular traces in addition to the main vascular bundles (Figs 34, 37, 38b, c). These resistant traces are indicated by arrows in Fig. 37. To the inside of the vallecular canals a strong dark line is sometimes present (arrows in Fig. 36) in the position where one would expect the endodermis. Inside this line the soft tissues are not preserved for more than about two rows of cells (Fig. 36). Thus the xylem of the main bundles is isolated in the middle. Most of the specimens have a ring of 28 or 30 vascular bundles, with only the metaxylem preserved. Each is a crescent or V-shaped mass of about 14 tracheids with the arms pointing to the outside (Figs 32, 35). Occasionally one or two protoxylem elements remain at the point of the V. The xylem is sometimes seen longitudinally (Fig. 33) with either annular or spiral thickenings.

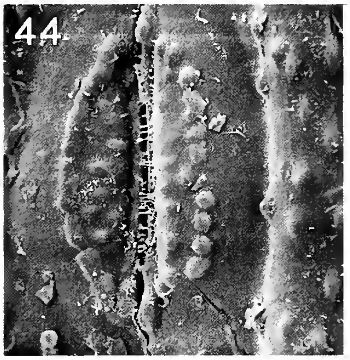
The specimen shown in Figs 36 and 38d is perhaps near a node at the very base of the shoot, or even on the rhizome. It bears an appendage which appears to be a small root with a central vascular strand. It also differs from most other sections in having a much smaller ring of vascular bundles, no vallecular canals and no subsidiary vascular bundles (Fig. 36). Of course close to the node one would expect some indication of the bundles joining to form the nodal ring, but there is no such indication.

Figure 38b–d comprises diagrams of three specimens in









Figs 39–42 *Equisetites lyellii* (Mantell). 39, SEM montage of leaf sheath of aerial shoot showing sculptured cells of the commissures; dotted lines indicate positions of leaf tips broken during preparation; from fragment parting, V.63060, × 50. 40, naturally oxidized piece of internode cuticle from fragment parting showing stomata in broad band, probably internode of aerial shoot from above ground level; V.63076, × 125. 41, 42, two of the stomata (only 5 or 6 were found) from specimen in Fig. 39; × 1000.

Figs 43–44 *Equisetum sylvaticum* Linnaeus. Internode stomata of living species, showing silicified surface closely resembling *E. lyellii*; × 1000.

transverse section, and a reconstructed section which is mostly based on the available information, but has added features which are purely conjectural. The exact position of the surface ridges is not clear as it appears to vary, but the arrangement in slide V.44949 (Fig. 35) is taken as typical. It should be pointed out that in living species of *Equisetum* the surface ridges are on the same radii as the vascular bundles. In none of the sections have we been able to identify the leaf-sheath surrounding the stem. One should consider the possibility that the layer we have identified as outer cortex might in fact be the leaf sheath very closely pressed into the contours of the stem surface. This interpretation would produce sharply defined shallow notches separating broad, flat ridges opposite the vascular bundles.

Discussion. One of the outstanding differences from modern horsetails is the large amount of metaxylem in *E. lyellii*, but an even more anomalous feature is the presence of the ring of small vascular traces which, as far as we can tell, are between the vallecular canals (Fig. 37) and on the same radii as the main vascular bundles. The normal arrangement of the vascular tissue in extant *Equisetum* is shown in Fig. 38f, but there is some disagreement about the exact nature of such a stele. The various viewpoints which revolve around whether the internodal bundle is a composite structure or a single unit have been summarized with great clarity by Parihar (1965). In general terms the internodal bundles may be considered to trifurcate at the node with the median strand passing out as a leaf trace. The lateral strands diverge to the left and right and unite with adjacent strands to form the alternating ring of bundles in the next internode above. In this process of splitting and reuniting, which is condensed at the node, a continuous ring of xylem is produced. The evidence we have for *E. lyellii* indicates that the vascular arrangement at the node was very similar to that in extant *Equisetum*. We know that the vascular bundles of *E. lyellii* normally alternate in successive internodes, but not invariably. Specimen V.51137 (Figs 21, 22), which is an internal mould of the hollow rhizome with ferruginous impressions of the vascular bundles, shows this non-alternation in several places. This specimen is also of special interest in apparently displaying leaf-gaps at some of its nodes (Fig. 22). The presence of leaf-gaps in living *Equisetum* is a little-known feature described originally by Browne (1939) and later in detail by Moore (1941) from several species. We also know that the whorls of leaves usually alternate at successive nodes, and although we cannot actually demonstrate that the leaves alternate with the bundles of the internodes above, the position of the probable leaf gaps (Figs 21, 22) strongly supports this. Assuming it to be so, we can only account for the small bundles by suggesting that they are leaf traces which depart from the main bundle at some distance below the node (Fig. 39g). They would thus be on the same radius as the bundle from which they arise and also the leaf above into which they would pass as the leaf trace. On the other hand the presence of the small leaf gaps seems to us at variance with this arrangement, since we assume the traces would diverge into the leaves without further disturbance to the main vascular bundles. However, we are working at the very limits of the material and at this stage we can only speculate that such anomalous leaf departure was not universally present. Alvin & Hluštik (1979) have demonstrated a similar situation in the Lower Cretaceous cheirolepidiaceous conifer *Frenelopsis alata* (K. Feistmantel), where the steles of side branches sometimes depart from below the node.

From the above evidence it is clear that the anatomical features of *E. lyellii* are rather further removed from the modern genus *Equisetum* than the external morphology suggests, and it is in the light of this that we prefer to retain it in the genus *Equisetites* Sternberg.

Amongst modern botanists there are still differences of opinion concerning the status of the genus *Equisetum* and its subdivisions. Here we need not consider more than the two major sub-groups, subgenus *Equisetum* and subgenus *Hippochaete*, which are easily distinguishable (see Page 1972*a*, 1974). The main features of the former, commonly called the horsetails, have been listed above under the discussion of *Equisetum burchardtii*. To these details it may be added that the stomata occur in a broad scattered band along each furrow of the stem. The stomatal cells are level with the surface and covered in a microscopic ornamentation of silicified beading, as in the stomata of *Equisetum sylvaticum* shown in Figs 43 and 44.

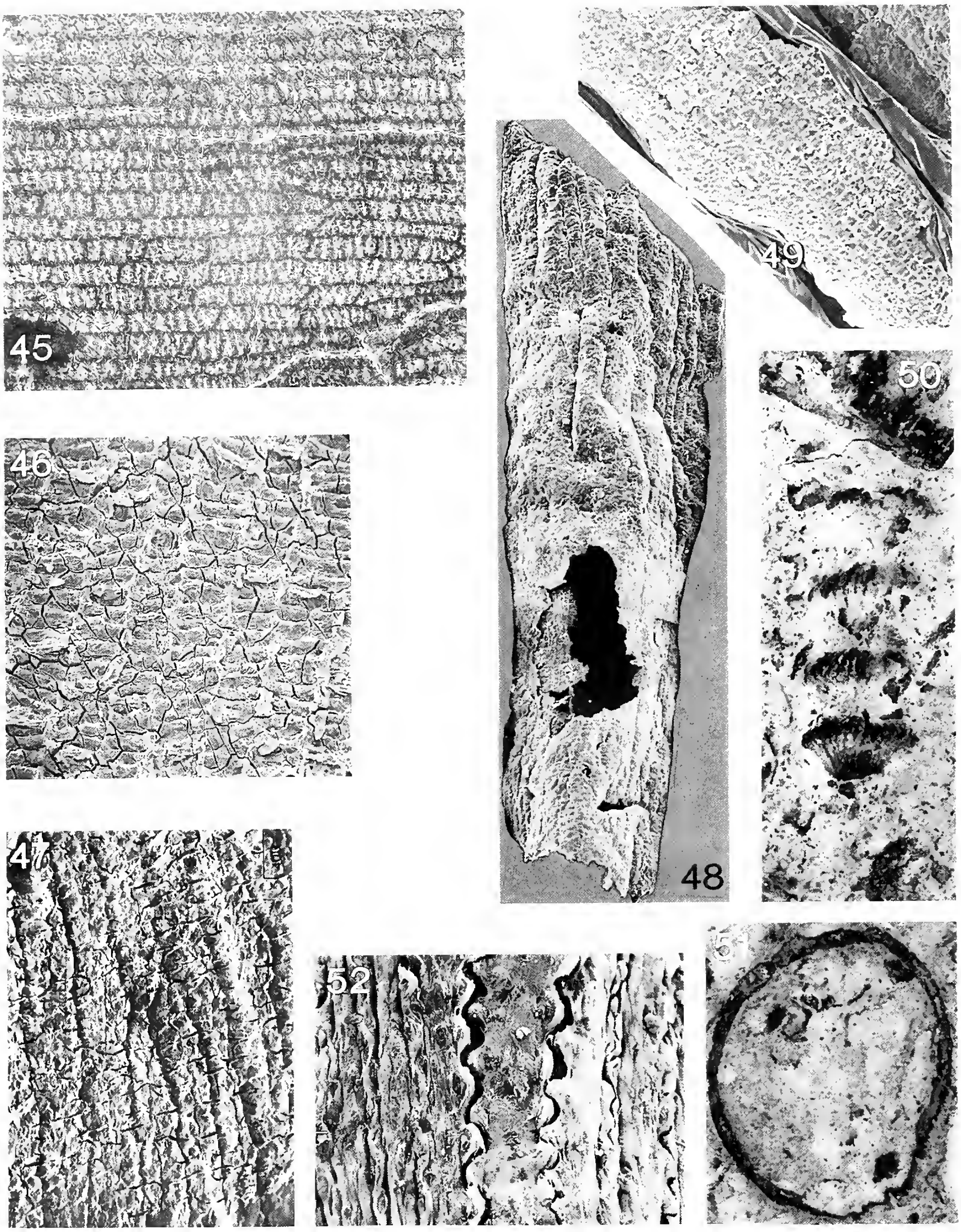
Members of the genus *Equisetum* subgenus *Hippochaete*, commonly known as the scouring rushes, are characterized by having hard, winter-green shoots which persist for up to three years. The rhizome has a large central canal and is never found with tubers. The aerial shoot has a relatively large number of leaves per node and the branches resemble the main shoot in being rounded and hollow. The stomata are arranged in one or two regular longitudinal files along the stem and are sunken in crater-like pits. The stomatal cells are non-beaded but there is coarse silica thickening around the rim of the crater (see Page 1972*a*).

It is quite obvious that *E. lyellii*, whilst displaying many of the features of the subgenus *Hippochaete* in its gross morphology, has stomata which both in distribution and structure are entirely typical of the subgenus *Equisetum*. Page (personal communication) considers that it should be regarded as at least subgenerically distinct from the two groups of modern species, i.e. as representing a now extinct third subgenus. Preliminary studies of the stomata of several Jurassic and Triassic species suggest that this subgenus may have been worldwide in the Mesozoic; see Page (1972*b*, 1974) for discussion of evolutionary evidence within the Equisetales and older articulates.

Suggested anatomical and morphological reconstructions of *Equisetites lyellii* are presented in Figs 38e and 67 respectively. The reconstructed transverse section of the aerial shoot internode (Fig. 38e) includes phloem and carinal canals which form in extant species by breakdown of the protoxylem during elongation. It seems reasonable to suppose that phloem was present between the arms of the crescent of metaxylem. The question of carinal canals is less clear as the presence of protoxylem elements in some of the bundles could be taken as an indication that these canals were absent.

The suggested reconstruction of *E. lyellii* (Fig. 67) is based on the new information given above, together with all the detailed measurements and field observations given by Allen (1941), though of necessity several features have been included for which there is absolutely no evidence. As with the reconstruction of *E. burchardtii* the choice between suggesting monomorphic or dimorphic habit was fairly, though not entirely, arbitrary. All extant members of the subgenus *Hippochaete* have only one kind of shoot but on balance we favour a dimorphic habit for *E. lyellii* for two reasons. The paucity of branches on aerial shoots in the fragment beds observed by Allen in the field (1941) must mean that many of the shoots were unbranched. The lack of a complete fertile cone but the relative abundance of isolated sporangiophores suggests that this part of the plant decayed rapidly on reaching maturity. One should also note that the sporangiophore heads of *E. lyellii* are rounded in shape, unlike modern species in which they become pentagonal as the result of close-packing. This further suggests a less robust structure, and we thus opt for the attractive notion of long, pale, fertile shoots bearing their delicate cones above the water, shedding their spores and soon becoming fragmented.

Comparison. Because of the exceptional material available for study this species is now known in more detail than any other Mesozoic member of the family. This makes useful comparisons even more difficult than before. The name

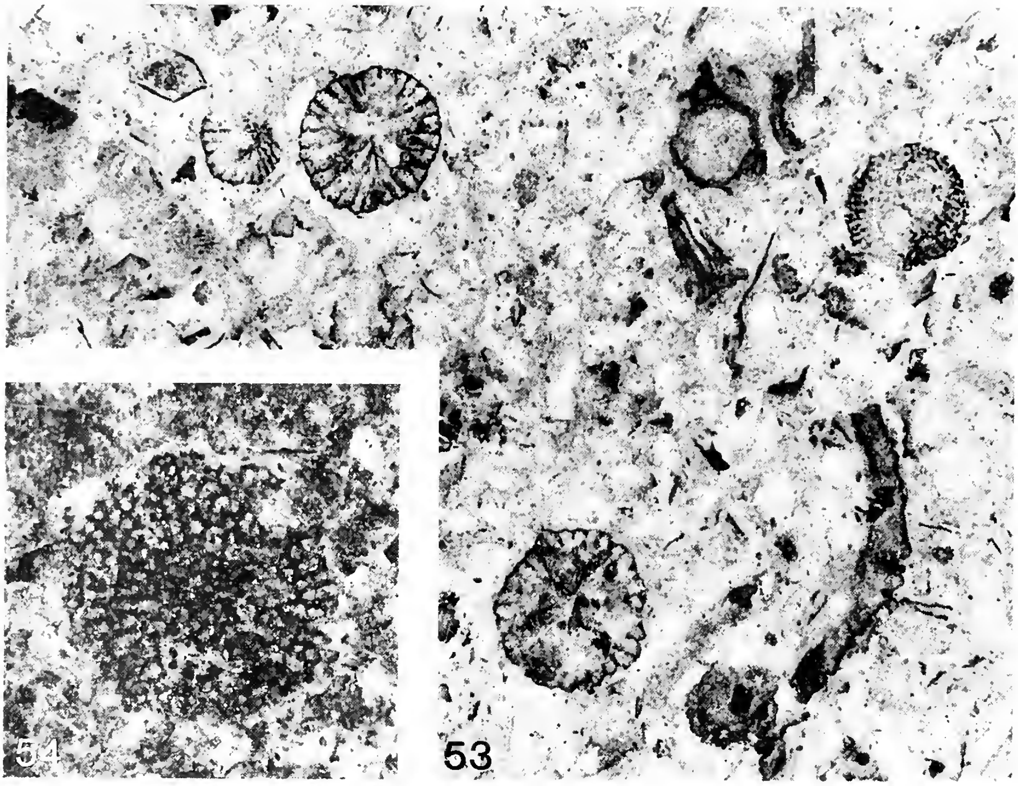


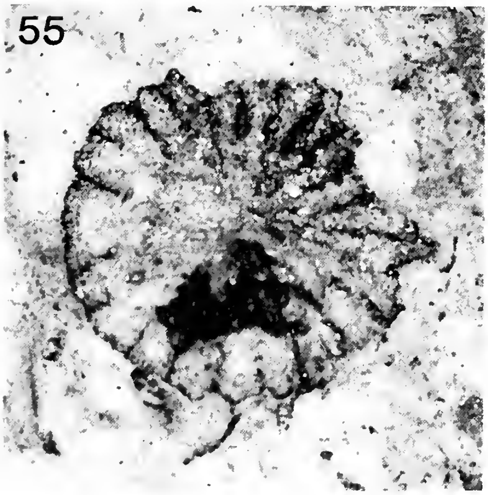
Figs 45–51 *Equisetites lyellii* (Mantell). All specimens from fragment beds. 45, rhizome cuticle naturally oxidized, showing transverse bars of thickening on cells; V.63075, × 100. 46, 47, similar pieces of cuticle in SEM; 46, inner surface, V.63060, × 250; 47, outer surface, V.63062, × 250. 48, small cylinder of cuticle presumed to be a branch borne by aerial shoot; V.63063, × 25. 49, piece of cuticle broken from middle of specimen in Fig. 48, in SEM showing cells matching those of rhizome (Figs 45, 46); × 100. 50, probable unexpanded shoot apparently with whorls of branches; V.63967, × 8. 51, hollow shoot broken off at surface of fragment bed; V.63064, × 10.

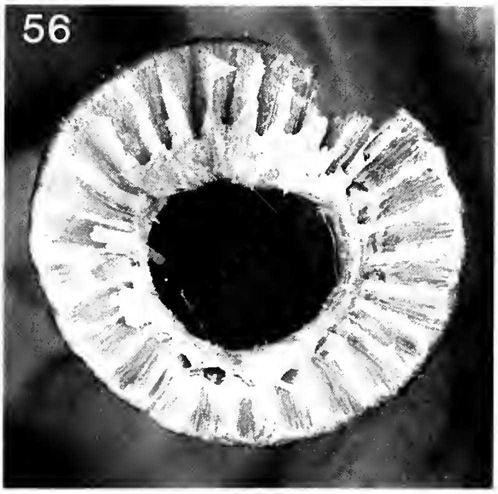
Fig. 52 *Equisetum telmateia* Ehrhart. Desilicified internode in living species, revealing elongate, sinuous cells similar to those of *E. lyellii*; × 1000.

Equisetites lyellii (Mantell) has been given to Lower Cretaceous equisetalean material from a number of countries worldwide, but at this stage it is impossible to assess the validity of these determinations. Some of them, such as the material from the Potomac Formation, U.S.A. (Fontaine 1889), are probably identical but new specimens are essential for study as Fontaine's originals are missing from the Smithsonian Institution.

The only other material known in comparable detail is that described by Gould (1968) from the Jurassic of Australia.

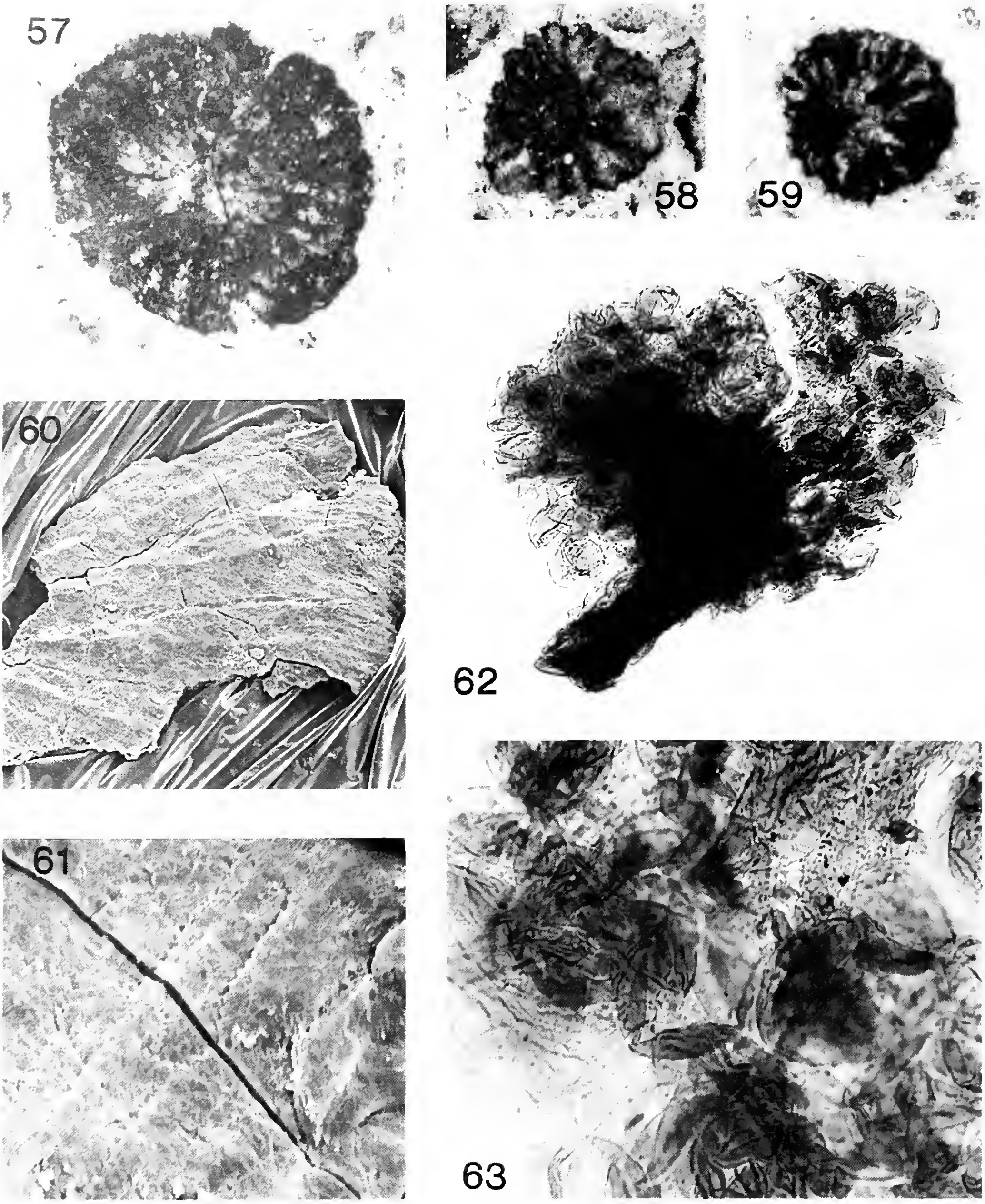






igs 53–55 *Equisetites lyellii* (Mantell). 53, typical surface of fragment bed photographed under paraffin showing nodal diaphragms etc.; V.63064, × 10. 54, spotted disc of type very common in fragment bed, derivation unknown; V.63069, × 20. 55, nodal diaphragm; V.63064, × 20.

ig. 56 *Equisetum telmateia* Ehrhart. 'Nodal diaphragm'; see p. 47 for discussion; × 8.



Figs 57–63 *Equisetites lyellii* (Mantell). 57–59, sporangiophore heads showing radiating ridges on outer surface; 57, V.63067; 58, V.63064; 59, V.63068; all × 20. 60, unmacerated portion of sporangiophore head in SEM, curved edge on right, surface ridges radiating from broken central point on left (background, heat-damaged sellotape); V.63065, × 100. 61, surface of same specimen showing cells with undulating walls very similar to rhizome cuticle; × 500. 62, 63, spore mass obtained by macerating sporangiophore head, presumed to be contents of a single sporangium, V.63066; 59, × 225; 60, × 700.

There are two species, *Equisetum laterale* Phillips and *Equisetum bryanii* Gould. Both are similar to *E. lyellii* in having scattered stomata and sinuous-walled epidermal cells with bars of thickening. It would be interesting to study this material again along with other Mesozoic species in the light of the phylogenetic considerations raised by the subgeneric status of *E. lyellii*.

SPORAE DISPERSAE

Genus *PILASPORITES* Balme & Hennelly

For remarks on *Pilasporites* see Batten, 1968.

Pilasporites allenii Batten Figs 64–66

1968 *Pilasporites allenii* Batten: 638, pl.123, figs 1–4, 6, 10–14.

DESCRIPTION. For the diagnosis and fully illustrated account of this species see Batten's (1968) original description. Figs 64–66, p. 56, are representative photomicrographs of these isolated dispersed spores.

The spores of *Pilasporites allenii* were spherical or subspherical in shape before being compressed in sediment. They consist of a comparatively thick exine (exospore) surrounded by a flimsy, crumpled, closely adhering perine (perispore) which commonly bears a surface deposit of scattered granules. Despite its fragile appearance the outer membrane is clearly tough and resistant to chemical treatment, including oxidation. The exine is unornamented and devoid of a trilete or monolete aperture (Figs 63–65). In these respects the spores are entirely comparable to those of extant *Equisetum* (see for example Gullvåg 1968, Lugardon 1970, Guervin *et al.* 1972, Good 1975, Tryon & Tryon 1982, Kurmann & Taylor 1984).

Despite the alete appearance, a darkened patch is displayed on some specimens (Figs 64, 65) which resembles the 'stopper' found by Lugardon (1970) in the wall of spores of extant *Equisetum maximum*, but its diameter is more than three times as great. In this respect it suggests a closer relationship to the proximal area of geologically older spores with diminutive triradiate marks that are referred to *Calamospora*. If it did function as an operculum, which is unlikely, then the mode of germination of the spores of Cretaceous *Equisetites* may have varied, because others clearly had a tendency to split, as commonly seen in acetolysed products of extant species. Where opened in this way the exine along the margins is often slightly folded inwards.

DISCUSSION. Acetolysis, a chemical method frequently used for preparing modern and Quaternary palynomorphs for examination by transmitted light microscopy, is known to dissolve the elaters of extant *Equisetum* spores which, when coiled, envelop the perispore. No Wealden specimens have yet been found with these extra-perinous elements. The possibility that they were removed during sediment diagenesis or by chemical treatment of rock samples in the laboratory has been mentioned previously by Batten (1968). He also suggested that they might not have had them in the first place. Similar spores were reported by Gould (1968) from cones of the Australian Jurassic species identified as *E. laterale* Phillips. These also lack elaters, as do specimens isolated much earlier by Halle (1908) from compressions of *Equisetites* and those encountered in cones found more recently by Vozenin-Serra & Laroche (1974, 1976).

The pre-Quaternary fossil record of vascular plant spores with elaters is limited to associations with some Carboniferous calamites (Wilson 1943, 1963, Baxter & Leisman 1967, Good & Taylor 1974, 1975, Good 1975, 1977) and with two equisetaleans, from the Middle Jurassic (Harris 1978) and early Tertiary (Chandler 1964). Sphenophyllalean products are quite different (Taylor 1986). The calamite spores are trilete with three distally attached elaters; they are not closely similar to those of modern *Equisetum*, which are alete and have four elaters. They are thought likely to represent the most mature and best preserved specimens, whereas contemporaneous cones that yield spores lacking elaters are considered to be immature (Good 1975, 1977). Although a triradiate mark is typically present on calamite spores (Hartung 1933) its presence does not necessarily distinguish them from those of the Equisetaceae. Both Carboniferous and early Mesozoic equisetalean species have yielded spores of similar character (see for example Halle 1908 and Gastaldo 1981).

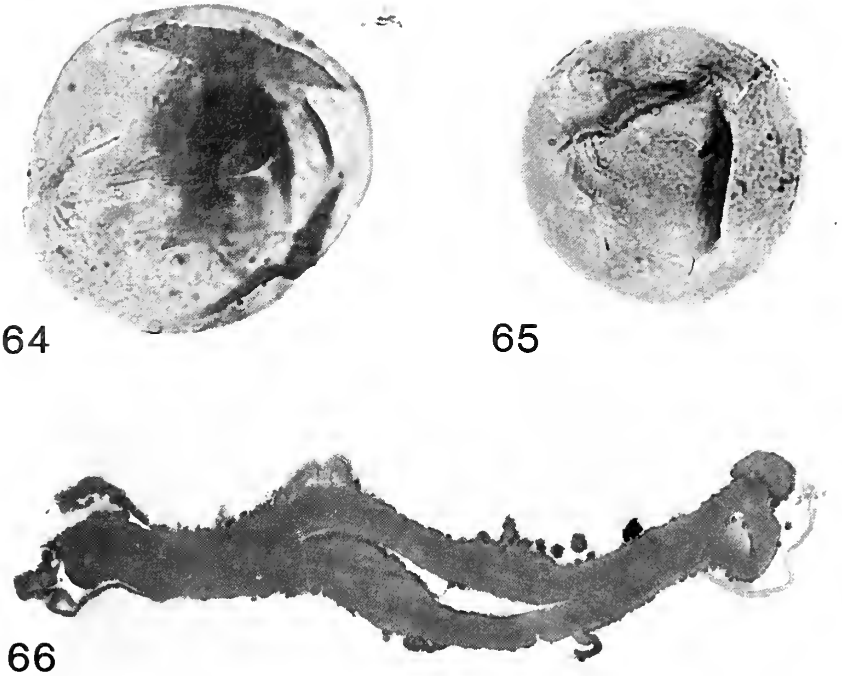
Harris (1978) found some round palynomorphs in rock matrix between sporangiophore heads of *Equisetum columnare* which seemed to bear fine threads resembling elaters. But he was not sure that they were produced by *E. columnare*, and he also noted that the threads visible on the two specimens he illustrated (Harris 1978: text-fig. 2D) were incomplete. By contrast the early Tertiary spores recovered from an *Equisetum* cone by Chandler (1964: plate 1, figs 3, 4) are remarkably similar to extant forms.

Did the spores of *Equisetites lyellii* bear elaters? If they did then surely one should find them preserved within the spore masses? Those remains of broken and decayed fertile cones which have been isolated from fragment partings without chemical treatment have so far failed to reveal any. Is this because they were immature at the time they were deposited (cf. Good 1975)? Hence, is the absence of elaters on specimens in masses a function of developmental factors, and on single and presumed fully mature spores because they decayed rapidly after dispersal? Or has the search proved fruitless because they were never developed? Species of *Equisetum* which produced elater-less spores could represent part of an extinct taxonomic grouping within the Equisetaceae, as suggested already on the basis of the morphology and anatomy of *E. lyellii*.

COMPARISON. Batten (1968, 1973) compared *Pilasporites allenii* with a number of dispersed miospores that had been referred previously to the Equisetaceae and with morphologically similar species which had not been linked to this family. Several additional records that fall into one or other of these categories are considered below.

Maljavkina (1956) referred triradiate spores she recovered from the Cretaceous of the eastern Gobi depression to a new, but invalid and superfluous, genus *Equisetacites*. Alete species included in different genera erected earlier by the same author (Maljavkina 1949) have also been linked by some Soviet palynologists to *Equisetites* or the Equisetaceae. Vinogradova (1971) described as new a palynomorph from the Jurassic of Mangyshlak and western Turkmenia which she named *Equisetites variabilis* (see also Bolkhovitina & Fokina 1971). McKellar (1974) erected *Peroaletes rugosus* for Jurassic spores from the Surat Basin of Australia; these appear to be similar to *Pilasporites allenii* but have a more rigid exine and lack the dark patch seen on some Wealden forms.

Burger (1976) identified *Concentrisporites hallei* (Nilsson) Wall from the Lower Cretaceous of the Great Artesian Basin of Queensland, Australia. This species was originally reported (as *Equisetosporites hallei*) from Rhaetian and early Jurassic rocks of Sweden and considered closely comparable to, if not identical with, the spores of *Equisetites* (*Equisetostachys*) *suecicus* (Nathorst) Halle (see Nilsson 1958: 66–67 and Batten 1968: 241). Similar, indeed probably identical, forms have been recorded from the Jurassic of France (Danzé-Corsin & Laveine 1963), Canada (Pocock 1970, referred to *Concentrisporites pseudosulcatus* (Danzé-Corsin & Laveine) Pocock) and Australia (Reiser & Williams 1969, identified as *Perinopollenites elatoides* Couper). More recently Taugourdeau-Lantz & Dubois (1979) described as new *Pilasporites petri* and *P. calabrensis* from the Middle Jurassic of Calabria, Italy. Both were considered to have probable equisetalean origins, whereas the spores referred to ?*Equisetum* by Mamczar (1986) are unlikely to have any connection with this group. Finally, a scanning electron micrograph of the surface of an inaperturate palynomorph, thought by



Figs 64–66 *Pilasporites allenii* Batten, the probable dispersed spore of *Equisetites lyellii* (Mantell). 64, 65, V.63073, × 1000. 64, spore showing subcircular patch of thickened exine and scattered granules on closely-adhering perine. 65, typical specimen of *P. allenii* with membranous perine closely enveloping and crumpled against the exine. 66, cross section of spore showing thick, homogeneous exine surrounded by a thin perine bearing scattered granular bodies; V.63074, × 4000.

Kedves (1979) to have possible algal origins and identified as *Psophosphaera intrapunctata* (Kedves) Kedves, displays the sort of crumpling and scattered granular bodies that characterize the perine of *Pilasporites allenii* (compare Batten 1973: pl. 42, figs 10, 11 with Kedves 1979: pl. 3, fig. 1). None of these palynomorphs is, however, unequivocally identical with the Wealden spores.

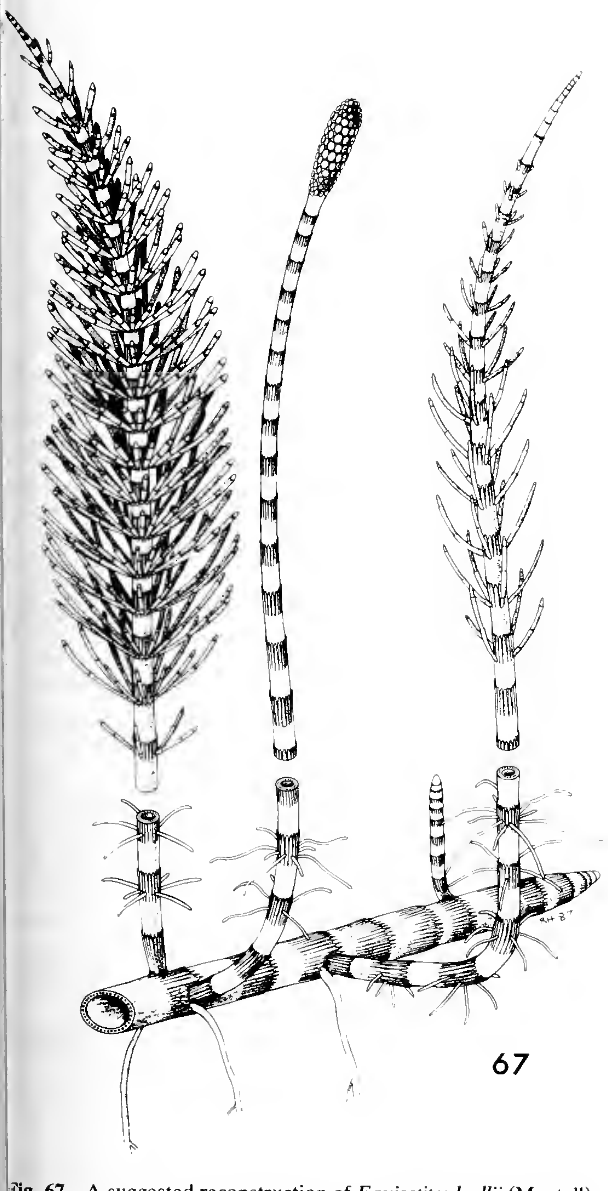
PALAEOENVIRONMENTAL SIGNIFICANCE

Where *Equisetites lyellii* is preserved in position of growth it is typically associated with thinly interbedded mudstones and siltstones. The latter commonly occur in lenticular units within the finer-grained deposits, forming the 'passage beds' of Allen (1959, 1976). These are subaqueous sedimentary accumulations and, although conveniently referred to as 'soil beds' for descriptive purposes, are generally not regarded as palaeosols *sensu stricto*. Allen, however, regards them as fossil aquatic soils at the 'wet end' of a continuous spectrum of soils, all supporting plants, from totally wet through reed-swamp and marsh to subaerial (1976 and personal communication). Well stratified weathering profiles indicating subaerial soils have been confirmed in the Wealden of northern France (Meyer 1976), but only suspected in southern England (Lake & Thurrell 1974, Allen 1976, 1981, Stewart 1981) where high rates of deposition and frequent erosion appear to have hindered their development. Red-mottled silts and clays with traces of roots in growth position and indications of iron-pan development in places imply fluctuating water tables, soil-forming alterations and local leaching, but exposure does not seem to have been long enough for weathering to have completed the pedogenic process.

All the *Equisetites lyellii* soil beds were probably under water to a depth of up to 0·5 m, if not permanently then at least more often than not. Possibly the plants could have withstood total immersion for short periods. The presence of only a few widely scattered stomata on the lower parts of the stems supports an aquatic habitat. By contrast, *Equisetum burchardtii* may have grown in better-drained sediment more often exposed or above the water table. This is suggested by its occurrence in sandier facies and by the presence of tubers on the rhizomes of the plant. In extant species of *Equisetum*, these are formed and consumed on a seasonal basis but it is possible that in *E. burchardtii* this happened in response to alternating wet and dry periods. Seasons need not be invoked. Tubers characterize only those members of the subgenus *Equisetum* which grow on dry land and have deciduous aerial parts. It follows, therefore, that the Wealden species was probably a herbaceous perennial which might well have died when its habitat became swampy or permanently flooded.

For *Equisetites lyellii* the combination of a subtropical climate and the preferred habitat being standing water suggests that, despite fluctuations in rainfall (Allen 1976, 1981, Sladen & Batten 1984), die-back occurred only sporadically during periods of drought and was not an annual event. This is consistent with the 'winter-green' interpretation of the species suggested and discussed here.

The plants are visualized as occupying extensive areas of the watery late Purbeck and Wadhurst mud-plains where



67

ig. 67 A suggested reconstruction of *Equisetites lyellii* (Mantell) as discussed in the text. Approximately × ½. © Joan Watson, 1990.

leposition took place slowly in quiet conditions. Some (e.g. he Brede Soil Bed) were clearly 'reed-swamp' communities ringing the shores of lakes and bays (Allen 1959). The hizomatous system of growth enabled communities not only o spread rapidly and keep pace with changes in water depth ut also prevented mud from smothering them by keeping up vith sedimentation. The scattered occurrences of *E. lyellii* in ther Wealden deposits (e.g. the Grinstead Clay) and the endency for their stems and rhizomes to be more slender may reflect a response to conditions that were less conducive to colonization and vigorous growth. These probably included slightly raised salinities.

The arenaceous units of the Wealden succession, whether interpreted as mainly representing sandy braidplains (Allen 1976, 1977, 1981) or, as previously invoked, deltaic accumulations on a large or small scale (e.g. Allen 1959, 1962, 1976, 1977, Lake 1977, Worssam 1977), were clearly inhospitable to *Equisetites* and *Equisetum*. Recent work on the distribution of dinoflagellate cysts and other algae (Batten 1982, 1985 and in preparation; Harding 1986) suggests that the Wadhurst waters were generally fresher than those of Grinstead and Weald Clay times. This could account for the scarcity of equisetalean remains in the younger formations which otherwise represent deposition in broadly similar mud-plain conditions. It could also confirm earlier suggestions (e.g. Allen 1959, Allen *et al.* 1973, Batten 1968, 1975, 1977) that the plants grew only where the water was usually fresh and hence provide an answer to the question—what killed off the established communities?

It is difficult to follow their upward development. Erect stems are commonly terminated by fragment partings, which suggests that the plants were destroyed catastrophically. Although it is possible that they could have been overwhelmed by a sudden influx of a large amount of sediment, there is generally no evidence for this. Even if it could be demonstrated, attempts by the plants to grow up through the overburden would surely be preserved. Allen (1938, 1959) found some evidence for this but it has not been proved beyond doubt. Rhizomes of modern *Equisetum* are able to grow upwards and continue above ground as aerial stems and have been found as much as fifteen feet (4·5 m) below ground in an evenly soft substrate, attached to the upper layers by thin vertical rhizomes. The fragment partings may indicate physical damage to communities (Allen 1947, 1959, Batten 1968) or sometimes merely consist of partly decomposed litter of old stems. Total destruction is not necessarily implied. Nevertheless this did take place, and the prime cause is likely to have been inundation with saline water. Complete immersion by fresh water for an extended period (years rather than months) is also a possibility. The former interpretation is supported by evidence from the ostracod and molluscan assemblages (e.g. Allen 1959, 1976, Allen *et al.* 1973, Anderson *et al.* 1967) and phytoplankton (Batten in preparation) recovered from beds that lack *E. lyellii*. Once the plants had died the stems broke off and sediment dropped into the hollow open ends, thus enhancing their chances of being preserved *in situ*.

ACKNOWLEDGEMENTS. During the long time this paper has been in preparation many people have assisted us and we thank them all most warmly. We are particularly indebted to Dr C. N. Page of the Royal Botanic Garden, Edinburgh, who put at our disposal his specialist knowledge of *Equisetum* with great enthusiasm. We thank Mr Richard Hartley who has skilfully brought our reconstructions to life. To Professor Perce Allen who has been most generous with material and information and has waited longer than anyone we offer our special thanks. We hope that his patience has now been rewarded.

REFERENCES

Allen, P. 1938. The Ashdown Sand–Wadhurst Clay Junction. *Geological Magazine*, London, **75**: 560–561.

—— 1941. A Wealden soil bed with *Equisetites lyelli* (Mantell). *Proceedings of the Geologists' Association*. London, **52**: 362–374.

—— 1947. Notes on Wealden fossil soil-beds. *Proceedings of the Geologists' Association*, London, **57**: 303–314.

—— 1959. The Wealden environment: Anglo-Paris Basin. *Philosophical Transactions of the Royal Society*, London, **242** (B): 283–346.

—— 1962. The Hastings Beds deltas: recent progress and Easter field meeting report. *Proceedings of the Geologists' Association*, London, **73**: 219–243.

—— 1976. Wealden of the Weald: a new model. *Proceedings of the Geologists' Association*, London, **86** [for 1975]: 389–437.

—— 1977. Wealden of the Weald—a new model. Reply. *Proceedings of the Geologists' Association*, London, **87** [for 1976]: 433–442.

—— 1981. Pursuit of Wealden models. *Journal of the Geological Society*, London, **138**: 375–405.

——**, Keith, M. L., Tan, F. C. & Deines, P.** 1973. Isotopic ratios and Wealden environments. *Palaeontology*, London, **16**: 607–621.

Alvin, K. L. & Hluštik, A. 1979. Modified axillary branching in species of the fossil genus *Frenelopsis*: a new phenomenon among conifers. *Botanical Journal of the Linnean Society*, London, **79**: 231–241.

Anderson, F. W., Bazley, R. A. B. & Shephard-Thorn, E. R. 1967. The sedimentary and faunal sequence of the Wadhurst Clay (Wealden) in boreholes at Wadhurst Park, Sussex. *Bulletin of the Geological Survey of Great Britain*, London, **27**: 171–235.

Batten, D. J. 1968. Probable dispersed spores of Cretaceous *Equisetites*. *Palaeontology*, London, **11**: 633–642.

—— 1973. Palynology of early Cretaceous soil beds and associated strata. *Palaeontology*, London, **16**: 399–424.

—— 1975. Wealden palaeoecology from the distribution of plant fossils. *Proceedings of the Geologists' Association*, London, **85** [for 1974]: 433–458.

—— 1977. Wealden of the Weald—a new model. Written discussion of a paper previously published. *Proceedings of the Geologists' Association*, London, **87** [for 1976]: 431–433.

—— 1982. Palynofacies and salinity in the Purbeck and Wealden of southern England. *In* Banner, F. T. & Lord, A. R. (eds), *Aspects of Micropalaeontology*: 278–308. London.

—— 1985. Two new dinoflagellate cyst genera from the non-marine Lower Cretaceous of Southeast England. *Neues Jahrbuch für Geologie und Paläontologie. Monatshefte*, Stuttgart, **1985/7**: 427–437.

Baxter, R. W. & Leisman, G. A. 1967. A Pennsylvanian calamitean cone with *Elaterites triferens* spores. *American Journal of Botany*, Lancaster, Pa., **54**: 748–754.

Berry, E. W. 1911. *In: Maryland Geological Survey. Lower Cretaceous*. 622 pp. Baltimore.

Bolkhovitina, N. A. & Fokina, N. I. (eds) 1971. Jurassic and Early Cretaceous spores and pollen of central Asia. *Trudy̆ Vsesoyuznogo Neftyanogo Nauchno-Issledovatel'skogo Geologo-Razvedochnogo Instituta*, Moscow, **104**. 214 pp. [In Russian].

Browne, I. M. P. 1939. Anatomy of the aerial axes of *Equisetum kansanum*. *Botanical Gazette*, Chicago, **101**: 35–50.

Burger, D. 1976. Some Early Cretaceous plant microfossils from Queensland. *Bulletin Bureau of Mineral Resources, Geology and Geophysics, Australia*, Melbourne, **160**: 1–22.

Chandler, M. E. J. 1964. *The Lower Tertiary Floras of Southern England. 4. A summary and survey of findings in the light of recent botanical observations*. xii + 151 pp. British Museum (Natural History), London.

Chatterjee, J. 1964. Stomata in *Equisetum ramosissimum* Desf. subsp. *ramosissimum. Phytomorphology*, Delhi, **14**: 451–457.

Danzé-Corsin, P. & Laveine, J.-P. 1963. Flore infraliasique du Boulonnais. B—Microflore. *In* Briche, P., Danzé-Corsin, P. & Laveine, J.-P., *Mémoires de la Societé géologique du Nord*, Lille, **13**: 57–110.

Dunker, W. 1846. *Monographie der norddeutschen Wealdenbildung*. xxxii + 83 pp. Braunschweig.

Ettingshausen, C. von 1852. Beitrag zur naheren Kenntniss der Flora der Wealdenperiod. *Abhandlungen der Geologischen Bundesanstalt*, Wien, **1**: 1–32.

Fontaine W. M. 1889. The Potomac or Younger Mesozoic Flora. *Monographs of the U.S. Geological Survey*, Washington, **15**: 1–377.

—— 1905. *In* Ward, L. F., Status of the Mesozoic Floras of the United States. *Monographs of the U.S. Geological Survey*, Washington, **48**. 616 pp.

Gastaldo, R. A. 1981. *Palaeostachya dircei* n. sp., an authigenically cemented equisetalean strobilus from the Middle Pennsylvanian of southern Illinois. *American Journal of Botany*, Lancaster, Pa, **68**: 1306–1318.

Good, C. W. 1975. Pennsylvanian-age calamitean cones, elater-bearing spores, and associated vegetative organs. *Palaeontographica*, Stuttgart, **153** (B): 28–99.

—— 1977. Taxonomic and stratigraphic significance of the dispersed spore genus *Calamospora. In* Romans, R. C. (ed.), *Geobotany*: 43–64. New York.

—— **& Taylor T. N.** 1974. The establishment of *Elaterites triferens* spores in *Calamocarpon insignis* microsporangia. *Transactions of the American Microscopical Society*, Lancaster, Pa., **93**: 148–151.

—— —— 1975. The morphology and systematic position of calamitean elater-bearing spores. *Geoscience and Man*, Baton Rouge, La, **11**: 133–139.

Gould, R. E. 1968. Morphology of *Equisetum laterale* Phillips, 1829, and *E. bryanii* sp. nov. from the Mesozoic of south-eastern Queensland. *Australian Journal of Botany*, Melbourne, **16**: 153–176.

Guervin, C., Laroche, J., Le Coq, C. & Bossy, J.-P. 1972. La spore de l'*Equisetum arvense* L.: stéréostructure de la périspore et mode d'insertion des élatères. *Compte rendu hebdomadaire de séances de l'Académie des Sciences*, Paris, **274** (D): 3385–3386.

Gullvåg, B. M. 1968. On the fine structure of the spores of *Equisetum fluviatile* var. *verticillatum* studied in the quiescent, germinated and non-viable state. *Grana Palynologica*, Stockholm, **8**: 23–69.

Halle, T. G. 1908. Zur Kenntnis der Mesozoischen Equisetales Schwedens. *Kungliga Svenska Vetenskapsakademiens Handlingar*, Uppsala & Stockholm, **43**. 38 pp.

Harding, I. C. 1986. An Early Cretaceous dinocyst assemblage from the Wealden of southern England. *Special Papers in Palaeontology*, London, **35**: 95–109.

Harris, T. M. 1961. *The Yorkshire Jurassic Flora*, **1**. Thallophyta Pteridophyta. ix + 212 pp. British Museum (Natural History), London.

—— 1978. A reconstruction of *Equisetum columnare* and notes on its elator-bearing spores. *Palaeobotanist*, Lucknow, **25**: 120–125.

—— 1981. Burnt ferns from the English Wealden. *Proceedings of the Geologists' Association*, London, **92**: 47–58.

Hartung, W. 1933. Die Sporenverhältnisse der Calamariaceen. *Arbeiten aus dem Institut für Paläobotanik und Petrographie der Brennsteine*, Berlin, **3**: 96–149.

Hauke, R. L. 1957. The stomatal apparatus of *Equisetum*. *Bulletin of Torrey Botanical Club*, New York, **84**: 178–181.

Hunter, W. P. 1835. Some Account of the Limestone Quarries and Petrifying Spring at Pounceford, in Sussex; with Preliminary Remarks on the Wealden Rocks. *Loudon's Magazine of Natural History*, London, **8**: 597–608.

Hyde, H. A., Wade A. E. & Harrison S. G. 1969. *Welsh Ferns, Clubmosses, Quillworts and Horsetails*. xii + 178 pp. National Museum of Wales, Cardiff.

Kedves, M. 1979. Scanning electron-microscopical investigations into the sporomorphes [*sic*] of the coal layers in the Dorog Basin. *Acta Biologica*, Szeged, **25**: 35–44.

Kennedy, W. J. & MacDougall, J. D. S. 1969. Crustacean burrows in the Weald Clay (Lower Cretaceous) of south-eastern England and their environmental significance. *Palaeontology*, London, **12**: 459–471.

Kurmann, M. H. & Taylor, T. N. 1984. Comparative ultrastructure of the sphenophyte spores *Elaterites* and *Equisetum*. *Grana*, Stockholm, **23**: 109–116.

Lake, R. D. 1977. Wealden of the Weald—a new model. Written discussion of a paper previously published. *Proceedings of the Geologists' Association*, London, **87** [for 1976]: 427–429.

—— **& Thurrell, R. G.** 1974. The sedimentary sequence of the Wealden Beds in boreholes near Cuckfield, Sussex. *Report of the Institute of Geological Sciences*, London, **74/2**. 60 pp.

Lugardon, B. 1970. Sur la structure fine des parois sporales d'*Equisetum maximum* Lamk. *Pollen et spores*, Paris, **11** [for 1969]: 449–474.

Maljavkina, V. S. 1949. [Index of spores and pollen; Jurassic–Cretaceous]. *Trudy̆ Vsesoyuznogo Neftyanogo Nauchno-Issledovatel'skogo Geologo-Razvedochnogo Instituta*, Moscow, **33**. 139 pp. [In Russian].

—— 1956. [Spores and pollen of the Lower Cretaceous of the eastern Gobi depression.] *Trudy̆ Vsesoyuznogo Neftyanogo Nauchno-Issledovatel'skogo Geologo-Razvedochnogo Instituta*, Moscow, **119**. 163 pp. [In Russian].

Mamczar, J. 1986. Palynostratigraphy of the uppermost Jurassic and Lower Cretaceous in the Polish Lowlands. *Prace Instytut Geologiczny*, Warsaw, **116**. 53 pp. [In Polish, summaries in Russian and English].

Mantell, G. 1827. *Illustrations of the Geology of Sussex*. xii + 92 pp., 20 pls. London.

—— 1833. *The Geology of the S.E. of England*. xix + 415 pp. London.

McKellar, J. L. 1974. Jurassic miospores from the upper Evergreen Formation, Hutton Sandstone, and basal Injune Creek Group, north-eastern Surat Basin. *Publications of the Geological survey of Queensland*, Brisbane, **361** (*Palaeontological Papers* **35**). 89 pp.

Meyer, R. 1976. Continental sedimentation, soil genesis and marine transgression in the basal beds of the Cretaceous in the east of the Paris Basin. *Sedimentology*, Oxford, **23**: 235–253.

Moore, R. 1941. The 'leaf gap' in *Equisetum*. *Canadian Journal of Research*, Ottawa, **19** (C): 80–84.

Nilsson, T. 1958. Über das Vorkommen eines mesozoischen Sapropelgesteins in Schonen. *Lunds Universitets årsskrift*, Lund, (N.F.) **2** (54). 111 pp.

Page, C. N. 1972*a*. An assessment of inter-specific relationships in *Equisetum* subgenus *Equisetum*. *New Phytologist*, Cambridge, **71**: 355–369.

—— 1972*b*. An interpretation of the morphology and evolution of the cone and shoot of *Equisetum*. *Botanical Journal of the Linnean Society*, London, **65**: 359–397.

—— 1974. *Equisetum* subgenus *Equisetum* in the Sino-Himalayan Region—a preliminary taxonomic and evolutionary appraisal. *Fern Gazette*, London, **11**: 25–47.

Parihar, N. S. 1965. *An Introduction to Embryophyta*, **II**. *Pteridophytes*. 272 pp. Allahabad.

Pocock, S. A. J. 1970. Palynology of the Jurassic sediments of western Canada, Part 1. Terrestrial species. *Palaeontographica*, Stuttgart, **130** (B): 12–136.

Reiser, R. F. & Williams, A. J. 1969. Palynology of the Lower Jurassic sediments of the northern Surat Basin, Queensland. *Publications of the Geological Survey of Queensland*, Brisbane, **339** (*Palaeontological Papers* **15**). 24 pp.

Riegel, W., Wilde, V. & Pelzer, G. 1986. Erste Ergebnisse einer paläobotanischen Grabung in der fluviatilen Wealden-Fazies des Osterwaldes bei Hannover. *Courier Forschungsinstitut Senckenberg*, Frankfurt-am-Main, **86**: 137–170.

Schenk, A. 1871. Beiträge zur flora der Vorwelt. IV. Die flora der nordwestdeutschen Wealdenformation. *Palaeontographica*, Stuttgart, **19**: 203–262.

—— 1876. Beiträge zur Flora der Vorwelt. V. Zur Flora der nordwestdeutschen Wealdenformation. *Palaeontographica*, Stuttgart, **23**: 157–163.

Seward, A. C. 1894. The Wealden Flora. I. Thallophyta–Pteridophyta. *Catalogue of Mesozoic Plants in the Department of Geology, British Museum (Natural History)*. xxxvii + 179 pp. London.

—— 1913. A contribution to our knowledge of Wealden floras with especial reference to a collection of plants from Sussex. *Quarterly Journal of the Geological Society of London*, **69**: 85–116.

Sladen, C. P. & Batten, D. J. 1984. Source-area environments of Late Jurassic and Early Cretaceous sediments in southeast England. *Proceedings of the Geologists' Association*, London, **95**: 149–163.

Sternberg, G. K. 1833. *Versuch einer geognostischen botanischen Darstellung der Flora der Vorwelt* **2** (5, 6): 1–80. Leipzig & Prague.

Stewart, D. J. 1981. A meander-belt sandstone of the Lower Cretaceous of Southern England. *Sedimentology*, Oxford, **28**: 1–20.

[Stokes, C. & Webb, P. B.] 1824. *In* Mantell, G., Description of some Fossil Vegetables of the Tilgate Forest in Sussex. *Transactions of the Geological Society of London* (ser. 2), **1**: 423–426 [The authors' names do not appear in this paper].

Taugourdeau-Lantz, J. & Dubois, R. 1979. Données palynologiques sur le Jurassique calabrais: argument pour le rapprochement Afrique–Europe et importance de nouvelles espèces de spores d'Equisetales. *Revue de Micropaléontologie*, Paris, **21**: 208–220.

Taylor, W. A. 1986. Ultrastructure of sphenophyllalean spores. *Review of Palaeobotany and Palynology*, Utrecht, **47**: 105–128.

Topley, W. 1875. *The Geology of the Weald*. xiv + 503 pp., 2 maps. London, Memoirs of the Geological Survey, England and Wales.

Tryon, R. M. & Tryon, A. F. 1982. *Ferns and allied plants (with special reference to tropical America)*. xii + 857 pp. New York.

Vinogradova, K. V. 1971. [Stratigraphy and palynology of Jurassic oil and gas bearing deposits of Mangyshlak and western Turkmenia]. *Academiya Nauk SSSR, Institut Geologii i Razrabotki Goryuchikh Iskopaemykh*. 71 pp. [In Russian].

Vozenin-Serra, C. & Laroche, J. 1974. Intérêt phylogénétique et stratigraphique de la découverte d'une Equisétacée fossile au Cambodge. *Compte rendue hebdomadaire des séances de l'Académie des sciences*, Paris, **279** (D): 41–43.

—— —— 1976. Presence d'une Equisétacée dans les formations de Chrès—Cambodge occidental. *Palaeontographica*, Stuttgart, **159** (B): 158–166.

Watson, J. 1983. Two Wealden species of *Equisetum* found *in situ*. *Acta Palaeontologica Polonica*, Warsaw, **28**: 265–269.

Wilson, L. R. 1943. Elater-bearing spores from the Pennsylvanian strata of Iowa. *American Midland Naturalist*, Notre Dame, Ind., **30**: 518–523.

—— 1963. *Elaterites triferens* from a Kansas coal ball. *Micropalaeontology*, New York, **9**: 101–102.

Worssam, B. C. 1977. Wealden of the Weald—a new model. Written discussion of a paper previously published. *Proceedings of the Geologists' Association*, London, **87** [for 1976]: 429–430.

APPENDIX: STRATIGRAPHIC OCCURRENCES

Details of specimens figured in this paper and other notable material not figured here.

Figure	Collection	Spec.No.	Locality	Horizon	Comments
Equisetum burchardtii					
1, 2, 3	Humboldt	57	Harrel bei Bückeburg	Berriasian	Neotype. Figd Watson 1983: pl.13, fig.1
4	,,	6	,,	,,	Figd Watson 1983: pl. 13, fig. 2
5, 6, 7, 8	,,	7	,,	,,	
9	B.M.(N.H.)	V.1070	Prob. Ecclesbourne, nr Hastings, E. Sussex	?Ashdown Beds	Figd Watson 1983: pl. 13, fig. 3
10	Humboldt	88	Harrel bei Bückeburg	Berriasian	Figd Schenk 1871: pl. 30, fig. 1
11	,,	87	,,	,,	
12	,,	85	,,	,,	
unfigured	B.M.(N.H.)	V.1070a	Ecclesbourne, E. Sussex	?Ashdown Beds	
,,	,,	V.2730b	,,	,,	Rufford Colln.
,,	Humboldt	1984/745	Harrel bei Bückeburg	Berriasian	Nice erect stems.
Equisetites yokoyamae					
13	B.M.(N.H.)	V.2335	Ecclesbourne, E. Sussex	?Ashdown Beds	Figd Seward 1894: fig. 3 (with incorrect specimen number) and fig. 3*
unfigured	,,	V.2834	Bexhill, E. Sussex	,,	Very small tubers and thin rhizomes discussed in text, p. 42.
Equisetites lyellii					
15	Sedgwick	K.2221	Brede, E. Sussex	Wadhurst Clay, Brede Soil Bed	Figd Allen 1941: pl. 24A; Watson 1983: pl. 13, fig. 4.
16	B.M.(N.H.)	3605	Poundsford, E. Sussex	top Purbeck	Lectotype. Figd Mantell 1833: 245, fig. 3.
17	,,	39123	,,	,,	Figd Mantell 1833: 245, fig. 2.
18, 27	,,	V.710	St Leonards, E. Sussex	Ashdown Beds	Very well preserved epidermis.
19	,,	V.59	,,	,,	Figd Seward 1894: pl. 1, fig. 4.

Figure	**Collection**	**Spec.No.**	**Locality**	**Horizon**	**Comments**
Equisetites lyellii, cont.					
20	B.M.(N.H.)	V.45457	SE Ashurst Wood, E. Grinstead, W. Sussex TQ 412367	Wadhurst Clay, Balcombe Soil Bed	Coll. C.H. Shute & P. J. Whybrow.
21, 22	,,	V.51137	,,	,,	Thickest known rhizome.
23	Sedgwick	K.2139	Baldslow Wood, Westfield, E. Sussex.	Wadhurst Clay, Brede Soil Bed	Figd Allen 1947: fig. 57A.
24	B.M.(N.H.)	V.63058	East Grinstead, W. Sussex. TQ 377387	Wadhurst Clay, High Brooms Soil Bed	Coll. C. H. Shute
25, 26, 28	,,	26a, V.63070 26b, V.28643 26c, V.63071 26d, V.63072	High Brooms Brick & Tile Co. pit, Nr Tunbridge Wells, Kent. TQ 417594	Wadhurst Clay, High Brooms Soil Bed	Coll. J. E. Owen
29	,,	V.63059	¼ mile S of Ashurst Wood, W. Sussex TQ 419364	Wadhurst Clay, High Brooms Soil Bed	Coll. C. H. Shute & P.J. Whybrow.
30–38 + other unfigd specs.	,,	V.44948 *et seqq.*, see Figs	,,	,,	Coll. P. J. Whybrow. Slides made from nodule.
39, 41, 42	,,	V.63060	Cuckfield No. 1 Borehole	Wadhurst Clay	42 figd Watson 1983: pl. 14, fig. 12
40	,,	V.63076	Danehill, W. Sussex TQ 382266	,,	Figd Watson 1983: pl. 14, fig. 11
45	,,	V.63075	,,	,,	Figd Watson 1983: pl. 14, fig. 2
46	,,	V.63060	Cuckfield No. 1 Borehole	,,	Figd Watson 1983: pl. 14, fig. 3
47	,,	V.63062	,,	,,	
48, 49	,,	V.63063	,,	,,	
50, 57	,,	V.63067	East Grinstead, W. Sussex. TQ 377387	Wadhurst Clay, frag. parting above High Brooms Soil Bed	50 figd Watson 1983: pl. 14, fig. 4
51, 53, 55, 58	,,	V.63064	,,	,,	53 figd Watson 1983: pl. 14, fig. 5.
54	,,	V.63069	,,	,,	
59	,,	V.63068	,,	,,	Figd Watson 1983: pl. 14, fig. 6.
60, 61	,,	V.63065	Cuckfield No. 1 Borehole	Wadhurst Clay	61 figd Watson 1983: pl. 14, fig. 9.
62, 63	,,	V.63066	,,	,,	63 figd Watson 1983: pl. 14, fig. 10.
64, 65	,,	V.63073	Danehill, W. Sussex	,,	
66	,,	V.63074	,,	,,	
unfigured	,,	3599	prob. Poundsford, E. Sussex	? top Purbeck	Mantell Colln. Rhizomes perfectly circular in cross section
,,	,,	38375	,,	,,	,,
,,	,,	10837	,,	,,	,,
,,	,,	38375	,,	,,	,,
,,	,,	V.60511	SE Ashurst Wood, W. Sussex	Wadhurst Clay	Longest rhizome spec. in Museum collns, 23 cm long with 16 internodes.

Bull. Br. Mus. nat. Hist. (Geol.) **46**(1): 61–152

Issued 31 May 1990

Cretaceous Bryozoa from the Faringdon Sponge Gravel (Aptian) of Oxfordshire

L. J. PITT

1 Lancaster Road, North Harrow, Middlesex HA2 7NN

P. D. TAYLOR

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

CONTENTS

Synopsis. The rich bryozoan fauna of the Faringdon Sponge Gravel is the most diverse known from the Aptian. Forty-nine species of cyclostome bryozoans and one species of cheilostome bryozoan are described in this systematic account, which revises the work of Canu & Bassler (1926), making extensive use of SEM to study type and other specimens. The following taxa are described for the first time: *Proboscinopora* gen. nov. (type species *Proboscina divisi* Vine), *Paracrescis* gen. nov. (type species *Paracrescis boardmani* sp. nov.), *'Stomatopora' melvillei* sp. nov., *Stomatoporina alternata* sp. nov., *Filisparsa gasteri* sp. nov., *Collapora hillmeri* sp. nov., *Hyporosopora constricta* sp. nov., *H. larwoodi* sp. nov., *H. mantelli* sp. nov., *Tholopora dightoni* sp. nov., and *T. hastingsae* sp. nov. A dichotomous key is given to assist species identification. Remarks are made concerning generic concepts and ranges of genera. A type species is designated for the genus *Reptomulticava* d'Orbigny, 1854.

Lectotypes are selected for the following species: *Ceata granulata* (Canu & Bassler), *Clausa zonifera* Canu & Bassler, *Entalophoroecia quadripartita* (Canu & Bassler), *Heteropora keepingi* Gregory, *Laterocavea intermedia* Canu & Bassler, *Meliceritites cunningtoni* (Gregory), *M. transversa* Canu & Bassler, *Petalopora cunningtoni* Gregory, *Plagioecia spissa* (Gregory), *Reptoclausa hagenowi* (Sharpe), and *Tetrocycloecia multiporosa* Canu & Bassler.

Aspects of bryozoan palaeoecology and preservation are discussed. A wide range of colony-forms occurs at Faringdon. Arborescent colonies with narrow cylindrical branches dominate, but more robust erect forms are also present, and encrusting colony-forms abound on sponge, shell and pebble substrates. Foliaceous colony-forms are notable for their extreme rarity. The richness of the bryozoan fauna suggests episodic sedimentation in an environment well provided with nutrient-laden currents, possibly at water depths of 100 m or more. Varying amounts of abrasion of fragmented colonies occurred prior to burial. Whereas some specimens are in pristine condition, diagenetic overgrowths of calcite obscures surface details in others.

The Faringdon bryozoan fauna contains a few species in common with faunas of similar age from south-eastern France and western Switzerland, and with poorly-known Lower Greensand faunas from elsewhere in England. However, other species appear to be endemics.

INTRODUCTION

The Sponge Gravels of Faringdon in Oxfordshire have been worked for at least three hundred years and their rich fauna of Aptian fossils is well known. The earliest recorded collection is that made by Edward Lhuyd (see Edmonds 1973), who was Keeper of the Ashmolean Museum, Oxford between 1690 and 1709. In the early 19th Century, Gideon Mantell collected at Faringdon, but in spite of the fact that many bryozoans collected by him survive in the BM(NH), he made no mention of bryozoan species in either edition (1844, 1854) of his 'The Medals of Creation…'. Sharpe collected extensively at Faringdon and listed 44 bryozoan species in a publication of 1854. Unfortunately he determined his material using d'Orbigny's 'Terrains Crétacés' (1851–54), and his misidentifications led him to believe that the deposit was a remanié of Danian age. Sharpe was the first geologist to describe from Faringdon a new species of bryozoan: *Lopholepis hagenowi* = *Reptoclausa hagenowi* (Sharpe, 1854). Although Meyer (1864) correctly dated the Faringdon deposit as Lower Greensand, the Rev. E. C. Davey largely followed Sharpe's misidentifications of bryozoan species when publishing a catalogue of his collection in 1877. This also listed 44 bryozoan species, though in a later, undated publication (thought from internal evidence to be have been published in the first decade of this century, ?1905) he listed 54 species. Davey sold his collection to the University of Oxford in 1872 (to pay for a law suit) and much of it is still recognizable in the Oxford University Museum. Vine (1891) listed 42 species from Faringdon.

J. W. Gregory described several Faringdon species and mentioned others in the two parts of his catalogue of Cretaceous Bryozoa in the British Museum (1899, 1909*a*). However, no comprehensive systematic work was completed until the publication in 1926 of Canu & Bassler's 'Studies on the cyclostomatous Bryozoa', in which 51 species of bryozoans were distinguished from Faringdon. Canu & Bassler did this joint work entirely by correspondence, sending material backwards and forwards between France and the U.S.A. Their material was collected for them by W. E. Crane; there is no evidence that either author ever visited Faringdon.

One of us (L. J. P.) started to work on the Faringdon bryozoan fauna with the late Henry Dighton Thomas but on the death of Thomas in 1966 this work was suspended. Two short papers (Pitt 1949, 1976) were published on new species from Faringdon before the work of producing a full revision was resumed in 1981 by the two of us.

METHODS AND MATERIAL

In addition to already sorted bryozoan specimens in various institutional collections, much material has been collected and sorted, either from bulk sediment samples or as individual specimens recognizable in the field as bryozoans or potentially bryozoan-encrusted substrates. Ultrasonic cleaning has been employed to remove weakly-adherent matrix, and some specimens have been further developed using a needle. All listed specimens have been examined with binocular microscopes and most of the measurements have been made with an eyepiece graticule. Macrophotographs were prepared from colonies coated lightly in ammonium chloride. Thin sections and acetate peels have been prepared mainly of the cerioporine and cancellate cyclostomes which offer fewer useful external characters. Prior to sectioning most of the specimens were embedded in blocks of resin. A large number of specimens have been studied using an ISI 60A scanning electron microscope (SEM) fitted with a CFAS system. This system enabled study of uncoated specimens, including types, up to about 10 cm in size. The images obtained are formed by back-scattered electrons and have qualities slightly different from conventional secondary electron images (see Taylor 1986*a*). Unless otherwise stated, all photographic illustrations are back-scattered electron micrographs. Magnifications are very approximate.

Institutional abbreviations are as follows: BM(NH), British Museum (Natural History), London; OUM, Oxford University Museum; BGS, British Geological Survey, Keyworth; USNM, United States National Museum (Smithsonian Institution), Washington, USA; MNHN, Muséum National d'Histoire Naturelle, Paris; MHNG, Muséum d'Histoire Naturelle, Geneva; SM, Sedgwick Museum, Cambridge.

For abbreviations of measured morphological characters, see p. 68 (Fig. 2).

GEOLOGICAL SETTING

A small outlier of Lower Greensand (Aptian) occurs in the neighbourhood of Faringdon, 25 km WSW of Oxford (Fig. 1). The Faringdon Lower Greensand (Arkell 1947; Casey 1961 and references therein), resting with unconformity on Kimmeridge Clay or Corallian limestones of Upper Jurassic age, is up to 58 metres thick and is divisible into the following units:

3. Sands with chert and ironstone
2. Sandy clays
1. Sponge Gravel
   b. Red Gravel
   a. Yellow Gravel

Nearly all of the rich fauna comes from the Sponge Gravel, especially the Yellow Gravel. The occurrence of the rare ammonites *Parahoplites nutfieldensis* and *P. maximus* in the Red Gravel (Casey 1961) enables the Faringdon Sponge Gravel to be dated as the lower half of the *nutfieldensis* Zone (*subarcticum* Subzone) of the Upper Aptian.

The Sponge Gravel consists of cross-bedded, bioclast-rich, gravels and sands which are variably ferruginous and differentially cemented. Quartzose, phosphatic and claystone pebbles and cobbles abound, particularly at certain horizons (e.g.

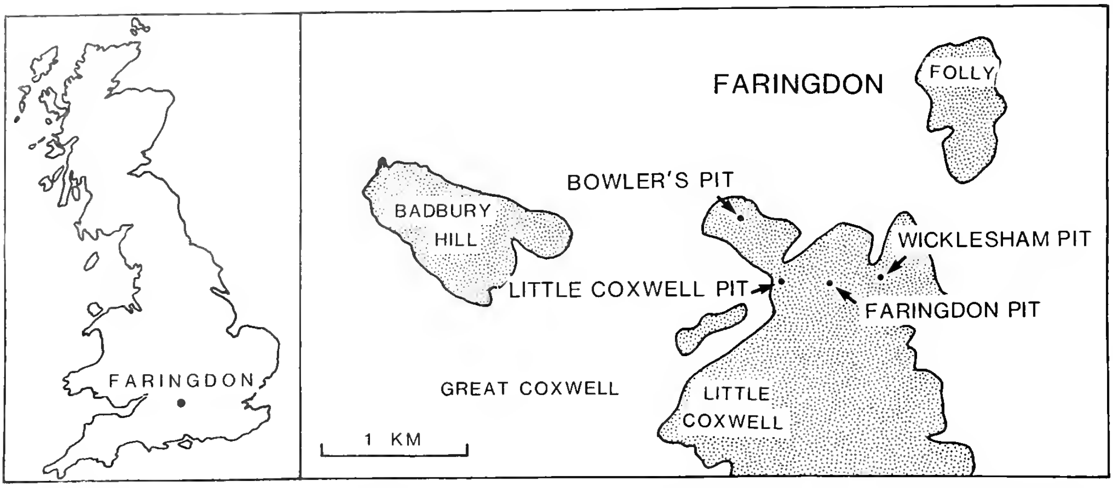


Fig. 1 Locality map of the Faringdon area in Oxfordshire (simplified after Arkell 1947: fig. 28). The outcrop of the Aptian Lower Greensand, which includes the Faringdon Sponge Gravel, is stippled; the remaining unstippled area consists of Jurassic rocks.

near the base of the Red Gravel). The fossils vary in their state of preservation from pristine to fragmented or heavily abraded; some (e.g. belemnites) are clearly derived from the Upper Jurassic. The indigenous fauna is dominated by large calcisponges (notably *Raphidonema* spp.) and other sponges together with bryozoans. Also common are brachiopods (see Middlemiss 1959), oysters, serpulids (see Ware 1975) and echinoids. Aragonitic fossils are generally not preserved, but their past presence is indicated by occasional moulds of gastropods which were overgrown by sponges or bryozoans.

It is thought that the Faringdon Sponge Gravel accumulated in submarine depressions a little way offshore (Arkell 1947). Krantz (1972) made a detailed study of the sedimentology and genesis of the Sponge Gravel, concluding that the deposit represented the transgressive conglomerate of a channel in-filling which incorporated an abundant hardground fauna. The channels were depressions aligned WNW to ESE, formed during an earlier period of marine erosion, and may have represented the 'upstream' end of a tidal, ebb-current dominated bed transport path which operated in a narrow gulf opening to the south and east (Bridges 1982).

Several pits have been worked in the Sponge Gravel (Fig. 1). The best known of these is Little Coxwell Pit (National Grid reference SU 286943) which has yielded the most abundant bryozoan fauna from the Yellow Gravel. Though still accessible at the present day, the workable area of Little Coxwell Pit is now much diminished and lower levels (beneath a cemented horizon) which once yielded the best-preserved material can no longer be reached. The adjacent Faringdon Pit (SU 288943) also exposes the Yellow Gravel, as did the now defunct Bowler's Pit (SU 282947). The large Wicklesham Pit (SU 292944) exposes only the overlying Red Gravel, in which bryozoans are less abundant and generally poorly preserved. There are also small exposures of Yellow Gravel on Badbury Hill (SU 260947).

BRYOZOAN PRESERVATION

Preservation of bryozoans from Faringdon is extremely variable, depending upon both the condition of colonies at the time of burial and subsequent diagenetic factors. Breakage and surficial abrasion occurred in many specimens before burial. Erect branching colonies are invariably preserved as branch fragments commonly less than 1 cm in length. However, rare examples exist of almost intact preservation of arborescent colonies (e.g. Fig. 90). Branch fragments may be extensively abraded, the zooecial frontal walls completely removed in many instances. Even encrusting colonies may be heavily worn and, as in erect colonies, signs of regenerative growth (e.g. Fig. 9B) indicative of pre-mortem fracturing are usually absent; i.e. much of the damage seems to have occurred after colony death (see also p. 65 below). Particularly vulnerable were gynozooecia whose roofs are frequently missing. At the other extreme are encrusting colonies occupying borings or hollows in the substrate in which are preserved very long and delicate peristomes (e.g. Fig. 46). Among erect species, the mixture of fragments showing differing states of preservation suggests more-or-less *in situ* breakdown and abrasion of colonies, the well-preserved fragments having been buried relatively quickly whereas the heavily abraded fragments must have lain for a long time on the sediment surface.

Diagenesis has had an important influence on the preservation of surface details. For example, the best preserved bryozoans show clearly the pseudopores of the frontal walls (e.g. Fig. 16D), and the mural spines which are visible within zooecial apertures (e.g. Fig. 50B). However, slight to profuse growth of crystals of calcite cement obscures these details (e.g. Fig. 26B) in the majority of specimens, particularly those from the Red Gravel. The presence of this cement may be related to dissolution of the aragonitic component of the Faringdon biota. Pressure solution pits (e.g. Fig. 131A, centre left) caused by sand grains juxtaposed to colony surfaces are common and care is needed to prevent these pits being interpreted under the optical microscope as features of bryozoan morphology. Unfortunately many type specimens are poorly-preserved (e.g. Fig. 47) and full characterization of external morphology in these species may be difficult. Calcite overgrowths inside the rims of zooecial apertures (e.g. Fig. 26B) are particularly troublesome when measuring apertural dimensions.

BRYOZOAN PALAEOECOLOGY

Bryozoans are sessile filter-feeders which require a firm substrate for larval settlement and metamorphosis. A wide variety of substrates were utilized by the bryozoans of the Faringdon Sponge Gravel, and this may partly explain the high species diversity. Certain species are characteristic of particular substrates, but others can be found attached to many different types of substrate. Oyster shells, brachiopods (e.g. Fig. 110), sponges (e.g. Fig. 44A) and intraclasts (e.g. Fig. 30) are the most frequently encountered substrates. Large cup-shaped sponges may support colonies of many different species, together with serpulid worms. The absence of an intact substrate in some colonies in which the base is preserved (e.g. Figs 54, 55) may signify attachment during life to a soft-bodied organism, either plant or animal. However, clear bioimmurations revealing the nature of these putative soft substrates have not been found (cf. the Maastrichtian bryozoan fauna described by Voigt, 1973). Echinoid spines are commonly encrusted by bryozoans, particularly *Charixa lhuydi* (see p. 146), which may have been associates of living echinoids. Bones of marine reptiles derived from the Jurassic may also be encrusted by species such as *Idmonea radiolitorum* (Fig. 36).

Wilson (1986) made a detailed study of bryozoans and other organisms encrusting or boring into claystone cobbles from the Red Gravel of Wicklesham Pit. He recognized 23 bryozoan species, most of which were found only within borings and other cavities. These 'coelobites' were apparently able to avoid epifaunal predators and physical abrasion. In contrast, a biota dwelling on cobble surfaces, including the bryozoan *Reptoclausa hagenowi*, is considered by Wilson to have been well-adapted to the rigours of this mobile hardground habitat.

Many different bryozoan growth-forms are present in the Faringdon Sponge Gravels. Among the encrusting species, sheet-like (e.g. Fig. 44A), ribbon-like (e.g. Fig. 16A) and unner-like (e.g. Fig. 3A) forms are all represented. Whereas sheet-like colonies have a high commitment to defending the ubstrate space they occupy, runner-like colonies are fugitives which are well adapted to locating spatial refuges on the ubstrate, and ribbon-like forms have an intermediate adapive strategy (see Taylor 1984). Multilamellar growth-forms haracterize some sheet-like tubuloporines, and the massive olonies of *Semimulticavea marginata* are also multilayered Figs 132, 135). Serpulids and other encrusting organisms are frequently found between layers of *S. marginata* colonies; as n some Pliocene cyclostomes with a similar growth-form Balson & Taylor 1982), these fouling organisms were overrown and entrapped by their living bryozoan substrates. Colonies of *S. marginata* probably underwent episodic ?seasonal) phases of growth and dormancy (cf. *Multicrescis uberosa* from the Hauterivian, see Flor & Hillmer 1970). A milar rhythmicity in growth may have characterized colonies f *Reptomulticava brydonei* and *Tholopora* spp. which have ubcylindrical branches made up of superimposed subcolonies.

Erect arborescent growth-forms dominate the Faringdon auna in terms of numbers of species and abundance. Foliaeous growth-forms are notably rare (cf. Walter 1985 on the eocomian of France and Switzerland), only a solitary fragment of *?Mesenteripora campicheana* being present. All the emaining arborescent bryozoans have subcylindrical, bifurating branches. These are polarized into a group of species with narrow branches, generally <2 mm in diameter (e.g. Fig. 90), and a less common group of species with robust branches (e.g. Fig. 109). The latter group, comprising *Echinocava raulinii, Heteropora keepingi* and *Ceriopora farringdonensis*, accord with the general observation of McKinney (1986) for thick-branched stenolaemates in possessing maculae which are thought to have been involved in channeling excurrents away from the colony surface.

The narrow-branched arborescent colonies which form the dominant element of the Faringdon fauna fit approximately within the vinculariiform category of growth-forms originally recognized for cheilostome bryozoans. Stach (1936) regarded this growth-form as adapted for life in deep or sheltered waters where wave action is absent and currents are weak. In their classic study of bryozoan growth-forms in the Recent sediments off the Rhône Delta, Lagaaij & Gautier (1965) found that vinculariiform bryozoans reached their highest percentages in deep-water (>120 m) calcareous sands, although minor percentages of this growth-form occurred across most of the area of study. Wass, Conolly & Macintyre (1970), working in southern Australia, noted that vinculariiform colonies commonly occurred at depths greater than 100 fathoms (*c.*180 m). However, it is unclear to what extent these environmental findings for Recent cheilostome-dominated faunas can be applied to the cyclostome assemblage of the Faringdon Sponge Gravel.

A quantitative study of fragments of 'vinculariiform' cyclostomes in samples of Yellow Gravel from Little Coxwell Pit has been undertaken by A. Butterworth, whose unpublished results are summarized here. In a sample from the A. G. Davis Collection, 40% of fragments were unidentifiable (usually because they were excessively worn), and of the 11 species distinguished in the identifiable portion, *Meliceritites dendroidea* and *Ceata granulata* were the most common, accounting for 14% and 13% respectively by weight of the sample. As might have been expected, the mean length of fragments of each species correlated strongly with the average branch thickness for that species; i.e. species with thin branches were broken into shorter fragments than species with thick branches. Counts were made of the number of fragments preserving growth tips and the number preserving branch bifurcations (Y-shaped fragments). Topological considerations dictate that the number of bifurcations in an arborescent colony should equal one less than the number of growth tips (see Cheetham, Hayek & Thomsen 1981: 78). As Faringdon bryozoan colonies were comparatively large when intact, in the absence of sorting the number of bifurcating fragments present in any given sample of branch fragments resulting from the mechanical breakdown of colonies should approximate to the number of growth tips present. This was found not to be so in the samples analysed. In the A. G. Davis sample, 249 bifurcations as against 37 growth tips were counted; i.e. bifurcations were 6·7 times as common as growth tips. A larger sample collected by one of us (P. D. T.) in 1985 yielded 721 bifurcations and only 210 growth tips; bifurcations were 3·4 times as common as growth tips. This under-representation of growth tips can be explained in two ways: by net transportation of growth tips away from the site of deposition (e.g. by branch tips breaking off in-situ colonies mechanically or as a result of the activity of predators), or by loss of growth tips during mechanical abrasion of colony fragments prior to their burial. The second interpretation is favoured because the more delicate species (e.g. *Entalophoroecia quadripartita, Siphodictyum gracile*) were found to

Table 1 List of bryozoan species from the Faringdon Sponge Gravel described in this paper, with a comparative list of names used by Canu & Bassler (1926) for these species.

This paper	**Canu & Bassler, 1926**
'*Stomatopora*' *melvillei* sp. nov.	—
Stomatoporina alternata sp. nov.	—
Voigtopora calypso (d'Orbigny)	*Stomatopora calypso* (d'Orbigny)
Stomatoporid sp. 1	—
Stomatoporid sp. 2	—
Proboscinopora marginata (d'Orbigny)	—
Oncousoecia coarctata (Canu & Bassler)	*Proboscina coarctata* sp. nov.
Oncousoecia depressa (d'Orbigny, *sensu* Canu & Bassler)	*Proboscina depressa* (d'Orbigny)
Oncousoecia parvula (Canu & Bassler)	*Berenicea parvula* sp. nov. *Microecia cornucopia* (d'Orbigny) *Proboscina virgula* (d'Orbigny)
Filisparsa gasteri sp. nov.	—
Reptoclausa hagenowi (Sharpe)	*Reptoclausa hagenowi* (Sharpe)
Idmonea denticulata (Canu & Bassler)	*Reptoclausa denticulata* sp. nov.
Idmonea radiolitorum d'Orbigny	*Proboscina radiolitorum* (d'Orbigny) *Proboscina zic-zac* d'Orbigny
Collapora hillmeri sp. nov.	—
Plagioecia orbifera (Canu & Bassler)	*Diaperoecia orbifera* sp. nov. *Berenicea pulchella* de Loriol (*partim*) *Berenicea (Reptomultisparsa) tenella* de Loriol
Plagioecia spissa (Gregory)	*Cellulipora spissa* (Gregory)
Hyporosopora constricta sp. nov.	—
Hyporosopora larwoodi sp. nov.	—
Hyporosopora mantelli sp. nov.	*Trigonoecia haimei* (de Loriol)
Mesonopora fecunda (Vine)	—
Cardioecia neocomiensis (d'Orbigny)	*Cardioecia faringdonensis* sp. nov. *Cardioecia pauper* sp. nov. *Notoplagioecia faringdonensis* sp. nov.
Ceata granulata (Canu & Bassler)	*Cea granulata* sp. nov.
?Mesenteripora campicheana (d'Orbigny)	—
Entalophoroecia quadripartita (Canu & Bassler)	*Clinopora quadripartita* sp. nov.
Unitubigera sp.	—
Meliceritites gracilis (Goldfuss)	—
Meliceritites dendroidea (Keeping)	*Lobosoecia semiclausa* (Michelin) *Meliceritites semiclausa* Gregory
Meliceritites cunningtoni (Gregory)	*Meliceritites cunningtoni* (Gregory)
Meliceritites transversa Canu & Bassler	*Meliceritites transversa* sp. nov.
'*Berenicea*' *filifera* Canu & Bassler	*Berenicea filifera* sp. nov.
'*Berenicea*' *faringdonensis* Canu & Bassler	*Berenicea faringdonensis* sp. nov.
'*Berenicea*' *grandipora* Canu & Bassler	*Berenicea grandipora* sp. nov.
'*Berenicea*' cf. *sowerbyi* (Lonsdale)	—
Siphodictyum gracile Lonsdale	*Siphodictyum gracile* Lonsdale *Siphodictyum irregulare* sp. nov.
Laterocavea dutempleana d'Orbigny	*Laterocavea dutempleana* d'Orbigny
Laterocavea? intermedia Canu & Bassler	*Laterocavea intermedia* sp. nov. *Clausa cranei* sp. nov.
Heteropora clavata, *sensu* Gregory	—
Heteropora keepingi Gregory	*Ceriopora dimorphocella* sp. nov. [?] *Heteropora nummularia* sp. nov.
Ceriopora farringdonensis Gregory	—
Tetrocycloecia multiporosa Canu & Bassler	*Tretocycloecia (?) multiporosa* sp. nov. *Tretocycloecia densa* sp. nov.
Clausa zonifera Canu & Bassler	*Clausa zonifera* sp. nov.
Semimulticavea marginata (Canu & Bassler)	*Multigalea marginata* sp. nov. *Multigalea canui* (Gregory) *Radiopora tuberculata* (d'Orbigny)
Seminodicrescis variolata (Gregory)	*Multicrescis mammilosa* sp. nov. *Seminodicrescis nodosa* d'Orbigny
Reptomulticava brydonei (Gregory)	*Reptomulticava fungiformis* Gregory
Tholopora dightoni sp. nov.	*Tholopora virgulosa* Gregory
Tholopora hastingsae sp. nov.	—
Tholopora thomasi Pitt	—
Echinocava raulinii (Michelin)	*Plethopora aptensis* sp. nov.
Paracrescis boardmani sp. nov.	—
Charixa lhuydi (Pitt)	—

have particularly low ratios of growth tips to bifurcations. Pre-burial abrasion of branch fragments was an important aspect of bryozoan taphonomy in the Faringdon Sponge Gravel.

Factors contributing to the richness of the Faringdon bryozoan fauna may have included:

1. High availability of hard substrates for attachment; 'primary' substrates may have been supplied by the erosion of fossils and concretions from the underlying Jurassic sediments, and 'secondary' substrates by the variety of organisms that developed on these primary substrates. The abundance and variety of substrates at Faringdon probably added to bryozoan richness, as Eggleston (1972) found for communities of Recent bryozoans living off the Isle of Man.
2. Episodic sedimentation allowing sufficient time for the colonization of the sea-bed by epibenthos before swamping and burial by migrating sandwaves.
3. Paucity of fine-grained sediment deposition.
4. Provision of nutrient-laden currents (cf. the present-day Otago Shelf of New Zealand where bryozoans attain maximum densities in areas in the path of the Southland Current according to Probert, Wilson & Batham 1979).

FAUNAL COMPOSITION AND COMPARISONS

The Faringdon fauna is the most diverse bryozoan fauna of early Cretaceous age currently recognized from anywhere in the world. A total of 50 calcareous bryozoan species are recognized (Table 1), all cyclostomes with the exception of a single cheilostome. To these must be added a boring ctenostome bryozoan described by Voigt & Soule (1973) as *Terebripora* (?) *bassleri* and questionably re-assigned to *Ropalonaria* by Pohowsky (1978). This figure of diversity compares with the 50 species listed by Canu & Bassler (1926: 2–3). However, some additional species are here recognized while several of those listed by Canu & Bassler are placed in synonymy. Canu & Bassler's neuroporid species (*Neuropora micropora, N. tenuinervosa, Neuroporella hemispherica*) are now thought to be sclerosponges rather than bryozoans (Kaźmierczak & Hillmer 1974), as is a fourth Faringdon species (not listed by Canu & Bassler) described by Gregory (1909*b*, see also 1909*a*) as *Reptomulticava fungiformis*.

Ryland (1970: 134) regarded the Lower Cretaceous as the zenith of the cyclostome bryozoans. Indeed, both the Faringdon cyclostome fauna and the diverse Valanginian fauna of Sainte-Croix in Switzerland (from which Walter (1972) recorded 37 species here regarded as cyclostomes) are appreciably richer in species than are the most diverse cyclostome faunas known from the Jurassic (see Walter 1970) or the pre-Jurassic. Although highly diverse bryozoan faunas continue into the Upper Cretaceous these contain an increasing proportion of cheilostomes which attain dominance over cyclostomes by about the end of the Santonian.

In terms of higher taxa, the Faringdon cyclostome fauna is dominated by tubuloporines (including melicerititids) of which there are 33 species (67%). The other cyclostome suborders are represented as follows: cerioporines—11 species (23%); cancellates—4 species (8%); rectangulates—1 possible species (2%). It should be noted, however, that the status of these suborders is currently that of evolutionary grades and not clades. Analysis of phylogenetic relationships in cyclostomes has yet to be attempted even at the most basic level.

Other Aptian bryozoan faunas in Britain are very poorly known. Although Casey (1961) gives a long list of species recorded from the British Aptian, many of these are species described by Canu & Bassler (1926) and known only from Faringdon. The work of Keeping (1883) on bryozoans from the Aptian of Upware (Cambridgeshire) and Brickhill (Bedfordshire) is greatly in need of revision. Both localities are now no longer accessible, but the material described by Keeping survives in the collections of the Sedgwick Museum, Cambridge. Keeping records 18 bryozoan species from Upware and 8 from Brickhill. At least two of the Upware species (*Meliceritites dendroidea* (Keeping) and *Echinocava raulinii* (Michelin)) occur also at Faringdon. Also in need of revision are the four putative bryozoan species described by Lonsdale (1849), apparently from the Atherfield Clay (Lower Aptian) of the Isle of Wight. These include *Siphodictyum gracile* Lonsdale which is a common species in the Faringdon Sponge Gravel. The BM(NH) collections contain a significant number of bryozoan specimens, many poorly-preserved, from Aptian Lower Greensand localities in Kent and Surrey. These too are in need of study.

Outside Britain Aptian bryozoans are mostly known from SE France and the Jura where Walter and colleagues have made several faunal studies (Delamette & Walter 1984; Masse & Walter 1974; Walter 1977; Walter & Busnardo 1971; Walter & Clavel 1979; Walter *et al.* 1975). It is difficult to assess how many species are shared between Faringdon and these French and Swiss localities. However, the following distinctive species occur in common: *Siphodictyum gracile* Lonsdale, *Laterocavea dutempleana* d'Orbigny, *Echinocava raulinii* (Michelin) and *Cardioecia neocomiensis* (d'Orbigny). All of these appear to be long-ranging species; *S. gracile* is recorded from the Barremian and Aptian (Walter *et al.* 1975), *L. dutempleana* from the Aptian and Albian (Voigt 1981), *E. raulinii* from the Hauterivian to Albian (Walter *et al.* 1975), and *C. neocomiensis* from the Hauterivian to Aptian (Hillmer 1971).

A considerable number of species found at Faringdon have not been recorded elsewhere. Whether or not these are truly endemic will only become clear after further studies of Lower Cretaceous bryozoan faunas. Among the more distinctive species apparently restricted to the Faringdon Sponge Gravels are the following: *Idmonea denticulata, Reptoclausa hagenowi, Meliceritites cunningtoni, Paracrescis boardmani*, and the three species of *Tholopora*.

SYSTEMATIC PALAEONTOLOGY

All known species of calcareous bryozoans present in the Faringdon Sponge Gravel are described. For description of the boring ctenostome *Terebripora* (?) *bassleri* Voigt & Soule, see Voigt & Soule (1973: 24) and Pohowsky (1978: 57).

Although this faunal study is not intended as a monographic revision of any particular taxa of cyclostomes, it has been necessary to make remarks concerning the status of many genera and the concepts of the genera as here employed. Problems encountered in defining genera emphasize the need for thorough revisions of generic type species, as done by Nye

(1976) for some of the cerioporine genera. Unfortunately many of these type species were founded by d'Orbigny (1851–54), who used large syntypic suites of specimens from more than one locality when describing his new species. Not only is it usually difficult or impossible to match any one syntype to d'Orbigny's stylized published figures, but each syntypic suite may comprise more than one species. A full revision of the d'Orbigny Collection (housed in the MNHN, Paris) is of paramount importance to the future progress of systematic studies of Cretaceous cyclostomes.

The generic ranges quoted below are highly tentative but are believed to represent an improvement in precision and accuracy on previously published data (Bassler 1953).

Abbreviations of measured morphological characters are shown in Fig. 2 and its caption. Additional abbreviations used in the text but not shown on this figure are: **BW**, branch width; **KAM**, kenozooecial apertural measurement; **LOPM**, longitudinal ooeciopore measurement; **LOSM**, longitudinal ooeciostome measurement; **TOPM**, transverse ooeciopore measurement; **TOSM**, transverse ooeciostome measurement.

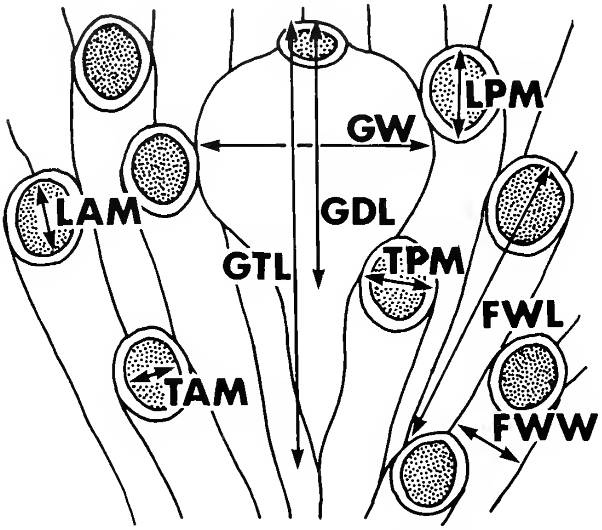


Fig. 2 Measured morphological characters in cyclostome bryozoans from the Faringdon Sponge Gravel. Abbreviations: **FWL**, frontal wall length (of autozooecia); **FWW**, frontal wall width; **GDL**, gynozooecium dilated length; **GTL**, gynozooecium total length; **GW**, gynozooecium width; **LAM**, longitudinal apertural measurement (of autozooecia); **LPM**, longitudinal peristome measurement; **TAM**, transverse apertural measurement; **TPM**, transverse peristome measurement.

It should be noted that measurements of zooecial and zoarial dimensions have generally been made from a limited number of specimens and may not encompass the entire range of values present in the species. Pseudopore densities have been calculated by placing a square of known area over SEM prints at a standard magnification of × 320, counting the number of pseudopores present and calculating how many would be present in an area of one mm^2.

To assist species identification, the key in the Appendix (p. 149) should be consulted.

Unless otherwise stated, all listed material is from the Faringdon Sponge Gravel of the Faringdon area. Exact locality and collection details are given when known. In cases where more than one specimen has been registered under a single number, this is indicated by a number or the word 'sample' in parenthesis after the specimen registration number.

Order **CYCLOSTOMATA** Busk, 1852
Suborder **TUBULIPORINA** Milne Edwards, 1838
Family **STOMATOPORIDAE** Pergens & Meunier, 1886

Genus ***STOMATOPORA*** Bronn, 1825

TYPE SPECIES. *Alecto dichotoma* Lamouroux, 1821, by monotypy; Bathonian, France.

REMARKS. *Stomatopora* is here used for encrusting uniserial or nearly uniserial tubuliporines lacking basal gynozooids. Different authors have applied the name in different ways: for example, Harmelin (1974*a*) included Recent species with peristomial gynozooids, Walter (1970) Jurassic species with erect branches, and Illies (1973) species exhibiting a variety of budding patterns. These interpretive problems arise in part because the type material of the type species was destroyed during the battle for Caen in 1944. Although Walter (1970) proposed a neotype for *Stomatopora dichotoma* (see Illies 1976), it is by no means clear whether this is conspecific with Lamouroux' original material. Also, the lack of peristomial gynozooids in fossil material may be a result of preservational factors rather than primary absence. Until the precise identity of the genus has been clarified, *Stomatopora* can be only loosely applied and it seems appropriate to write the name in quotations.

Early branches of the neotype of *S. dichotoma* are uniserial but later branches are narrowly multiserial with the proximal parts of later budded zooecia occurring side-by-side with the distal parts of earlier zooecia. The distinction between *Stomatopora* and the more obviously multiserial new genus *Proboscinopora* (see p. 74) is somewhat gradational, although in *Proboscinopora* zooecia budded at the same level often have their apertures side-by-side.

RANGE. Triassic (Carnian) to Recent.

'Stomatopora' melvillei sp. nov. Figs 3–6

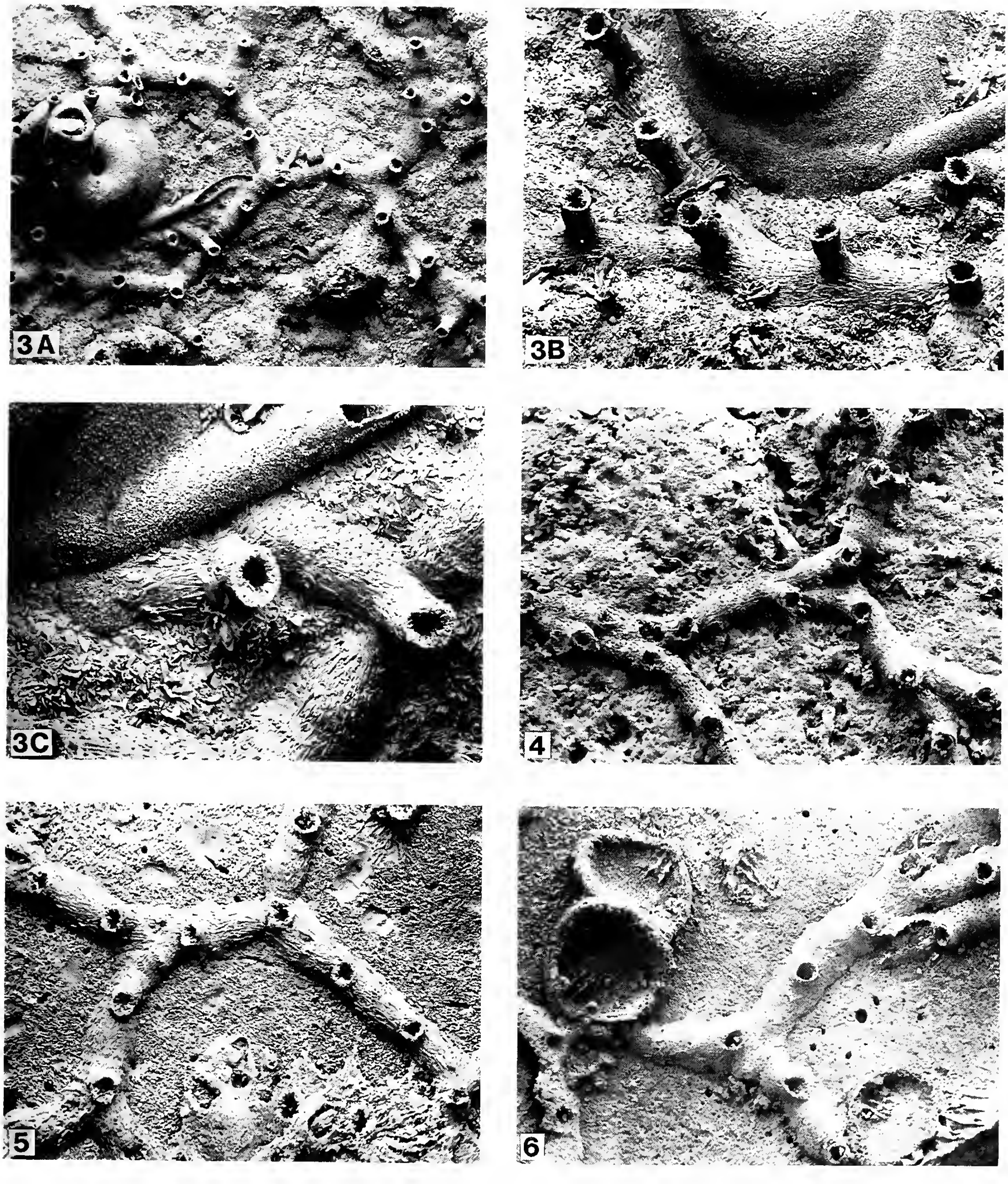
1899 *Proboscina crassa* (Roemer) var. *divaricata* (d'Orbigny); Gregory: 35 (*partim*); pl. 2, fig. 8.

HOLOTYPE. BM(NH) D53699, Faringdon Sponge Gravel, Little Coxwell Pit, A. G. Davis Colln.

PARATYPES. BM(NH) 60538, Cunnington Colln (figured by Gregory 1899: pl. 2, fig. 8, as *Proboscina crassa* var. *divaricata*); D6322, D6326, A. N. Davis Colln; D7979, D7982, Treacher Colln; D55111, D55358–9, D55361–2, Little Coxwell Pit, Gaster Colln; D55357, D55360, Bowler's Pit, Gaster Colln.

NAME. For Richard V. Melville, in recognition of his research on the Faringdon Sponge Gravel.

DESCRIPTION. Zoarium encrusting, with uniserial branches in early growth stages but in later stages branches are often biserial, particularly immediately after their division. The first internode consists of the ancestrula and one other zooid. Thereafter, branches bifurcate at variable intervals, with between 1 and 9 zooecia per internode. The first bifurcation is at a high angle (130°–170°), but later bifurcations occur at decreasing angles; e.g. in BM(NH) D6326 the first bifurcation angle is 170°, the second averages 125°, the third 116°, the



igs 3–6 *'Stomatopora' melvillei* sp. nov. Fig. 3, BM(NH) D53699, **holotype**; 3A, early zooecia sharing the same substrate as some serpulid worms, × 14; 3B, zooecia with well-preserved peristomes, × 27; 3C, ancestrula and first budded zooecium, × 60. Fig. 4, BM(NH) D6322, branch bifurcations with adherent sibling zooecia, × 15. Fig. 5, BM(NH) D6326, × 23. Fig. 6, BM(NH) D7979, broad zooecia budded during late astogeny, × 20.

urth 85°, and the fifth 105°. Angles in late astogeny are ccasionally so low that the two sibling zooecia are adherent r much of their lengths (Fig. 4).

Zooecia are moderately large, slender, almost parallelded, with smooth, convex frontal walls bearing large seudopores (approximately 900 per mm^2). Apertures are circular and moderately large. Peristomes may be well-raised, up to 0·25 mm when preserved in recesses on the substrate.

The ancestrula is present in BM(NH) D55111 in which the protoecium has a transverse diameter of 0·29 mm and the ancestrula a total length of 0·56 mm. A partly overgrown ancestrula occurs in BM(NH) D53699 (Fig. 3C). The primary

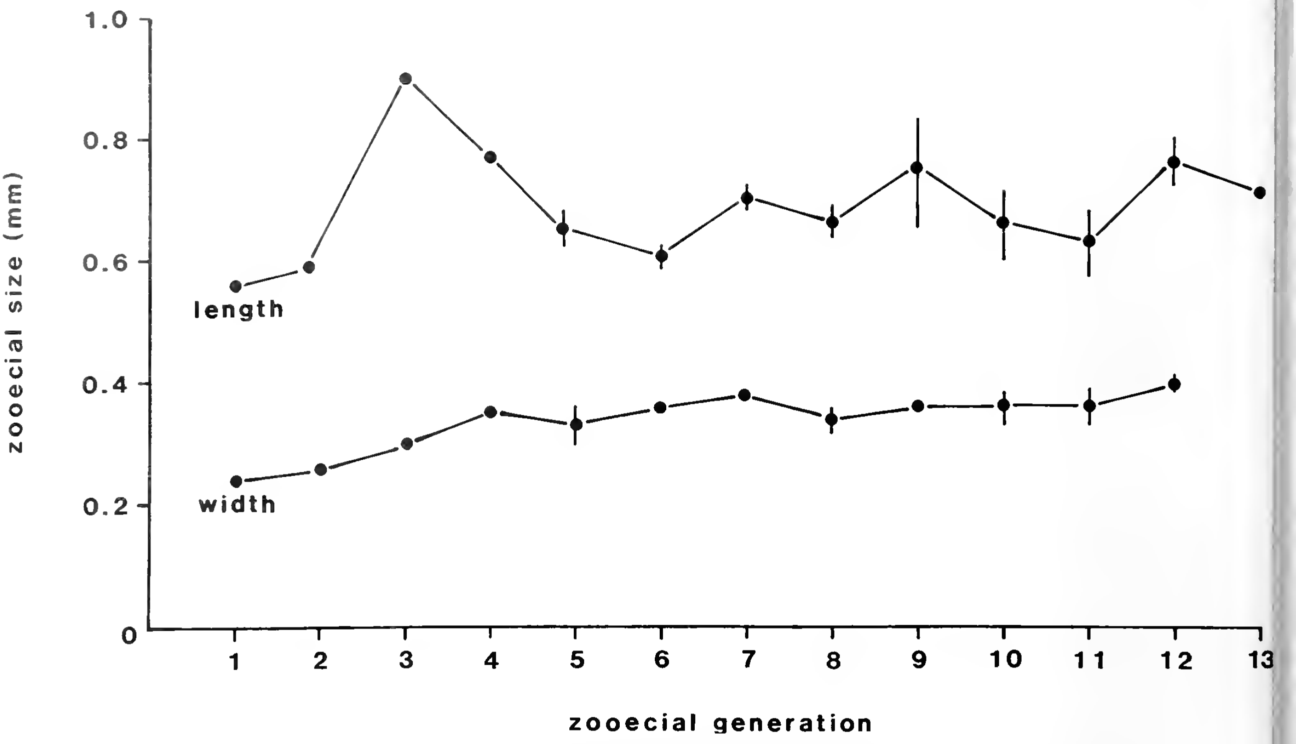


Fig. 7 Astogenetic gradients of zooecial length and width in a colony of *'Stomatopora' melvillei* sp. nov., BM(NH) D55111.

zone of astogenetic change for zooecial length is poorly differentiated and possibly brief, with relatively little difference in size between zooecia of different generations (Fig. 7). Zooecial width increases at a low rate for 10 or more zooecial generations.

MEASUREMENTS. TAM, 0·12–0·16 mm; TPM, 0·18–0·26 mm; FWL, 0·60–0·90 mm; FWW, 0·24–0·45 mm.

REMARKS. This species resembles the *S. granulata* (Milne Edwards, 1838) of Walter (1972: 293–294) but has shorter zooecia. It differs from *S. incrassata* (d'Orbigny, 1850) in the smaller zooecial dimensions.

'S.' melvillei is a common species at Faringdon and can be found encrusting a wide variety of substrates. It is most likely to be confused with *Voigtopora calypso* (below), which has zooecia of similar size. However, the parallel-sided zooecia of *'S.' melvillei* contrast with the slightly barrel-shaped zooecia of *V. calypso*, branches of *V. calypso* are never biserial, and lateral branching is known only in *V. calypso*.

Genus *VOIGTOPORA* Bassler, 1952

TYPE SPECIES. *Alecto calypso* d'Orbigny, 1850, by original designation; Senonian of Saintes, Charente-Maritime, France.

REMARKS. Illies (1976) has redescribed the type species of *Voigtopora*. This genus differs from typical *Stomatopora* principally in the occurrence of lateral branching. *Voigtopora* also has zooecia which extend proximally as long, narrow tubes flanking the proximal zooecium.

RANGE. Aptian (?Hauterivian) to Campanian.

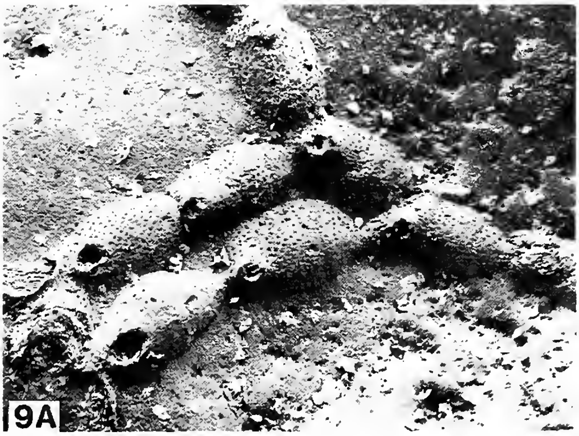
Voigtopora calypso (d'Orbigny, 1850) Figs 8–12

1850 *Alecto calypso* d'Orbigny: 265.
1851 *Alecto calypso* d'Orbigny; d'Orbigny: 844; pl. 630, figs 5–8.
1853 *Stomatopora calypso* (d'Orbigny) d'Orbigny: 841.
1926 *Stomatopora calypso* (d'Orbigny); Canu & Bassler: 5; pl. 26, fig. 11.
1974 *Voigtopora? calypso* (d'Orbigny) Illies: 133; fig. 2c.
1976 *Voigtopora calypso* (d'Orbigny); Illies: 108; figs 4–8.
1986 *Stomatopora calypso, sensu* Canu & Bassler; Wilson: 693.

MATERIAL. BM(NH) D7978, Treacher Colln; 60537a-b, Cunnington Colln; D55353, Little Coxwell Pit, A. G. Davis Colln; D55354, Little Coxwell Pit, Thomas Colln; D55355–6, Little Coxwell Pit, Gaster Colln; D52149, D57394, Little Coxwell Pit; D57418, Wicklesham Pit, Pitt Colln; D57736, Little Coxwell Pit, Voigt Colln.

DESCRIPTION. Colony encrusting, uniserial, branches generally dividing dichotomously at an angle of about 90°, with two to three zooecia occupying each internode. Rare lateral ramifications occur, daughter branches making an angle of about 90° to their parent branch. The ancestrula (observed only in D57736) buds a distal zooecium, and apparently two adventitious zooecia, one arising proximally (which is worn) and one laterally from the protoecium (Fig. 10A). The ancestrula has a protoecium 0·21 mm in diameter, and has a total length of 0·40 mm. A 'bipolar zooid pair' (*sensu* Taylor 1986*c*) consisting of two zooecia joined at their proximal ends (Fig. 9B) in one specimen indicates regenerative branch growth following damage.

Zooecia are moderately large, rather barrel-shaped in



Figs 8–9 *Voigtopora calypso* (d'Orbigny). Fig. 8, BM(NH) 60537, overgrowing branches, × 15. Fig. 9, BM(NH) D7978; 9A, barrel-shaped zooecia, × 28; 9B, bipolar pair of zooecia (junction arrowed), × 25; 9C, abraded zooecium preceeding a branch bifurcation and showing septal traces of the proximal parts of the daughter zooecia, × 50.

outline, sometimes with transverse wrinkles on the frontal wall. Most zooecia have a proximal portion, normally visible only in abraded specimens, of two narrow 'prongs' flanking the next proximal zooecium in linear series (Fig. 9C). However, each of the two daughter zooecia following branch dichotomy has only one 'prong' lateral to the proximal zooecium. Zooecial apertures are small and circular, and peristomes are usually only slightly raised, although a peristome 0·45 mm in length has been observed in a recess in the substrate. When visible pseudopores are large and circular (approximately 600 per mm^2).

MEASUREMENTS. TAM, mean 0·06 mm; TPM, mean 0·14 mm; FWL, mean 0·80 mm; FWW, mean 0·46 mm.

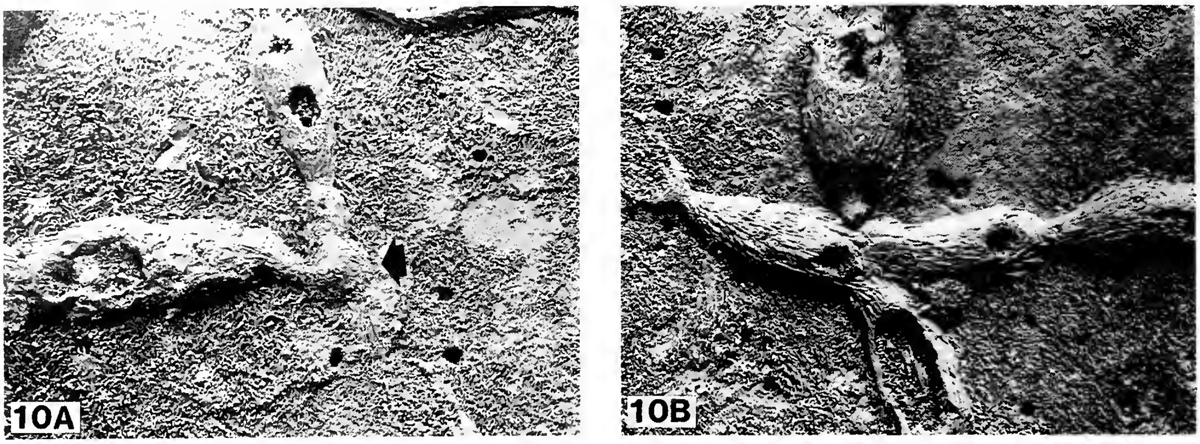
REMARKS. This species is very common in the Faringdon Sponge Gravel, and can be found encrusting phosphatic pebbles and other substrates. Colonies are characteristically fragmentary and early growth stages are usually absent.

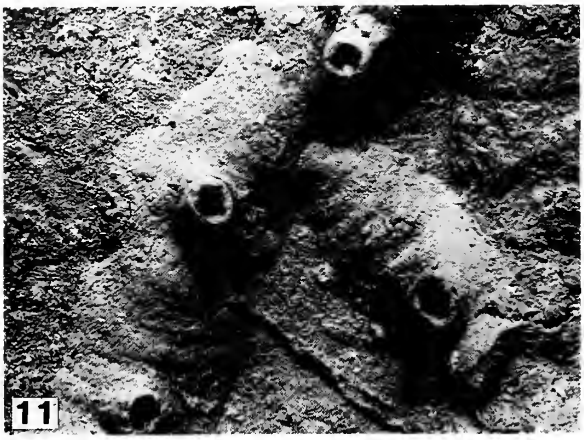
Lateral ramifications (Figs 10B, 11), the principal diagnostic character of *Voigtopora*, occur very infrequently in Faringdon populations of *V. calypso*. Early growth stages are unknown in type and other material of *V. calypso* from the Santonian of France. In the single known Faringdon colony to preserve early growth stages, a lateral and apparently a proximal bud (which is worn) emerge from the protoecium. Conspecific colonies from the Cenomanian of the Le Mans area have one of two growth patterns in early astogeny: in some colonies the ancestrula produced a proximal bud from the protoecium (cf. Illies 1974 in *Stomatopora multigemmans*); in other colonies such a bud is absent and a proximally growing branch arose as a strongly reflexed lateral branch from one of the early post-ancestrular zooecia. A population from the Cenomanian Del Rio Clay of Texas consists entirely of colonies with the second pattern.

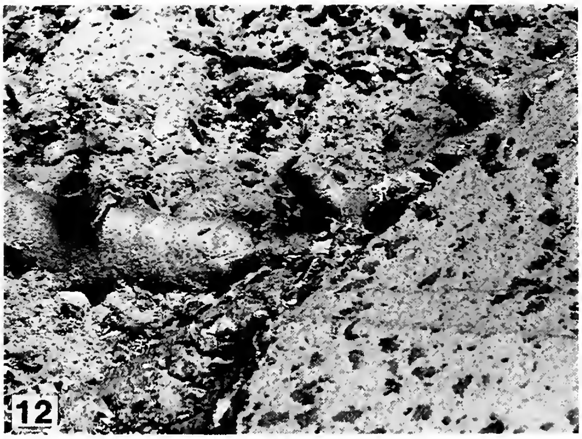
Genus ***STOMATOPORINA*** Balavoine, 1958

TYPE SPECIES. *Alecto incurvata* Hincks, 1860, by original designation; Recent (see Hayward & Ryland 1985).

REMARKS. *Stomatoporina* is characterized by colonies of uniserial, spiralling branches formed by zooecial budding along one margin of the branch only, but sometimes developing straight, biserial branches in later astogeny with zooecia budding from either side of the median line of the branch (see Illies 1975). Apart from the type species, one other species has been referred to the genus, *Stomatoporina spirata* (Walford) from the Middle Jurassic of Shipton Gorge, Dorset (Illies 1975).







Figs 10–12 *Voigtopora calypso* (d'Orbigny). Fig. 10, BM(NH) D57736; 10A, ancestrula (protoecium arrowed) giving rise to a distal zooecium and a left lateral zooecium which emerges from the protoecium, × 39; 10B, bifurcation and lateral ramification, × 32. Fig. 11, BM(NH) D57394, lateral ramification, × 40. Fig. 12, BM(NH) D57418, oblique view of zooecia with long peristomes, × 32.

RANGE. Bajocian to Recent.

Stomatoporina alternata sp. nov. Figs 13–15

HOLOTYPE. BM(NH) D55352, Little Coxwell Pit; Gaster Colln.

PARATYPES. BM(NH) D55348, D53225, Little Coxwell Pit, Taylor Colln; B1935 (2 colonies on *Neuropora* sp.), Little Coxwell Pit, Lee Colln.

NAME. 'By turns'.

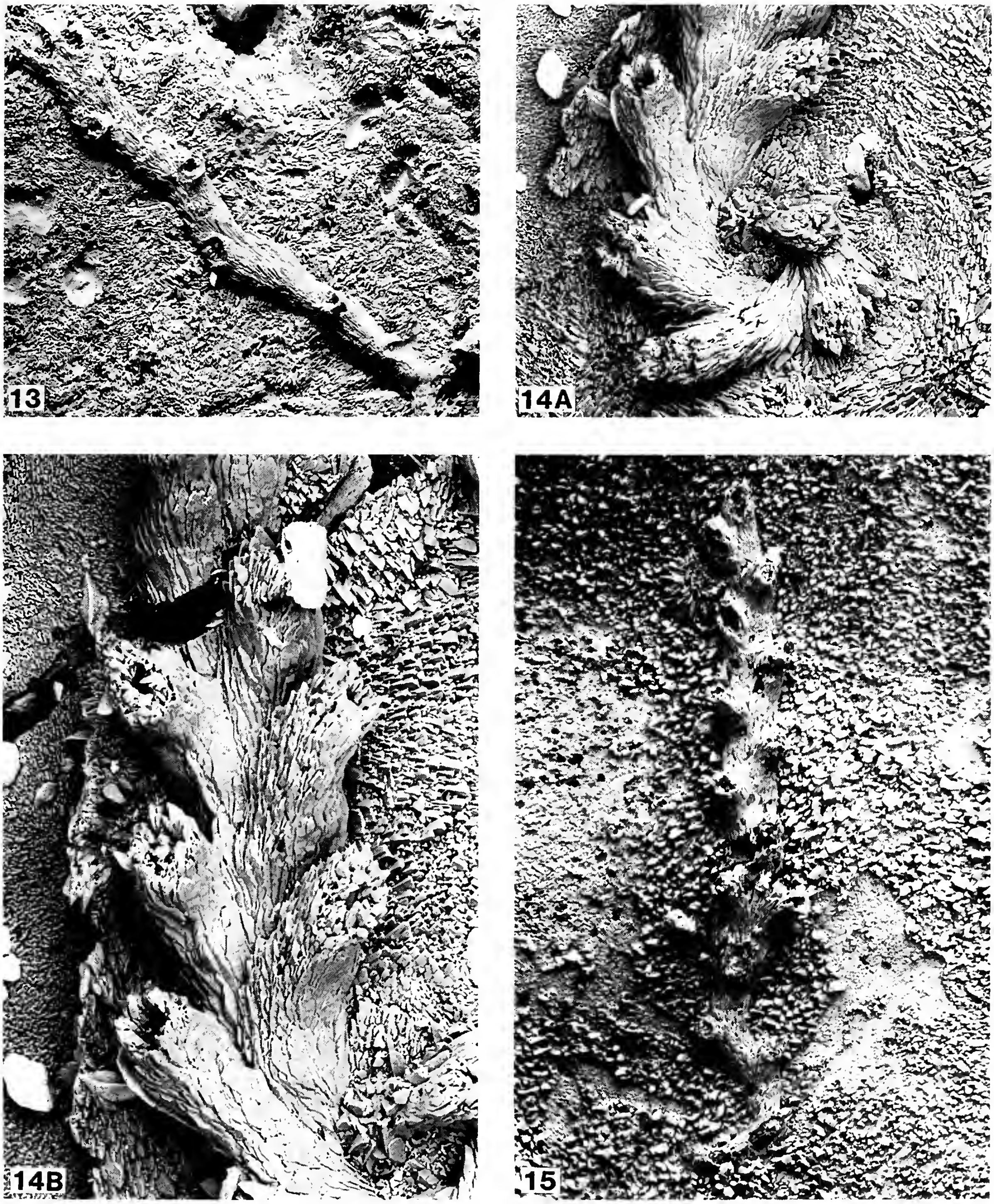
DESCRIPTION. Zoarium encrusting, initially uniserial (Fig. 14A) with zooecial apertures opening on one side; later biserial, with zooecia budding alternately to the left and right sides of the narrow branches (Fig. 13), which zigzag gently. Branches are 0·12 to 0·25 mm wide and bifurcate dichotomously at 60°–90°. Both daughter branches are biserial. Internodes are generally long, e.g. BM(NH) D55348 preserves the colony origin and about 16 generations of zooecia in a branch 3 mm long which does not bifurcate.

Zooecia are small, short in the early stages of the zoarium but longer in later stages, slender, proximally tapering, with circular apertures. Peristomes are offset from the midline of the branches and slightly raised. Pseudopores are not clearly visible in the poorly-preserved material available. The ancestrula, known from two abraded examples, is about 0·27 mm long and has an apertural diameter of 0·07 mm and a protoecium 0·12 mm in transverse width. Gynozooecia have not been observed.

MEASUREMENTS. TAM, 0·04–0·06 mm; TPM, 0·07–0·09 mm; FWL, 0·38–0·60 mm; FWW (proximal), 0·12–0·15 mm.

REMARKS. This new species appears to be the only described Cretaceous stomatoporid with a biserial budding pattern of regularly alternating, zigzag zooecia. There is a close resemblance with *Stomatoporina spirata* (Walford) from the Bajocian, redescribed by Illies (1975), which can show both uniserial and biserial growth, the uniserial branches taking the form of a tight spiral of zooecia. However, *S. alternata* differs in having longer zooecia, and in dichotomizing to give two biserial daughter branches; biserial branches in *S. spirata* divide to give one biserial daughter and one lateral daughter branch which is uniserial.

Within species variation in zooecial length has a considerable effect on the morphology of branches. Colony BM(NH) D53225 has relatively short zooecia and the branches consequently appear wider and have apertures more closely-spaced than is usual.



Figs 13–15 *Stomatoporina alternata* sp. nov. Fig. 13, BM(NH) D55352, **holotype**, × 41. Fig. 14, BM(NH) D53325; 14A, spiral arrangement of coarsely-preserved early zooecia, × 72; 14B, zooecia opening alternately to left and right, × 119. Fig. 15, BM(NH) D55348, small weathered colony, × 39.

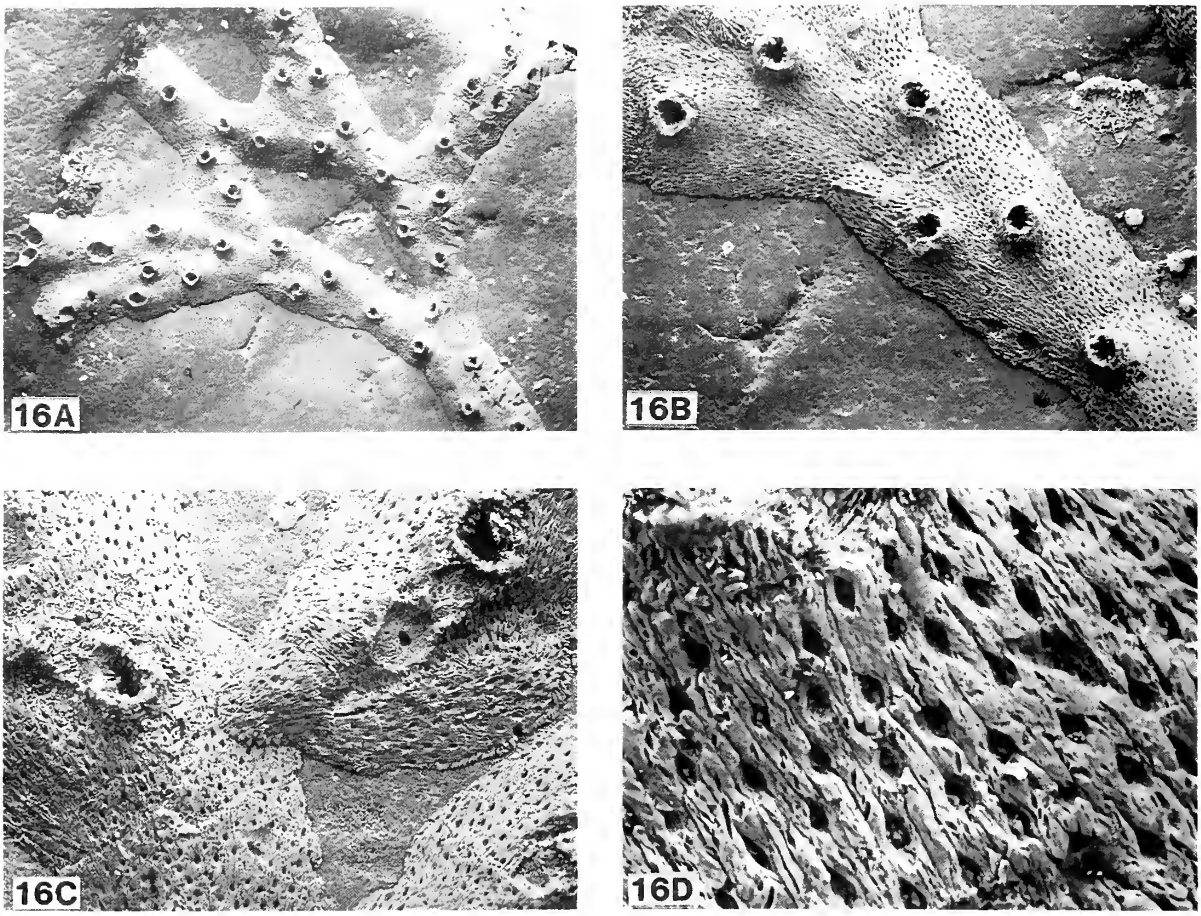


Fig. 16 *Proboscinopora marginata* (d'Orbigny), BM(NH) D7982; 16A, bifurcating and anastomosing branches, × 17; 16B, medial autozooecia flanked by kenozooecia whose outlines are not visible, × 32; 16C, origin of a lateral ramification, × 64; 16D, pseudopores, × 290; see also Fig. 17.

Genus ***PROBOSCINOPORA*** nov.

TYPE SPECIES. *Proboscina divisi* Vine, 1893; Middle Jurassic, Cornbrash (probably basal Callovian), Thrapston, Northamptonshire.

DIAGNOSIS. Colony encrusting with regularly oligoserial branches which may bifurcate and occasionally produce lateral ramifications; basal gynozooecia lacking.

NAME. Like *Proboscina*.

REMARKS. Among Mesozoic and Cenozoic cyclostomes generally referred to the genus *Proboscina* Audouin, 1826 are several species in which gynozooecia have not been found in spite of the availability of large populations for study. Although recognizing the need for a new genus to accommodate such multiserial stomatoporids, Canu & Bassler (1920: 659) followed the tradition of using the name *Proboscina* while acknowledging that the type species of *Proboscina*, the Recent *P. boryi* Audouin, possessed a gynozooecium. In order to 'conserve' the name *Proboscina* for species without gynozooecia, they erected a new genus *Peristomoecia* (1920: 692) for *Proboscina*-like species possessing gynozooecia. *Peristomoecia* comprised, as well as its type species *Stomatopora divergens* Waters, 1904, two other species, one of which was *Proboscina boryi*. By this action they made *Peristomoecia* a subjective junior synonym of *Proboscina*, and did not solve the problem of the need for a genus to accommodate prosbosciniiform species lacking gynozooecia. Therefore, the new genus *Proboscinopora* is here created for species with colonies resembling those of *Proboscina* but lacking basal gynozooecia. These stomatoporids are characterized by their ribbon-like, narrowly multiserial (oligoserial) branches which maintain a relatively constant width and bifurcate at intervals. Branches are usually of low profile and smooth-surfaced.

The species composition of *Proboscinopora* has yet to be fully established; many species which possibly belong to the genus are too poorly described or known from too few specimens for the absence of basal gynozooecia to be inferred with confidence.

RANGE. Uncertain; species are known to occur in the British Bathonian, and at least one species, *Proboscinopora toucasiana* (d'Orbigny), is found in the Upper Cretaceous (Coniacian–Santonian, ?Campanian).

Proboscinopora marginata (d'Orbigny, 1853)

Figs 16–17

1853 *Proboscina marginata* d'Orbigny: 849; pl. 631, figs 12–14.

1899 *Proboscina crassa* (Roemer) var. *divaricata* d'Orbigny; Gregory: 35; pl. 2, fig. 8.

MATERIAL. BM(NH) 60538, Cunnington Colln (figd as *Proboscina crassa* (Roemer) var. *divaricata* (d'Orbigny) by Gregory, 1899: pl. 2, fig. 8); D5150 (2 specimens), D5151, Cunnington Colln; D6325, A. N. Davies Colln; D7982–3, Treacher Colln; D55319, Little Coxwell Pit, Gaster Colln; D55320, Bowler's Pit, Gaster Colln (questionably assigned to this species); D55412, Little Coxwell Pit, Taylor Colln.

DESCRIPTION. Zoarium adnate, with narrow multiserial, ribbon-like branches, generally 2–3 autozooecia in width, bifurcating irregularly and, less commonly, giving rise to lateral branches at right angles. Branches are low and flat, sometimes anastomosing, with a gently tapering selvedge of narrow kenozooecia (visible in wetted specimens).

Autozooecia are elongate, with small circular apertures a variable but large distance apart, and usually have short peristomes, though peristomes up to 0·3 mm have been observed; frontal walls are ornamented by rounded diamond-shaped pseudopores, about 1000 per mm^2.

MEASUREMENTS. TAM, 0·10–0·14 mm (mean 0·12 mm); TPM, 0·20–0·24 mm (mean 0·23 mm); FWL, 0·90–1·20 mm; FWW, mean 0·30 mm; BW, 0·50–1·00 mm.

REMARKS. The Faringdon material agrees well with d'Orbigny's original description of *P. marginata* from the Aptian of Les Croûtes (Aube), which emphasizes the presence of marginal kenozooecia ('cellules bordées'). Although d'Orbigny (1853) found an ancestrula from Les Croûtes, ancestrulae have not been observed in Faringdon specimens, with the exception of a small colony (BM(NH) D55320) tentatively assigned to *P. marginata* but not developing the characteristic selvedge of kenozooecia (which is possibly a late astogenetic feature, cf. Illies 1981). In this colony the protoecium is large (0·24 mm transverse diameter), and the ancestrula is 0·38 mm long with an aperture 0·09 × 0·08 mm; the earliest branch division occurs at a high angle.

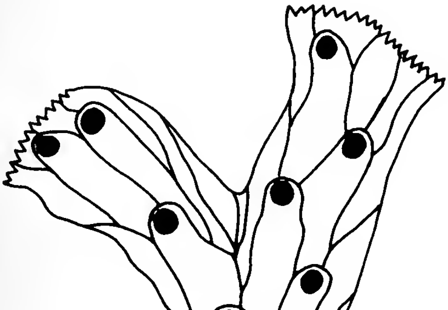


Fig. 17 Drawing of part of a branch of *Proboscinopora marginata* (d'Orbigny) in specimen BM(NH) D7982 showing the medial autozooecia and marginal kenozooecia whose outlines are visible when the specimen is immersed in water; × 21; see also Fig. 16.

Pergens (1889) regarded *P. marginata* and *P. ricordeauana* d'Orbigny, 1853 as conspecific, but this opinion seems unlikely on the basis of d'Orbigny's figures. Pergens also stated that d'Orbigny's specimens of these two species were worn, but this contradicts d'Orbigny's figures and suggests that Pergens may not have had d'Orbigny's original figured material at hand.

Faringdon specimens are usually found encrusting phosphatic or quartzose pebbles.

Stomatoporid sp. 1

Fig. 18

MATERIAL. BM(NH) D55115, Little Coxwell Pit, Gaster Colln; D55363, Little Coxwell Pit, Pitt Colln.

DESCRIPTION. Zoarium with branches of uniserially-arranged zooecia; new branches arise laterally, almost at right angles to the parent branch and about midway along a zooecium in the parent branch. Zooecia are extremely long and narrow; apertures are very small with no significant peristomes preserved. Pseudopores are not visible in the poorly-preserved specimens available. The ancestrula is unknown.

MEASUREMENTS. TAM, 0·07 mm; TPM, 0·14 mm; FWL, 0·6–1·0 mm; FWW, 0·16 mm.

REMARKS. This apparently undescribed species is represented by only two very poorly-preserved and fragmentary specimens, one (D55115) encrusting an oyster and the other (D55363) a sponge. The slender zooecia and lateral branching are quite characteristic, but in view of the preservation and absence of early growth stages it would be unwise to establish a new species.

In size and shape the zooecia resemble *Stomatopora longiscata* d'Orbigny (1853: pl. 629, figs 9–11), from the Cenomanian of northern France, which from d'Orbigny's figure appears to have a pattern of lateral branching. However, Pergens (1889) revised d'Orbigny's type of *S. longiscata* and showed the branching pattern to be dichotomous; the Faringdon species is therefore not regarded as conspecific with *S. longiscata*.

Lateral branching is a characteristic of *Voigtopora* among stomatoporids. Unlike the present Faringdon stomatoporid, however, species of *Voigtopora* have broad zooecia with long proximal prolongations flanking the next proximal zooecium in series (see p. 70). Generic attribution of the present species is therefore equivocal.

Stomatoporid sp. 2

Fig. 19

MATERIAL. BM(NH) D55106 (with *Plagioecia orbifera* and *'Berenicea' faringdonensis*), Little Coxwell Pit, Gaster Colln; D57596, Wicklesham Pit, Wilson Colln; D57724, Little Coxwell Pit, Elliott Colln; D57725, Little Coxwell Pit, Pitt Colln.

DESCRIPTION. Zoarium with branches of uniserially arranged zooecia. Branches bifurcate frequently, commonly at angles of about 90°, but varying between 45° and 100°. Internodes comprise between one and four zooecia, many having one or two zooecia. Early astogeny is unknown. Zooecia are small and slender, typically at their narrowest proximally.

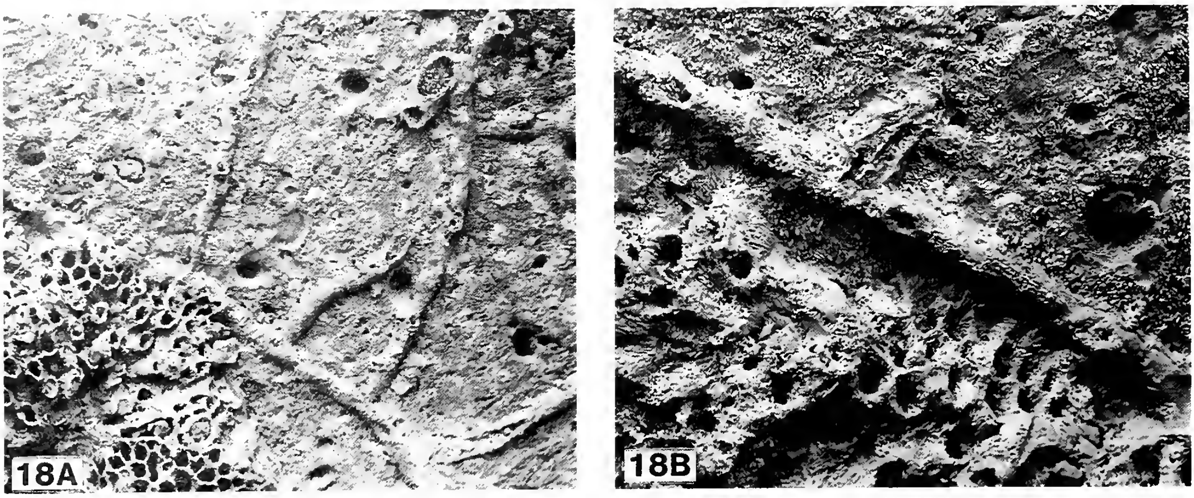


Fig. 18 Stomatoporid sp. 1, BM(NH) D55115; 18A, branches with lateral ramifications, × 14; 18B, elongate zooecia, × 40.

Apertures are small, and peristomes of significant length have not been observed.

Measurements. FWL, 0·39–0·51 mm; FWW (distal), 0·09–0·15 mm; FWW (proximal), 0·03–0·05 mm.

Remarks. Most of the available material of this species is fragmentary and poorly-preserved, with surface detail obscured by calcite cement or a ferruginous coating. The species is, however, clearly distinguishable from 'Stomatoporid sp. 1' by its smaller zooecia and bifurcating branches.

Family **ONCOUSOECIIDAE** Canu, 1918

Genus ***ONCOUSOECIA*** Canu, 1918

Type species. *Tubulipora lobulata* Hincks, 1880 (=*Alecto dilatans* Johnston, 1847; see Hastings 1963), by original designation; Recent.

Remarks. It was common practice for early palaeontologists (e.g. Gregory 1896, 1899) to assign all tubuliporinid species with ribbon-like encrusting colonies (probosciniform) to the Recent genus *Proboscina* Audouin (see above, p. 74). Several Mesozoic species of '*Proboscina*' possess gynozooecia (e.g. Walter 1970) which resemble those of the Recent type species of *Oncousoecia*. The gynozooecium in *Oncousoecia* is typically small, has a longitudinally elongate distal part and a transversely elliptical ooeciopore a little smaller than an autozooecial aperture.

Range. Aalenian to Recent.

Oncousoecia coarctata (Canu & Bassler, 1926)

Figs 20–22

1926 *Proboscina coarctata* Canu & Bassler: 8; pl. 28, fig. 1.
1926 *Proboscina ricordeauana* (d'Orbigny); Canu & Bassler: 7; pl. 27, figs 7–8.
1986 '*Proboscina coarctata*' Canu & Bassler; Wilson: 693.

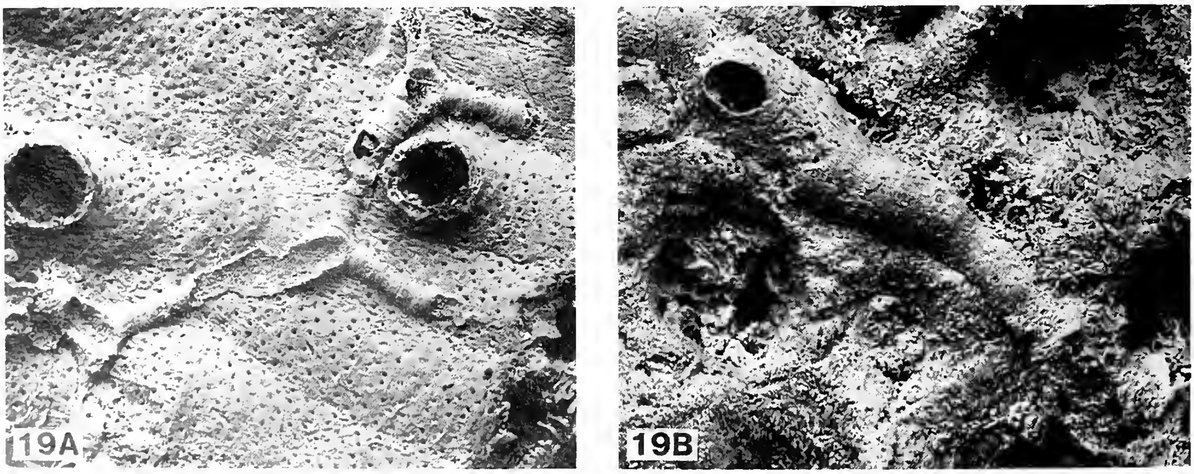
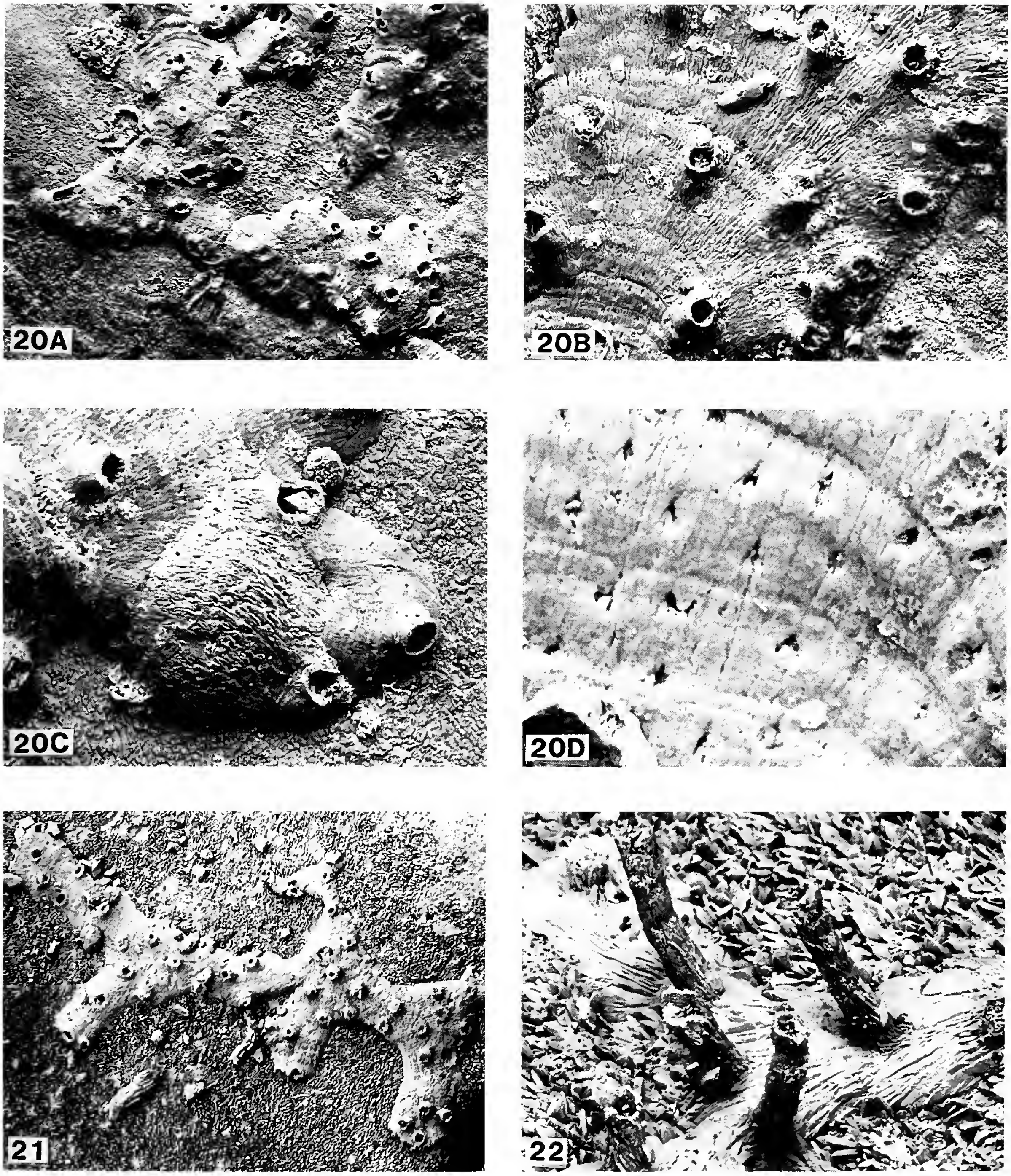


Fig. 19 Stomatoporid sp. 2, BM(NH) D55106; 19A, abraded zooecia overgrowing '*Berenicea*' *faringdonensis*, × 79; 19B, well-preserved zooecium, × 142.



Figs 20–22 *Oncousoecia coarctata* (Canu & Bassler). Fig. 20, USNM 69000, holotype; 20A, fractured lobate branches, × 26; 20B, autozooecia, × 73; 20C, gynozooecium, × 100; 20D, autozooecial pseudopores, × 400. Fig. 21, BM(NH) D55095, small colony, × 17. Fig. 22, BM(NH) D55094, exceptionally long peristomes, × 78.

HOLOTYPE. USNM 69000, figd by Canu & Bassler (1926: pl. 28, fig. 1).

OTHER MATERIAL. BM(NH) 60537 (with *Voigtopora calypso*); D6326 (with *'Stomatopora' melvillei*), A. N. Davies Colln; D55094–5, D55189–90, D57393, D57395, Little Coxwell Pit, Pitt Colln; D55188, Bowler's Pit, Pitt Colln; D55432, D55434 Wicklesham Pit, Wilson Colln.

DESCRIPTION. Colony adnate, consisting of narrow oligoserial branches usually between 2 and 8 zooecia wide, sometimes flabellate. Branches have a characteristically low relief and flat surface. Branch division is normally dichotomous at angles between 60° and 80°, but branches occasionally trifurcate. Episodic growth is suggested by the occurrence of flabellate branches with rounded distal margins from which proximally constricted daughter branches arise; apparent severing of one such daughter branch from its parent is observable in the holotype. Ancestrulae are rarely preserved; in specimen BM(NH) D57395 the ancestrula is 0·23 mm long and has a protoecium 0·14 mm in transverse diameter.

Autozooecia are small, slender, immersed (i.e. their frontal outlines are poorly visible) and sometimes have a transversely wrinkled frontal wall. Pseudopores are sparse (750–900 per mm^2.) and dart-shaped (Fig. 20D). Apertures are widely spaced, small, circular or transversely elliptical, usually with a thin-walled, low peristome; however, peristomes up to 0·45 mm long are preserved in a recess in specimen BM(NH) D55094 (Fig. 22).

Gynozooecia (Fig. 20C) are small, orbicular, slightly longer than wide, and have a terminal ooeciopore which is a little smaller than an autozooecial aperture.

MEASUREMENTS. LAM, 0·06–0·09 mm; TAM, 0·06–0·09 mm; FWL, 0·59–0·74 mm; FWW, 0·14–0·15 mm; GDL, 0·32–0·40 mm; GW, 0·25–0·39 mm; LOPM, 0·05 mm; TOPM, 0·06 mm; BW, 0·27–0·90 mm.

REMARKS. Unfortunately, Canu & Bassler (1926) chose an exceptional specimen as their type of *Proboscina coarctata*. This specimen has strongly flabellate branches (Fig. 20A), constricted at intervals and giving rise to daughter branches, and lacks the dichotomously branching pattern of most apparently conspecific specimens from Faringdon. The gynozooecia (Fig. 20C) present in this specimen apparently went unnoticed by Canu & Bassler.

The *Proboscina ricordeauana* d'Orbigny of Canu & Bassler (1926) appears identical to *P. coarctata*, and is unlike true *P. ricordeauana* d'Orbigny in which the branches are more convex. According to Pergens (1889), *P. ricordeauana* is probably conspecific with *P. marginata* (see p. 74), an opinion not supported by d'Orbigny's (1853) figures of the two species.

O. coarctata is a common species at Faringdon and can be found encrusting a variety of substrates including phosphatic pebbles, oyster shells and sponges.

Oncousoecia parvula (Canu & Bassler, 1926)

Figs 23–24

1926 *Berenicea parvula* Canu & Bassler: 10; pl. 28, figs 8–9.

1926 *Microecia cornucopia* (d'Orbigny); Canu & Bassler: 37; pl. 28, figs 5–7.

1926 *Proboscina virgula* (d'Orbigny); Canu & Bassler: 8; pl. 27, figs 9–10.

1986 *'Proboscina'* sp. B; Wilson: pl. 53, fig. 3.

MATERIAL. BM(NH) D52200 (8 specimens), D55180, Little Coxwell Pit, Pitt Colln; D55124 (with *Idmonea denticulata* and *Reptoclausa hagenowi*), Little Coxwell Pit, Gaster Colln; D55179, Little Coxwell Pit, Curry Colln; D53225 (with *Stomatoporina alternata*), Little Coxwell Pit, Taylor Colln; D55181, D57425–6, Little Coxwell Pit, Thomas Colln; D55422 (figd as *'Proboscina'* sp. B by Wilson 1986: pl. 53, fig. 3), D55435, Wicklesham Pit, Wilson Colln. USNM 69837 (figd as *Proboscina virgula* (d'Orbigny) by Canu & Bassler 1926: pl. 27, figs 9–10); 69882 (figd as *Microecia cornucopia* (d'Orbigny) by Canu & Bassler 1926: pl. 28, figs 5–7).

DESCRIPTION. Colony adnate, consisting of narrow (up to 0·90 mm wide), oligoserial branches (Fig. 24A), seldom bifurcating, usually 3–5 zooecia wide, sometimes flabellate, and flat to slightly convex in cross section.

Autozooecia are very small, visible for most of their length, with transversely wrinkled, convex frontal walls (Fig. 24C). Apertures are small, longitudinally elongate, arranged roughly in quincunx and are closely-spaced with moderately raised peristomes.

Gynozooecia (Figs 23B, 24D) are small, with an orbicular distal part which may be bulbous. The ooeciopore is terminal and slightly transversely elongated, a little larger than an autozooecial aperture, with a prominent but short ooeciostome.

MEASUREMENTS. LAM, 0·06–0·08 mm; TAM, 0·04–0·06 mm; FWL, 0·20–0·36 mm; FWW, 0·09–0·12 mm; GDL, 0·50 mm; GW, 0·30 mm; LOSM, 0·08 mm; TOSM, 0·12 mm.

REMARKS. This species was originally described by Canu & Bassler (1926) as *Berenicea parvula*, although their description and figures clearly indicate that the colony-form of their material was probosciniform rather than bereniciform. The type specimen of *B. parvula* is apparently missing from the collections of the USNM; a specimen bearing the registration number of the type (USNM 69842) belongs to a different species with much larger zooecia.

The *Microecia cornucopia* (d'Orbigny) of Canu & Bassler (1926), here synonymized with *O. parvula*, is not conspecific with d'Orbigny's species which is from the Upper Cretaceous of France. D'Orbigny's figures (1853: pl. 634, figs 7–9) are comparatively uninformative, but Gregory (1899) described some British Upper Cretaceous specimens as *P.cornucopia* which resemble the specimens figured by d'Orbigny. These specimens are not conspecific with *O. parvula*, which has narrower and less clearly flabellate branches and smaller zooecia. Canu & Bassler (1926) also mis-assigned specimens of *O. parvula* to *Proboscina virgula* (d'Orbigny), a Cenomanian species with branches distinctly subtriangular in cross-sectional shape (see d'Orbigny 1853: pl. 631, figs 15–17).

Specimens of *O. parvula* occur as small, delicate colonies mostly encrusting fragments of bivalves, brachiopods and other bryozoans.

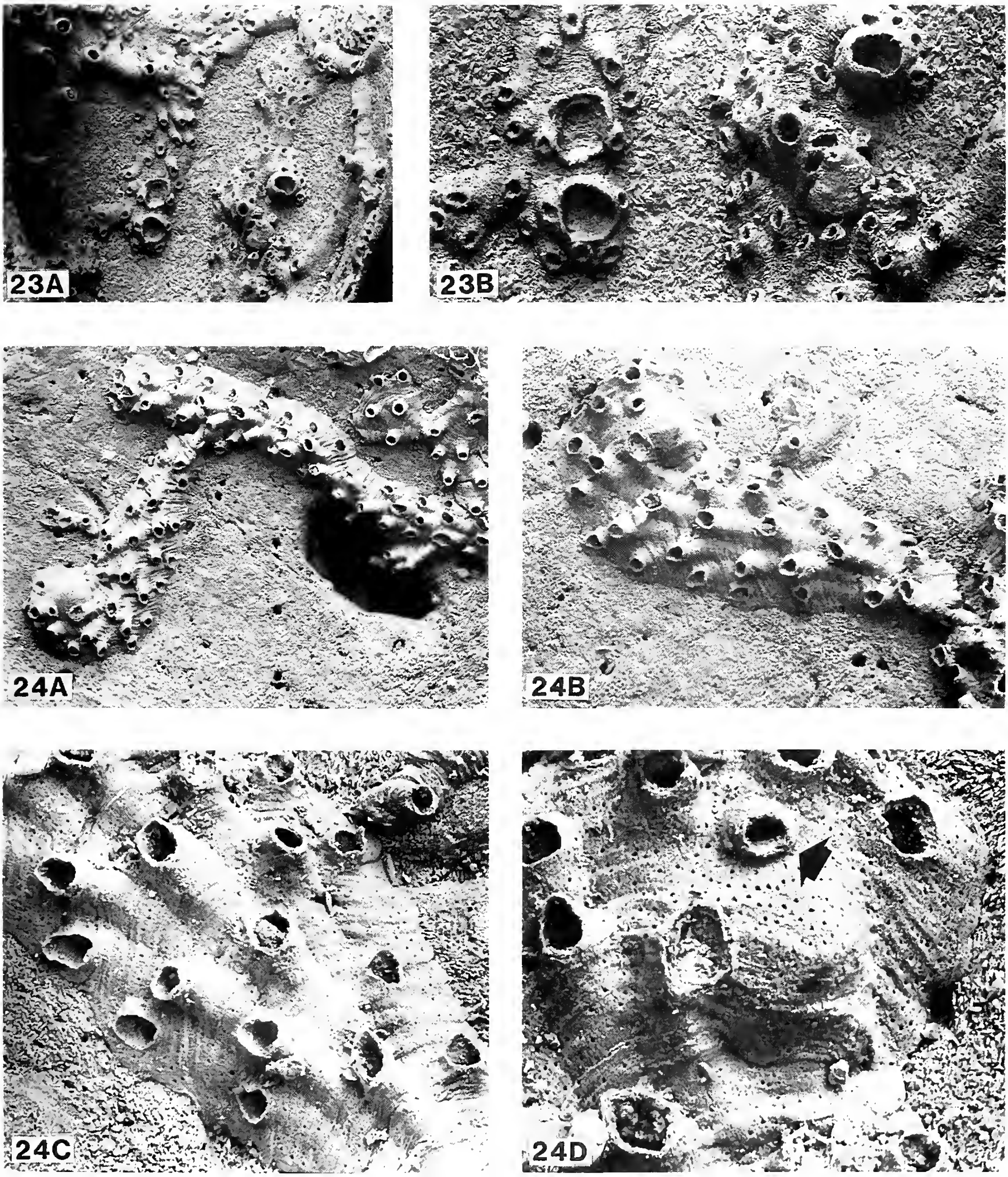
Oncousoecia depressa (d'Orbigny, 1850, *sensu* Canu & Bassler, 1926)

Figs 25–26

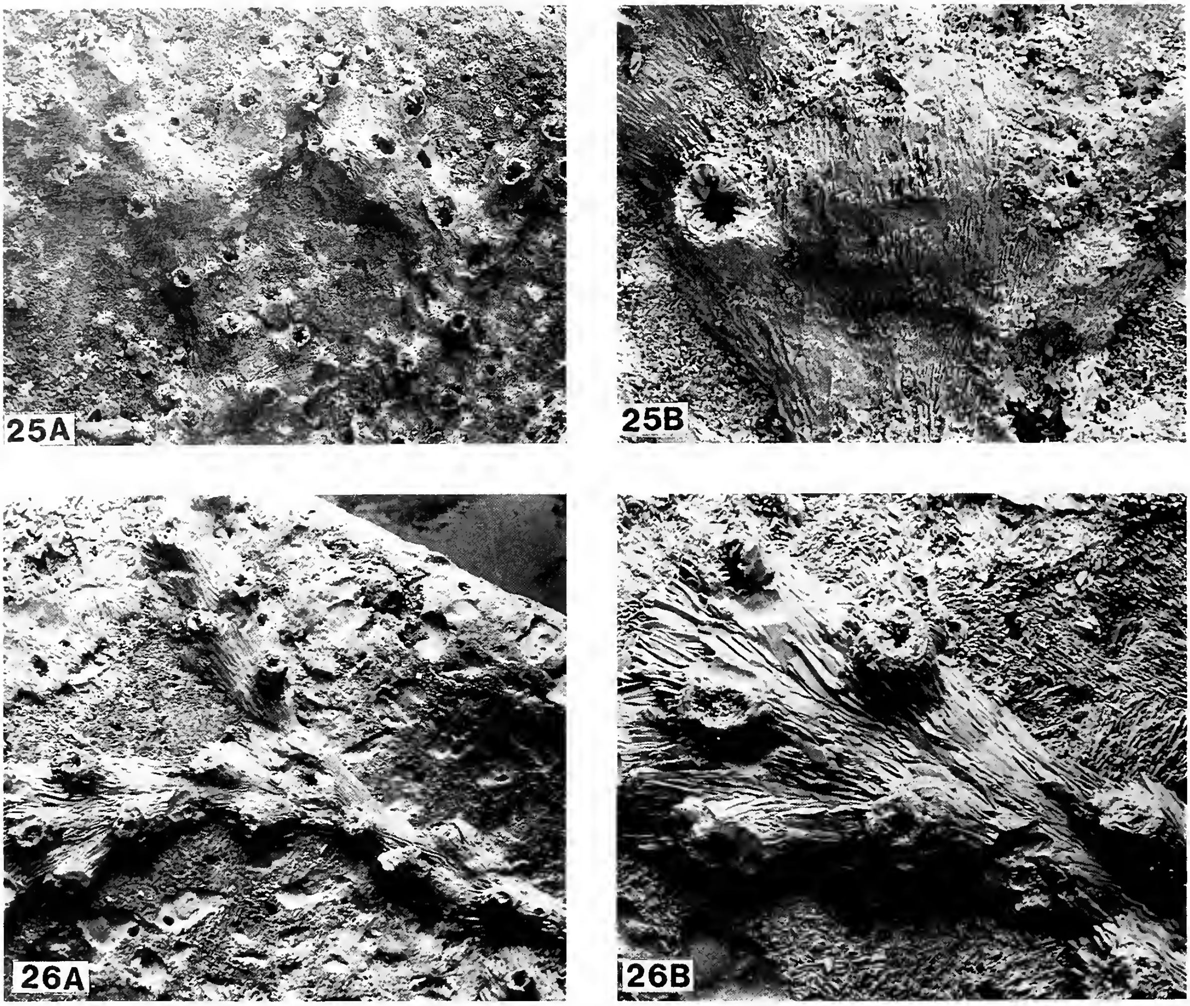
?1850 *Idmonea depressa* d'Orbigny: 109.

?1853 *Proboscina depressa* (d'Orbigny) d'Orbigny: 849; pl. 631, figs 12–14.

1926 *Proboscina depressa* (d'Orbigny); Canu & Bassler: 8; pl. 27, figs 5–6.



Figs 23–24 *Oncousoecia parvula* (Canu & Bassler). Fig. 23, BM(NH) D55422; 23A, colony branches encrusting the interior of a bivalve boring along with *Stomatopora*, × 16; 23B, numerous gynozooecia in two branches growing in opposite directions, × 35. Fig. 24, BM(NH) D55124; 24A, × 27; 24B, × 41; 24C, autozooecia, × 99; 24D, gynozooecium with ooeciopore arrowed, × 130.



Figs 25–26 *Oncousoecia depressa* (d'Orbigny, *sensu* Canu & Bassler). Fig. 25, BM(NH) D57430; 25A, × 19; 25B, gynozooecium (ooeciopore apparently obscured by calcite cement), × 48. Fig. 26, BM(NH) D55313; 26A, × 21; 26B, coarsely-preserved autozooecia, × 50.

MATERIAL. BM(NH) D55313, Little Coxwell Pit, Gaster Colln; D57430, Little Coxwell Pit, Pitt Colln. USNM 69483 (figd by Canu & Bassler, 1926: pl. 27, figs 5–6).

DESCRIPTION. Zoaria are encrusting, initially uniserial but becoming oligoserial, with somewhat flabellate branches, 2–3 zooecia wide, which bifurcate frequently. Branches are relatively flat and low.

Autozooecia are moderately large but of variable size, with slightly convex frontal walls visible for most of their length. Apertures are circular or longitudinally elliptical and widely spaced, and peristomes are little raised.

Gynozooecia (Fig. 25B) have small, inverted pear-shaped distal frontal walls and a transversely elongate ooeciopore.

MEASUREMENTS. LAM, 0·11–0·15 mm; TAM, 0·12–0·15 mm; FWL, 0·86–1·07 mm; FWW, 0·21–0·30 mm; GW, 0·50 mm; GDL, 1·10 mm; TOSM, 0·08 mm; LOSM, 0·04 mm; TOPM, 0·04 mm; LOPM, 0·03 mm.

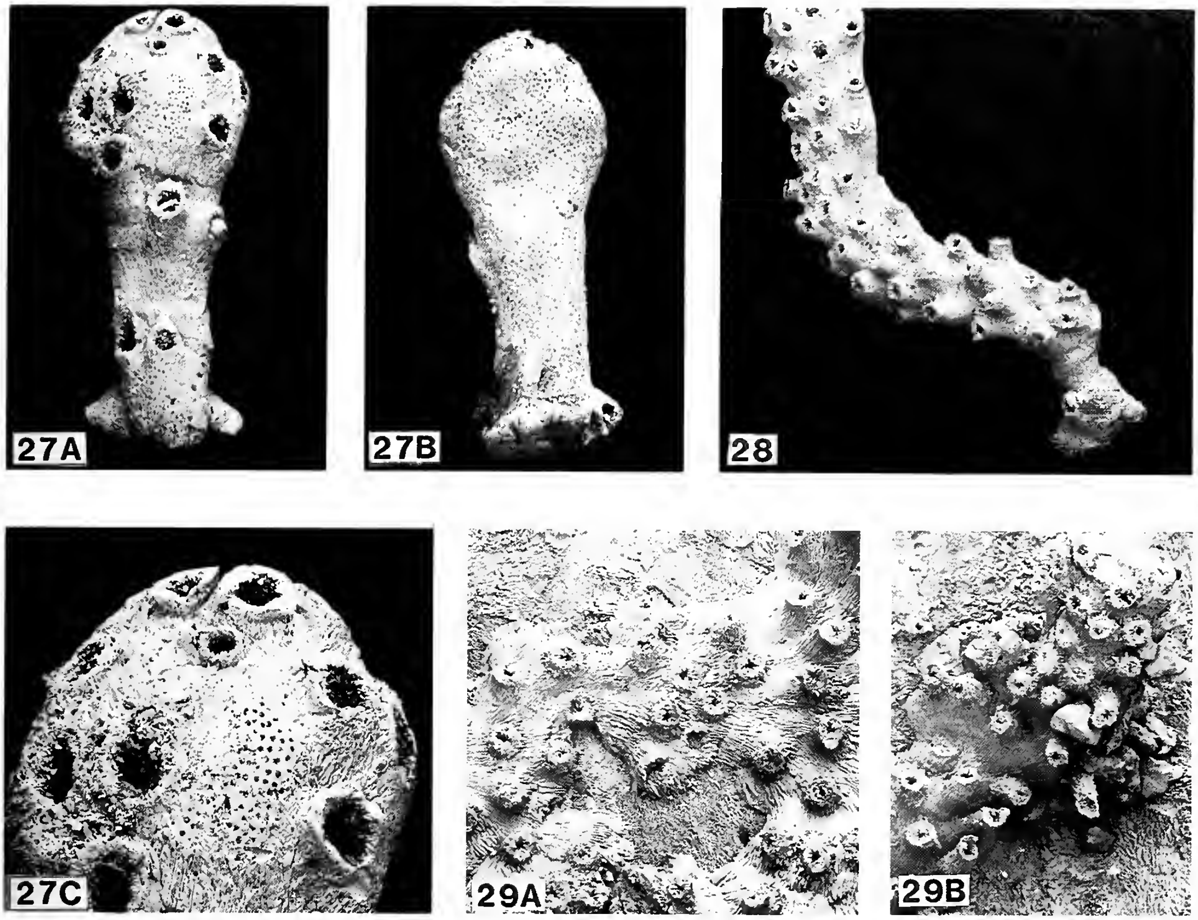
REMARKS. D'Orbigny (1850, 1853) described a species from the Neocomian of France which Canu & Bassler (1926) later identified from Faringdon under the name *Proboscina depressa* (d'Orbigny). However, it is difficult to be certain that the French and Faringdon specimens are conspecific in view of the relatively undistinctive morphology of the species and the absence of a revision of d'Orbigny's type material; Pergens (1889) merely records the occurrence of a worn colony in the d'Orbigny Collection. Therefore, the Faringdon material is here redescribed as *depressa, sensu* Canu & Bassler, 1926.

The gynozooecia and low profile of the branches allow generic assignment to *Oncousoecia.* The species can be distinguished from other Faringdon species of *Oncousoecia* by its larger zooecia.

Genus ***FILISPARSA*** d'Orbigny, 1853

TYPE SPECIES. *Filisparsa neocomiensis* d'Orbigny, 1853, by subsequent designation of Gregory, 1899; Neocomian, France.

REMARKS. *Filisparsa* is an oncousoeciid in which colonies develop erect branches with autozooecia opening only on the obverse surfaces of branches; reverse surfaces comprise exterior basal walls of the autozooecia. Walter (1972) regarded the type species, *F. neocomiensis* d'Orbigny, as an erect form of



Figs 27–29 *Filisparsa gasteri* sp. nov. Fig. 27, BM(NH) D55379, **holotype**; 27A, obverse side of branch, × 25; 27B, reverse side of branch, × 23; 27C, gynozooecium, × 70. Fig. 28, BM(NH) D55381, branch obverse, × 18. Fig. 29, BM(NH) D57427, colony base; 29A, encrusting zooecia, × 24; 29B, base of erect stem, × 20.

Stomatopora granulata (Milne Edwards), and therefore rejected the genus *Filisparsa*.

Gynozooecia have apparently not been described in *F. neocomiensis*, but the occurrence of ovoidal gynozooecia in *F. gasteri* sp. nov. (see below) and in several Upper Cretaceous species assigned to *Filisparsa* by Brood (1972), implies that *Filisparsa* is not a stomatoporid. Brood (1972) proposed a new family, Filisparsidae, with *Filisparsa* as type genus. This was necessary because he did not accept the family Oncousoeciidae. The Filisparsidae is here regarded as synonymous with the Oncousoeciidae.

Hinds (1975) described the mode of growth of *Filisparsa* and similar genera, noting that the diagnosis of the genus is broad and *Filisparsa* may be polyphyletic.

RANGE. Lower Cretaceous (Neocomian) to Recent.

Filisparsa gasteri sp. nov. Figs 27–29

HOLOTYPE. BM(NH) D55379, Little Coxwell Pit, Pitt Colln.

PARATYPES. BM(NH) D55380, Little Coxwell Pit, Thomas Colln; D55381, D55383, Little Coxwell Pit; D55382, D57427, Little Coxwell Pit, Pitt Colln; D55384, D55385, Little Coxwell Pit, Elliott Colln; D55386, Little Coxwell Pit, Taylor Colln.

NAME. For Christopher T. A. Gaster, who presented his large collection of Cretaceous invertebrates, including many Bryozoa, to the BM(NH) in 1938 and 1950.

DESCRIPTION. Known specimens are small, the largest observed erect branch being 4·3 mm high and 0·70 mm wide (BM(NH) D55381). Erect branches are compressed and have an obverse surface bearing autozooecial apertures in 3–4 rows, and a flat reverse surface comprising the exterior basal walls of the autozooecia (Fig. 27B); they have not been observed to bifurcate. Branch edges may be smooth or may have a serrated appearance due to the projecting peristomes of the marginal zooecia. The encrusting base (Fig. 29) is fairly extensive and consists of bifurcating oligoserial branches about 3–4 zooecia in width; several erect branches may arise from the colony base, each formed by the upturning of the distal end of an encrusting branch.

Autozooecia are variable in length and have elongate, slightly convex frontal walls, small circular to longitudinally elongate apertures, and moderately raised peristomes.

Gynozooecia (Fig. 27C) are borne on the erect branches, and are very small with longitudinally ovate dilated distal frontal walls, very short proximal frontal walls, and a small transversely elliptical ooeciopore.

MEASUREMENTS. TAM, 0·08–0·10 mm; FWL, 0·27–0·50 mm;

FWW, 0·17–0·20 mm; GTL, *c.* 0·78 mm; GW, *c.* 0·34 mm; LOSM, *c.* 0·08 mm; TOSM, *c.* 0·10 mm; LOPM, *c.* 0·05 mm; TOPM, *c.* 0·06 mm.

REMARKS. This uncommon species differs from *F. neocomiensis* d'Orbigny by having more closely-spaced apertures (see d'Orbigny 1853: pl. 760, figs 10–13), and lacking the distinct cresent-shaped growth lines depicted by d'Orbigny on branch reverse surfaces. However, a precise evaluation of the distinctions and relationships between the two species must await a modern revision of d'Orbigny's type specimens.

Family **MULTISPARSIDAE** Bassler, 1935
(= MACROECIIDAE Canu, 1918)

Genus ***REPTOCLAUSA*** d'Orbigny, 1853

TYPE SPECIES. *Reptoclausa neocomiensis* d'Orbigny, 1853, by subsequent designation of Bassler, 1935; Valanginian of Ste Croix (Switzerland).

REMARKS. The type species of *Reptoclausa* has been revised by Hillmer (1971). The genus is distinguished by its characteristic colony form; colonies are sheet-like and have autozooecia located on ridges which form subcolonies separated by expanses of kenozooecia. *Reptoclausa* appears to be closely related to *Idmonea* (see below, p. 84). The autozooecial ridges may be homologous with the branches of the latter genus, and the kenozooecia equivalent to the kenozooecia which often form a selvedge on the flanks of the branches of *Idmonea*.

Species of *Reptoclausa* differ from one another in the shapes and relationships of the autozooecial ridges. In *R. neocomiensis* the ridges are short and taper both distally and proximally; new ridges arise from areas of kenozooecia and are not connected with established ridges. A similar arrangement occurs in *R. hagenowi* (see below), but the ridges are typically longer. Furthermore kenozooecia in *R. hagenowi* are extremely slender, whereas those of *R. neocomiensis* have hexagonal frontal walls only slightly smaller in area than the autozooecial frontal walls. A Jurassic species of *Reptoclausa*, *R. porcata* Taylor, 1980, has kenozooecia which resemble those of *R. hagenowi*, but the autozooecial ridges are more rounded in profile and new ridges arise by the bifurcation of established ridges.

RANGE. Aalenian to Maastrichtian.

Reptoclausa hagenowi (Sharpe, 1854) Figs 30–33

1854	*Lopholepis hagenovii* [sic] Sharpe: 196; pl. 5, fig. 7a–d.
1899	*Idmonea hagenowi* (Sharpe) Gregory: 150; pl. 8, figs 1a–b.
1926	*Reptoclausa hagenowi* (Sharpe) Canu & Bassler: 82; pl. 18, figs 2–5.
1981	*Reptoclausa neocomiensis* d'Orbigny; Voigt: fig. 1i.
1986	*Reptoclausa hagenowi* (Sharpe); Wilson: pl. 53, fig. 9.

LECTOTYPE. BGS 7560, Sharpe Colln, designated herein as lectotype.

PARALECTOTYPE. BGS 7561, Sharpe Colln.

OTHER MATERIAL. BM(NH) 55110 (figd by Gregory 1899: pl. 8, fig. 1a, b); 51164, J. Sharp Colln; D3026, D3139, D50392, ?Colln; D3140, D3141, Charlesworth Colln; D4503 (4), Cunnington Colln; D7166, Ellis Colln; D50391, Wicklesham Pit, Pitt Colln; D52185–6, Little Coxwell Pit, Pitt Colln; D55118, D55124 (with *Oncousoecia parvula* and *Idmonea denticulata*), D55322–3, Little Coxwell Pit, Gaster Colln; D55119, Gaster Colln; D55321 (12), D57436, Little Coxwell Pit, Cleevely Colln; D55324, ?Little Coxwell Pit, Cleevely Colln; D55420 (figd by Wilson 1986: pl. 53, fig. 9), D55434, Wicklesham Pit, Wilson Colln; D57433–4, Little Coxwell Pit, Thomas Colln; D57435, Hinde Colln.

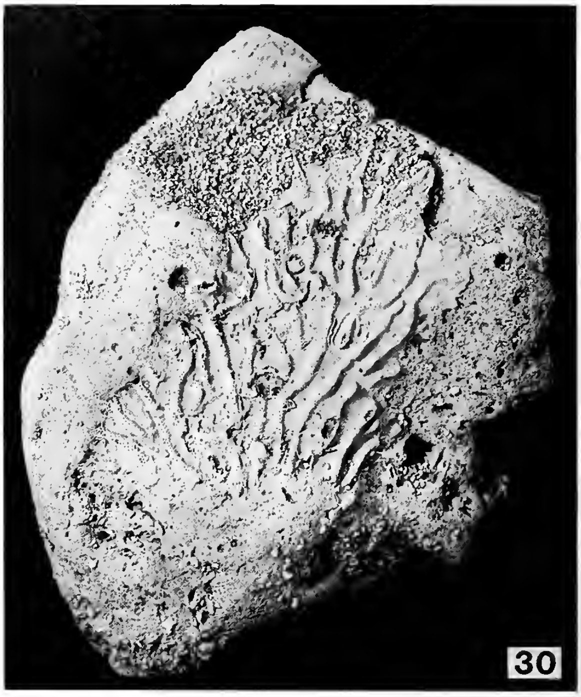
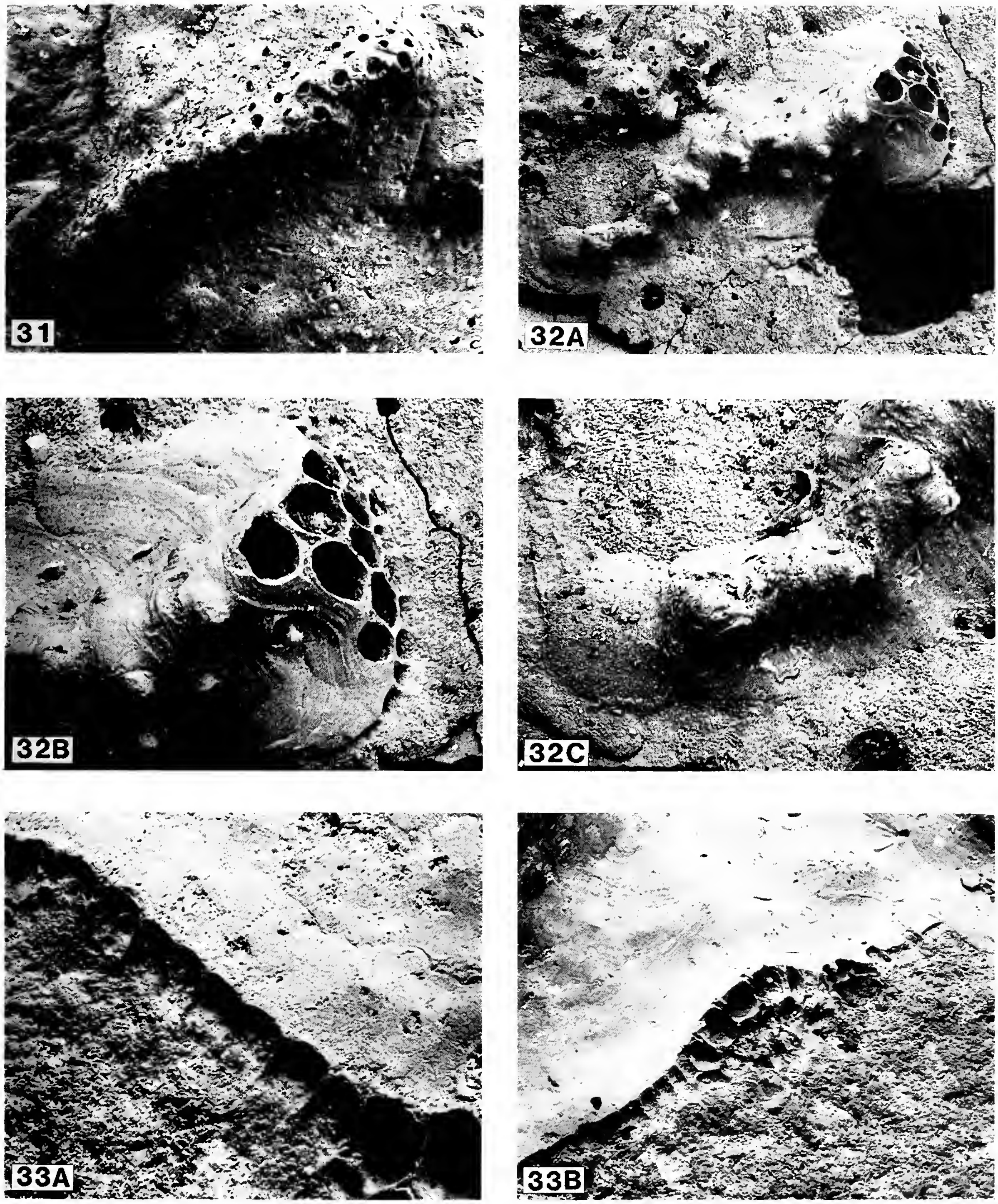


Fig. 30 *Reptoclausa hagenowi* (Sharpe), BM(NH) D50391, optical photograph of large colony encrusting a cobble, × 1·5.

DESCRIPTION. Zoarium adnate, sheet-like, with ridges composed of autozooecia forming elongate subcolonies (up to 12 mm long by 0·6–0·8 mm wide) separated by depressed areas of kenozooecia (Fig. 30). Autozooecial ridges may be sinuous. New ridges arise at the growing edge between existing ridges (i.e. individual subcolonies are not in continuity with one another), and ridges may taper in height and width and disappear distally. Zoaria are very thin and their surfaces are featureless between ridges.

The ancestrula has a large protoecium (diameter 0·35 mm) and a short distal tube (0·45 mm) which bends to one side (Fig. 32C). Early post-ancestrular zooecia also bend, some to the right and some to the left. Young colonies are V-shaped wedges (Fig. 32A) and consist of a single autozooecial ridge increasing in elevation distally and flanked by a selvedge of kenozooecia. During later growth the ancestrula is overgrown, and new autozooecial ridges are added in orientations approximately at right angles to the initial autozooecial ridge.

Autozooecia are immersed, have slight peristomes and subcircular apertures which are sometimes occluded by terminal diaphragms, especially in autozooecia at the bases of

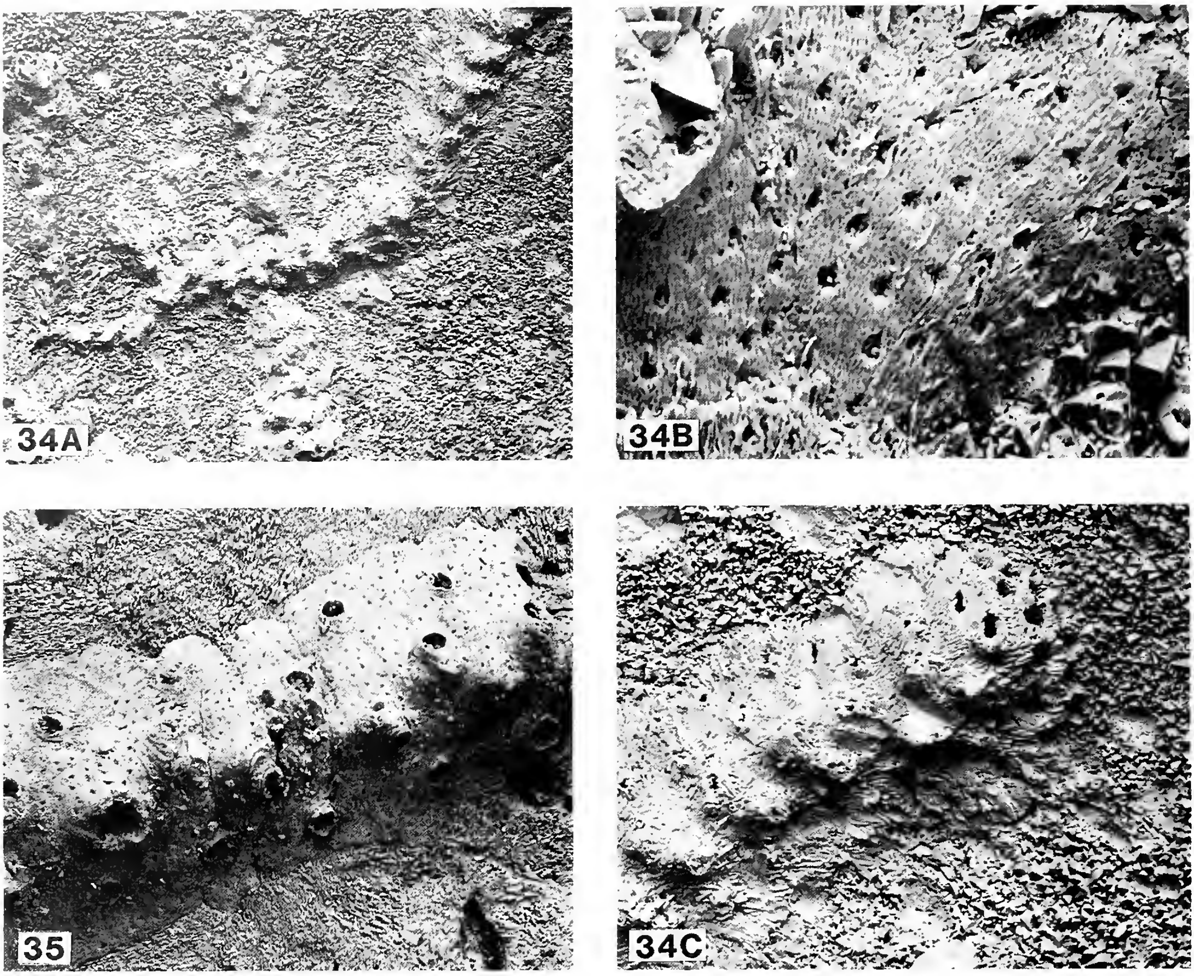


Figs 31–33 *Reptoclausa hagenowi* (Sharpe). Fig. 31, BM(NH) D55119, ridge of autozooecia, ×15. Fig. 32, BM(NH) D55124, small colony; 2A, × 19; 32B, growth margin, × 43; 32C, ancestrula (with large protoecium) and early budded zooecia, all with apertures turned to the right, × 81. Fig. 33, BM(NH) D55118; 33A, kenozooecial buds at the growth margin, ×120; 33B, newly-forming autozooecial ridge, × 31.

he ridges adjoining the regions of kenozooecia. Apertural liameter characteristically increasing from the base to the rest of the ridges, and apertures on either side of the ridge rest are arranged in alternating rows. About 1600 pseudo-ores per mm^2 occur on autozooecial frontal walls.

Kenozooecia are immersed, poorly defined, and have slender frontal walls; they are most easily visible as tiny buds at the growing edge between the autozooecial ridges (Fig. 33A).

Gynozooecia are situated on ridge crests, may be very



Figs 34–35 *Idmonea denticulata* (Canu & Bassler). Fig. 34, USNM 69936, holotype; 34A, early parts of colony with lateral branch ramifications, × 17; 34B, autozooecial pseudopores, × 340; 34C, growth tip, × 39. Fig. 35, BM(NH) D55124, × 58.

inconspicuous and are usually abraded. They have a longitudinally elliptical shape with a minute ooeciopore.

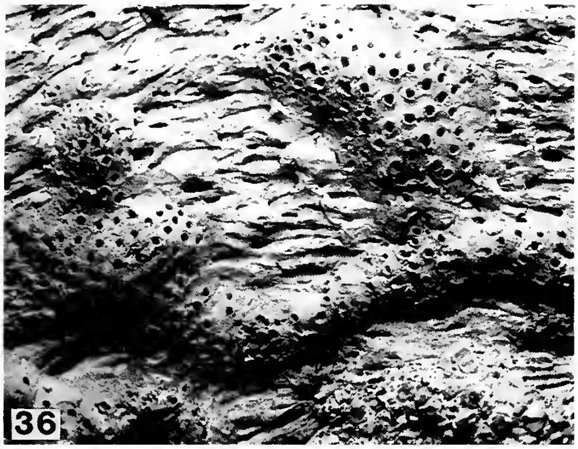
MEASUREMENTS. TAM (top of ridges), 0·10–0·12 mm; TAM (sides of ridges), 0·06–0·08 mm; GDL, *c*. 1·0 mm; GW, *c*. 0·75 mm.

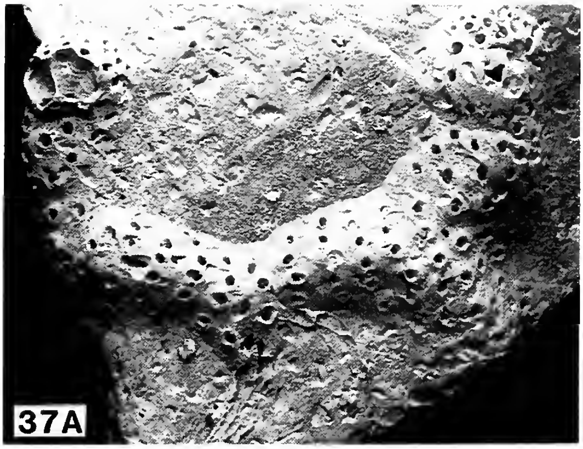
REMARKS. This is a very common and distinctive species at Faringdon. Colonies are often found encrusting quartzose or claystone pebbles (e.g. Fig. 30), but may also occur on bivalve shells and sometimes on brachiopods and echinoid spines. Wilson (1986) interpreted *R. hagenowi* as being well-adapted to the physically rigorous habitats afforded by the exteriors of claystone pebbles in the Red Gravels. However, the robust construction of the colonies may also have contributed to their occurrence in this habitat. Indeed, many specimens of *R. hagenowi* evidently survived extensive abrasion, probably post-mortem, which often resulted in truncation of the ridge crests.

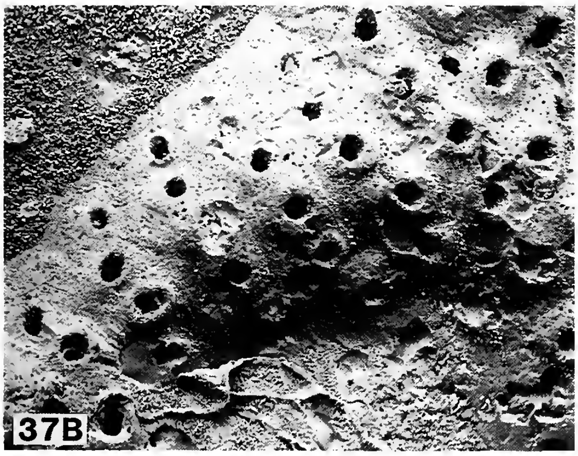
Genus ***IDMONEA*** Lamouroux, 1821.

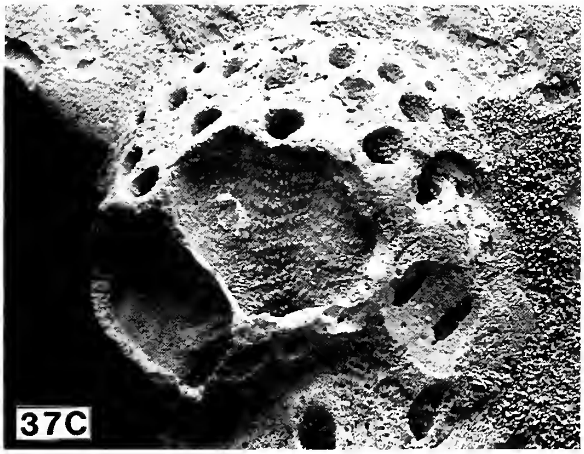
TYPE SPECIES. *Idmonea triquetra* Lamouroux, 1821, by monotypy; Bathonian, Normandy (see Mongereau & Walter 1965; Walter 1970).

REMARKS. *Idmonea* has been used by Mesozoic palaeontologists in a way different from neontologists. The latter have commonly referred erect tubuloporine species with branches of a subtriangular cross section to this genus (but cf. Harmelin 1976). However, the Jurassic type species is a tubuloporine with encrusting branches, subtriangular in cross section and with a selvedge of kenozooecia which does not coalesce with that of other branches to form a continous sheet (cf. *Reptoclausa*). 'Adventitious' branches sometimes originate from the kenozooecial selvedge. From the encrusting base erect branches may arise, having an ovoidal cross-sectional shape with autozooecial apertures opening on one side of the branch and kenozooecia on the other. These erect branches









Figs 36–37 *Idmonea radiolitorum* d'Orbigny. Fig. 36, BM(NH) D55201, colony encrusting a bone, × 13. Fig. 37, BM(NH) D52199; 37A, colony encrusting a shell fragment, × 14; 37B, autozooecia, × 30; 37C, gynozooecia with worn frontal walls, × 65.

are quite unlike the erect branches of so-called *Idmonea* from the Recent. It is uncertain whether any of the numerous erect post-Mesozoic species which have been assigned to *Idmonea* really belong to this genus (see Hinds 1975 for a revision of some Tertiary species of '*Idmonea*').

RANGE. Aalenian to ?Recent.

Idmonea denticulata (Canu & Bassler, 1926)

Figs 34–35

1926 *Reptoclausa denticulata* Canu & Bassler: 82; pl. 18, fig. 1.

HOLOTYPE. USNM 69936, figd Canu & Bassler 1926: pl. 18, fig. 1.

OTHER MATERIAL. BM(NH) D50392, ?Colln; D55124 (with *Reptoclausa hagenowi* and *Oncousoecia parvula*), D55237, D55244, Little Coxwell Pit, Gaster Colln; D55233, Little Coxwell Pit, Pitt Colln; D55438, D57596, Wicklesham Pit, Wilson Colln.

DESCRIPTION. Zoarium adnate, with gently sinuous branches of subtriangular section, seldom dividing (Fig. 35). Branches are generally about 0·6 mm in width and have a narrow selvedge of kenozooecia which are often inconspicuous. New branches arise occasionally by bifurcation but more often 'adventitiously' (Fig. 34A) from the selvedge of kenozooecia at the margin of the parent branch with which they make an angle of about 90°. Branch growth tips are rounded (Fig. 34C).

Autozooecia have short frontal walls, convex distally (particularly in zooecia at branch crests) but well immersed proximally. Distal parts of zooecia close to the branch crest are turned away from the crest. Apertures are small and circular, somewhat transversely elongated; those close to the branch crest are often slightly larger than apertures immediately adjacent to the kenozooecial selvedge, where terminal diaphragms are more frequently developed. Preserved peristomes are short and diverge from the midline of the branch. Pseudopores (Fig. 34B) are teardrop-shaped, pointed distally, and occur at a density of about 1900 per mm^2.

Gynozooecia have not been observed.

MEASUREMENTS. LAM, 0·05 mm; TAM, 0·05–0·06 mm; FWL, 0·27–0·41 mm; FWW, 0·12–0·15 mm.

REMARKS. Canu & Bassler (1926) assigned this species to the genus *Reptoclausa* d'Orbigny. However, the basal selvedge of kenozooecia only surrounds the individual branches and does not occupy the area of substratum between branches in the manner of *Reptoclausa* (see p. 82).

In the absence of gynozooecia, assignment to *Idmonea* must be provisional. Gynozooecia in the type species of *Idmonea* (*I. triquetra* Lamouroux) are longitudinally elongate.

Canu & Bassler's holotype of *I. denticulata* is a poor specimen in which the 'denticulated peristomes' are apparently a result of growth of diagenetic calcite crystals. The kenozooecial selvedge of *I. alipes* Gregory, 1899, with which Canu & Bassler compared their new species, is much broader than that of *I. denticulata*. *I. triquetra*, from the Middle Jurassic, differs in having branches which bifurcate more regularly and autozooecia with slightly raised margins to their subhexagonal frontal walls.

This is a relatively rare species at Faringdon where it is found encrusting oyster shells and pebbles. It is recognizable by the rather straggly, seldom-dividing branches.

Idmonea radiolitorum d'Orbigny, 1850 Figs 36–37

1850 *Idmonea radiolitorum* d'Orbigny: 200.
1851 *Proboscina radiolitorum* (d'Orbigny) d'Orbigny: 854; pl. 633, figs 8–10.
?1853 *Proboscina ricordeauana* d'Orbigny: 850; pl. 759, figs 6–7.
1899 *Proboscina radiolitorum* (d'Orbigny); Gregory: 48; pl. 3, fig. 5.
1926 *Proboscina radiolitorum* (d'Orbigny); Canu & Bassler: 7; pl. 27, figs 1, 2.
1926 *Proboscina zic-zac* d'Orbigny; Canu & Bassler: 7; pl. 29, fig. 7.
1971 *Proboscina* cf. *radiolitorum* (d'Orbigny); Hillmer: 38; pl. 2, fig. 1.

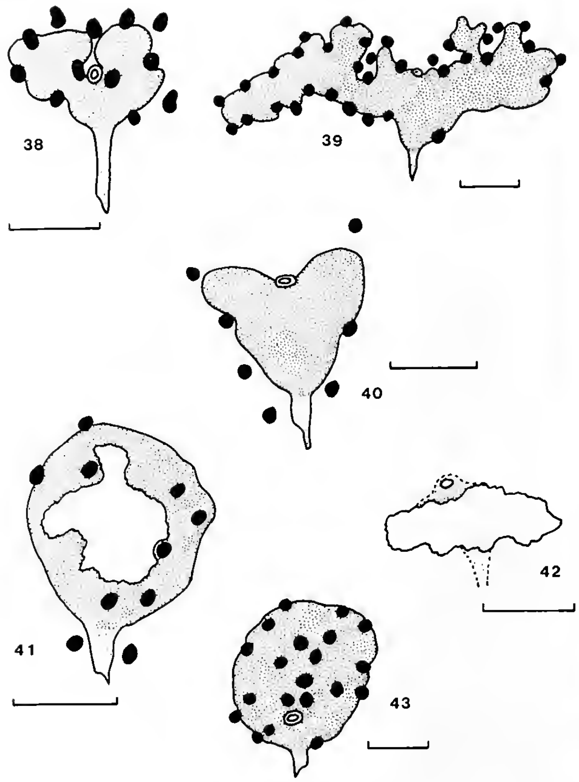
HOLOTYPE. MNHN d'Orbigny Colln 6975 (Voigt photocard 5827), Turonian, Angoulême, France.

OTHER MATERIAL. BM(NH) D7981, Treacher Colln; D52199, D52201, Little Coxwell Pit, Pitt Colln; D55240, D55243, D55244, Little Coxwell Pit, Gaster Colln; D55241 (3), Hinde Colln; D55242, D55245, Little Coxwell Pit, Thomas Colln.

DESCRIPTION. Zoarium adnate, consisting of round-topped, ribbon-like branches 4 or 5 zooecia across and 0·9–1·8 mm wide (Figs 36, 37A). Branches are typically uniform in width but may be constricted, and are often gently curved. Branching is infrequent (except during early growth stages) and occurs by bifurcation or, less often, by formation of an adventitious lateral branch almost at right angles to the parent branch. A marginal selvedge of kenozooecia is developed. Growing tips of branches are well rounded. In profile, branches are rounded and moderately high.

Autozooecia are moderately large, their frontal walls immersed and not clearly visible, especially proximally. Preserved peristomes are short but thick-walled, and apertures are of moderate size (largest in zooecia at the centre of the branches), subcircular or longitudinally elongate, and arranged in indistinct rows transverse to growth direction (Fig. 37B). Short mural spines may be visible within apertures. Pseudopores are slightly longitudinally elliptical, and occur at a density of about 1700 per mm^2.

Gynozooecia are rare but can be paired; small, bulbous, and slightly longer than wide. Short mural spines, similar to those seen in autozooecia, occur on the floor of gynozooecia (Fig. 37C). Ooeciopores have not been observed, all available gynozooecia being worn.



Figs 38–43 Gynozooecia in various species of bereniciform tubuloporines from the Faringdon Sponge Gravel. Dilated frontal walls are heavily stippled, ooeciopores are unshaded, and associated autozooecial apertures are shown in black. Scale bars represent 0·5 mm. Fig. 38, *Hyporosopora constricta* sp. nov., BM(NH) D55232; holotype; see also Fig. 51. Fig. 39, *Mesonopora fecunda* (Vine), BM(NH) D55155 (broken frontal wall restored); see also Fig. 60. Fig. 40, *Hyporosopora mantelli* sp. nov., USNM 69886a, holotype; see also Fig. 59. Fig. 41, *Plagioecia spissa* (Gregory), BM(NH) D5790; lectotype; see also Fig. 49. Fig. 42, *Hyporosopora larwoodi* sp. nov., BM(NH) D55099 (frontal wall broken); see also Fig. 52. Fig. 43, *Plagioecia orbifera* (Canu & Bassler), USNM 69901 (frontal wall broken and ooeciopore not visible); holotype; see also Fig. 47.

MEASUREMENTS. LAM, 0·12–0·15 mm; TAM, 0·11–0·12 mm; FWL, 0·36–0·75 mm; FWW, 0·18–0·27 mm; GW, *c*. 0·50 mm.

REMARKS. This is a common species at Faringdon and occurs on many substrates, including derived bone fragments (e.g. Fig. 36). There is no great difference between Faringdon specimens and the type specimen of *I. radiolitorum*, which is a worn specimen from the French Turonian. Possibly conspecific with *I. radiolitorum* is a second species described by d'Orbigny (1853), *Proboscina ricordeauana* from the French Aptian, represented by specimen 5694 in the d'Orbigny Colln at the MNHN. However, not only are the zooecia larger in this specimen than in the type of *I. radiolitorum*, but the type status of the specimen is dubious; it is clearly not the specimen figured by d'Orbigny.

The species is tentatively assigned to *Idmonea* on the basis of the colony growth-form, the occurrence of a marginal zone of kenozooecia and the high, rounded branches. It differs from *I. triquetra*, the Jurassic type species of *Idmonea*, notably in having rounded rather than sub-triangular branches and in the relatively short gynozooecium. Of the Cretaceous species assigned by Gregory (1899) to *Idmonea*, one (*I. hagenowi*) is a *Reptoclausa*, and the other two (*I. alipes* and *I. cristata*) have much larger marginal zones of kenozooecia than in *I. radiolitorum*.

Genus *COLLAPORA* Quenstedt, 1881

TYPE SPECIES. *Millepora straminea* (Phillips, 1829), by original designation; Bajocian of Yorkshire.

REMARKS. *Collapora* is a multisparsid with vinculariiform branches arising from an encrusting colony base.

Haplooecia Gregory, 1896 is an objective junior synomym of *Collapora* as the two genera have the same type species, *Millepora straminea* Phillips, 1829. This species has been redescribed by Illies (1968), Walter (1970) and Nye (1976). Walter (1970) incorrectly assigned the species to *Ceriocava* d'Orbigny, 1852 which is a cerioporine genus.

RANGE. Aalenian to Cenomanian.

Collapora hillmeri sp. nov. Figs 169–170 (p. 145)

HOLOTYPE. BM(NH) D58208, Little Coxwell Pit, Pitt Colln.

PARATYPES. BM(NH) D55169, Little Coxwell Pit, Thomas Colln; D55541, Little Coxwell Pit, A. G. Davis Colln; D58209–11, Little Coxwell Pit, Pitt Colln.

NAME. For G. Hillmer, West German bryozoan worker.

DESCRIPTION. Zoarium vinculariiform, arising from a small base in D58211, with dichotomizing branches about 1 mm in diameter. Growth tips have not been observed but one branch has a flattened distal end where it evidently grew against an unpreserved obstacle (Fig. 169A).

Autozooecia without clearly visible zooecial boundaries, about 12 occupying the circumference of a branch. They are variable in size, typically arranged in transverse bands of longer zooecia separated by the bands of shorter zooecia (Fig. 169B). Apertures (Fig. 169C) are of moderate diameter, subcircular or transversely elliptical in shape, with the peristome reduced to a low apertural rim. Pseudopores are circular with a density of about 2000 per mm^2.

Gynozooecia (Fig. 170A) are little inflated, longitudinally pyriform in outline, about 0·6 mm wide distally and 1·25 mm long. The ooeciopore (Fig. 170B) is located terminally and is distinctly transversely elliptical.

MEASUREMENTS. TAM, 0·08–0·12 mm; LAM, 0·05–0·08 mm; TOSM, 0·17 mm; LOSM, 0·08 mm; TOPM, 0·07 mm; LOSM, 0·03 mm.

REMARKS. This species differs from the Jurassic *Collapora straminea* in having shorter gynozooecia and a smaller, more transversely elliptical ooeciopore. The bands of alternately long and short zooecia seen in *C. hillmeri* have not been observed in *C. straminea*, but do occur in the Upper Cretaceous species *Heterohaplooecia monticulifera* Voigt & Viaud, 1983. This latter species, however, has larger autozooecia and thicker branches than *C. hillmeri*. Gynozooecia are unknown in *H. monticulifera*.

Among Faringdon bryozoans, *C. hillmeri* can be difficult to distinguish from *Entalophoroecia quadripartita* (see p. 103). The distinction between these two species was made at a late stage during the present study, following the discovery of a specimen of *C. hillmeri* with a gynozooecium. The gynozooecium is V-shaped in *E. quadripartita* but pyriform in *C. hillmeri*. *E. quadripartita* usually has numerous kenozooecia interspersed between the autozooecia, and the branches are often thinner and more straggly in appearance.

Family PLAGIOECIIDAE Canu, 1918

Genus *PLAGIOECIA* Canu, 1918

TYPE SPECIES. *Tubulipora patina* Lamarck, 1816, by original designation; Recent (see Harmelin 1976).

REMARKS. *Plagioecia* is one of several genera of superficially similar tubuloporines which were once assigned to *Berenicea* Lamouroux, a genus now regarded as a *nomen dubium* (see Taylor & Sequeiros 1982). The large, crescentic gynozooecia, pierced by autozooecia, of the type species are very distinctive. Other species commonly assigned to the genus may possess gynozooecia which are less broad but which share with the type species the presence of piercing autozooecia. The Jurassic species of *'Plagioecia'* described by Walter (1970) lack these piercing autozooecia and are more suitably placed in the genus *Hyporosopora* (see Taylor & Sequeiros 1982).

RANGE. Valanginian to Recent.

Plagioecia orbifera (Canu & Bassler, 1926) Figs 43–47

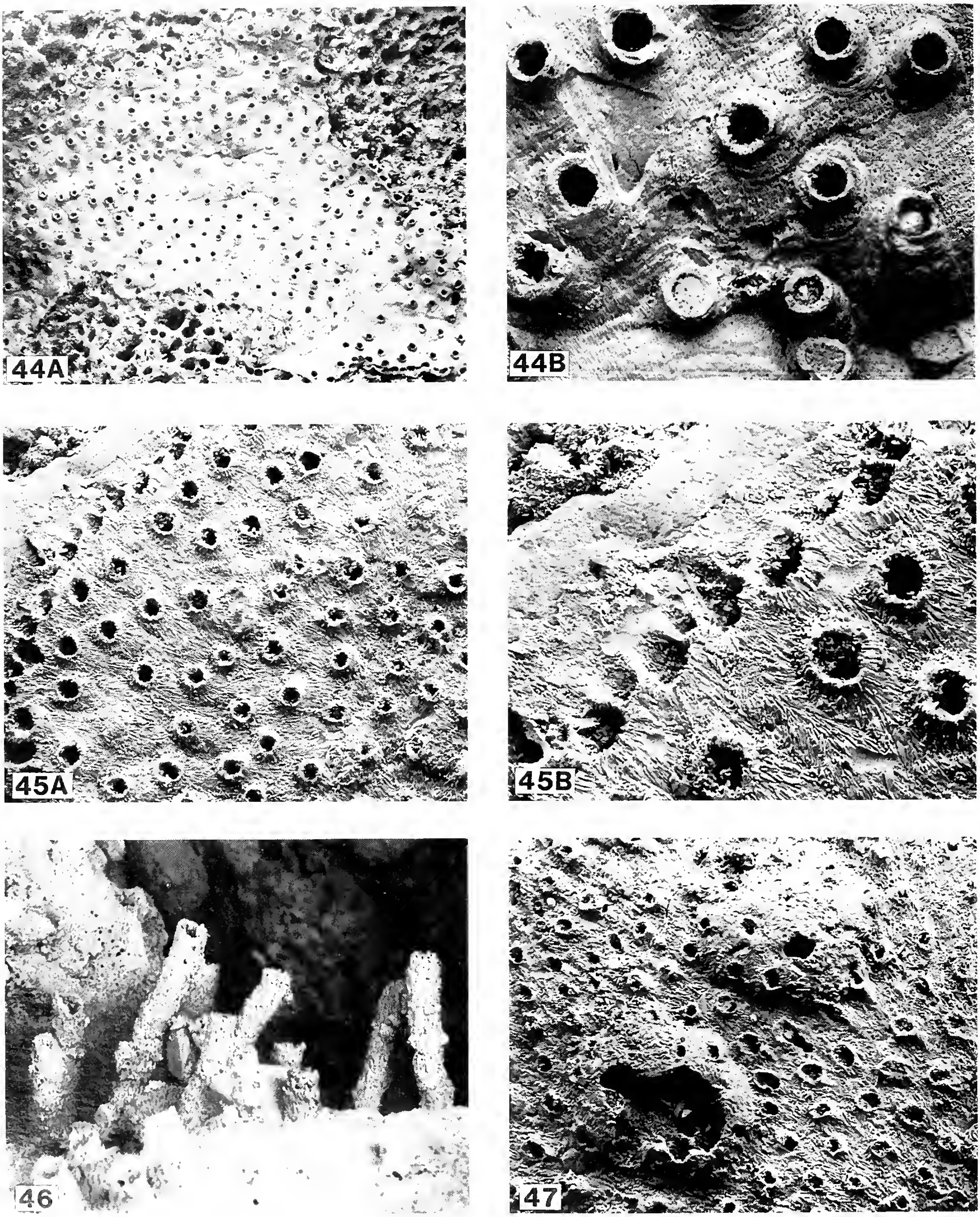
1926 *Diaperoecia orbifera* Canu & Bassler: 51; pl. 8, fig. 17
1926 *Berenicea pulchella* de Loriol; Canu & Bassler: 10 (*partim*); pl. 28, fig. 4.
1926 *Berenicea (Reptomultisparsa) tenella* de Loriol; Canu & Bassler: 12; pl. 29, figs 1–2.

HOLOTYPE. USNM 69901, figd Canu & Bassler (1926: pl. 8, fig. 17).

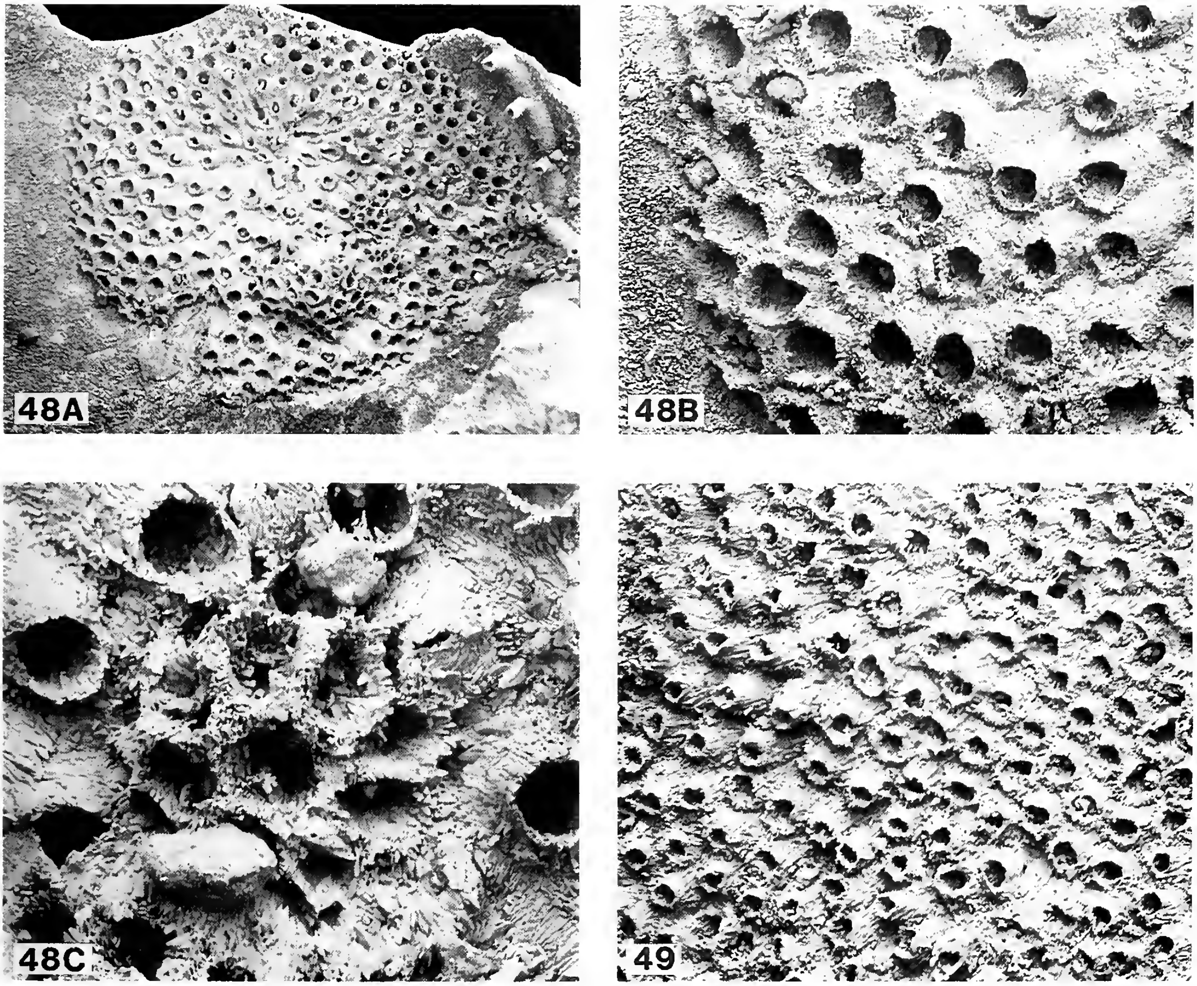
OTHER MATERIAL. BM(NH) 50781, Morris Colln; D52515, sewer trench, Little Coxwell Rd, Faringdon, Cleevely Colln; D52223, D55307 (9), Little Coxwell Pit, Pitt Colln; D55308–10, Bowler's Pit, Pitt Colln; D55311, Little Coxwell Pit, Gaster Colln: D55104, D55106 (with *'Berenicea' faringdonensis* and Stomatoporid sp. 2), Little Coxwell Pit, Thomas Colln; D55312, Little Coxwell Pit, Whiteley Colln; D55427–8, D55438–9, Wicklesham Pit, Wilson Colln.

DESCRIPTION. Zoarium adnate, bereniciform, often attaining a large size and sometimes becoming multilamellar. Growth margin thin, generally showing only one generation of zooecial buds (Fig. 45B). The discoidal form of the colony is attained rapidly with overgrowth of the ancestrula.

Autozooecia are moderately small, their frontal walls slightly convex and rather short; apertures are small, subcircular, usually surrounded by a low but distinct rim (Fig. 44B), although long peristomes (>0·7 mm) may be present in hollows on the substratum (Fig. 46). Frontal walls are crossed by irreglar transverse wrinkles in well-preserved zooecia, and have a pseudopore density of about 1300 per mm^2. Sparsely pseudoporous terminal diaphragms may be present at a level a little above that of the frontal wall.



Figs 44–47 *Plagioecia orbifera* (Canu & Bassler). Fig. 44, BM(NH) D55106; 44A, colony encrusting a sponge, × 17; 44B, autozooecia, × 90. Fig. 45, BM(NH) 50781; 45A, × 36; 45B, growth margin, × 93. Fig. 46, BM(NH) D55104, long peristomes preserved in a hollow on the substrate, × 53. Fig. 47, USNM 69901, holotype, autozooecia and two gynozooecia, × 32; see also Fig. 43.



Figs 48–49 *Plagioecia spissa* (Gregory). Fig. 48, BM(NH) D55105; 48A, small colony, × 9; 48B, growth margin showing crowded autozooecial apertures, × 37; 48C, newly-forming frontally budded subcolony, × 87. Fig. 49, BM(NH) D5790, **lectotype** (herein selected), variably spaced autozooecial apertures, × 24; see also Fig. 41.

Gynozooecia are very rare, being known only from the holotype specimen in which two poorly-preserved gynozooecia occur (Fig. 47). They are greatly inflated distally, roughly circular in outline shape, and penetrated by autozooecia (Fig. 43). The ooeciopore has not been observed; it is abraded or obscured by calcite cement overgrowth in both examples.

MEASUREMENTS. TAM, 0·06–0·08 mm; TPM, 0·09–0·12 mm; FWL, *c.* 0·60 mm; FWW, *c.* 0·18 mm; GDL, 0·88–0·91 mm; GW, 0·84–1·00 mm.

REMARKS. This is an extremely common species at Faringdon, where it is often found encrusting pebbles and sponges in association with *Hyporosopora mantelli*, *'Berenicea' grandipora* and *'B.' faringdonensis*. Autozooecial dimensions are considerably smaller than in the latter two of these, and a little larger than in *H. mantelli*, and the autozooecia have a distinct apertural rim absent in *H. mantelli*.

The fact that the gynozooecium is pierced by autozooecia suggests assignment to *Plagioecia*, although the distal dilated part is almost equidimensional whereas most species of *Plagioecia* have transversely elongate gynozooecia.

Berenicea pulchella de Loriol, 1863 and *B. tenella* de Loriol, 1868 are difficult to interpret from the original descriptions or from material in the MHNG. However, it is doubtful if either of these Swiss Valanginian species is the same as *P. orbifera* from Faringdon. Walter's (1972) redescription of *B. pulchella*, which he refers to *Plagioecia*, notes the heart-shaped gynozooecium, which is unlike that of *P. orbifera*. According to Walter (1972), *B. tenella*, also reassigned to *Plagioecia*, has a colony formed of subcircular subcolonies. Such structures are not present in *P. orbifera*.

Plagioecia spissa (Gregory, 1899) Figs 41, 48–49

1899 *Berenicea spissa* Gregory: 108; pl. 7, fig. 4.
1926 *Cellulipora spissa* (Gregory) Canu & Bassler: 6; pl. 26, figs 8–9.
1967 *'Cellulipora' spissa* (Gregory); Walter: 58; pl. 12, figs 5–6.
1972 *Cellulipora spissa* (Gregory); Buge & Voigt: 140.
?1984 *Cellulipora spissa* (Gregory); Delamette & Walter: 33; pl. 5, figs 1–2.

LECTOTYPE. BM(NH) B5790 (figd Gregory 1899: pl. 7, fig. 4), old collection, selected herein as the lectotype.

PARALECTOTYPES. BM(NH) D3024, Caleb Evans Colln; D3029, old collection.

OTHER MATERIAL. BM(NH) D55105, Little Coxwell Pit, Pitt Colln; D55314 (5), locality presumed to be Faringdon, *ex* Durham University Colln; D55315, D55316 (4), Little Coxwell Pit, Whiteley Colln; D55317 (3), Little Coxwell Pit, Cleevely Colln.

DESCRIPTION. Zoarium a discoidal sheet (bereniciform), often relatively large (diameter sometimes 20 mm). Growing edge usually revealing only one generation of zooecial buds (Fig. 48B); distal fringe of basal lamina wide, extending up to 0·5 mm away from the budding zone. Ancestrula and early zooecia apparently overgrown by lateral lobes of the initially fan-shaped zoarium. Multilamellar zoaria are occasionally produced by the frontal budding of discoidal subcolonies (Fig. 48C).

Autozooecia in primary zone of astogenetic change are slender with longitudinally elongate apertures; those in the zone of astogenetic repetition are short with subcircular or transversely elongate apertures (Fig. 48B) which are crowded, variable in size and lack peristomes. Areas of autozooecia with long frontal walls and widely-spaced apertures may be developed (Fig. 49), forming maculae (cf. the branching erect tubuloporine *Heterohaplooecia* Voigt & Viaud, 1983).

Gynozooecia are diffuse, longitudinally ovoidal, and penetrated by numerous autozooecia (Fig. 41); the ooeciopore is transversely elongate, smaller than an autozooecial aperture and positioned well proximally.

MEASUREMENTS (made from the lectotype). LAM, 0·09–0·18 mm; TAM, 0·12–0·15 mm; FWL, 0·36–0·57 mm; FWW, 0·21–0·30 mm; GDL, *c*. 1·4 mm; GW, *c*. 1·3 mm.

REMARKS. The lectotype specimen consists of two colonies of similar size which originate on the interior surface of the pedicle valve of a brachiopod, apparently fuse with one another, and extend onto the exterior surface of the brachiopod. Gregory's figure (1899: pl. 7, fig. 4) depicts a worn area of colony on the exterior of the brachiopod.

This is a common species at Faringdon which is distinctive by virtue of the closely-spaced apertures in zones of astogenetic repetition. Although apparently unknown elsewhere in the British Cretaceous, Canu & Bassler (1926) recorded *P. spissa* from the Aptian of d'Ervy, Switzerland, and Buge & Voigt (1972) from the Hauterivian of Hauteville, France. Assignment to the genus *Cellulipora*, as suggested by Canu & Bassler (1926), is doubtful because the Faringdon species lacks the well-defined, regularly-arranged, polygonal subcolonies bounded by zones of kenozooecia which are present in the type species, *C. ornata* from the Cenomanian of Le Havre, France (see Buge & Voigt 1972). The gynozooecium suggests placement in *Plagioecia*.

Genus ***HYPOROSOPORA*** Canu & Bassler, 1929

TYPE SPECIES. *Hyporosopora typica* Canu & Bassler, 1929, by original designation; Bathonian of France.

REMARKS. This genus of bereniciform tubuloporines is distinguished by the form of the gynozooecium which is moderately broad and varies in outline from subtriangular (as in the type species) to boomerang-shaped with lateral lobes extending distally of the level of the ooeciopore (see Taylor & Sequeiros 1982). Autozooecia do not penetrate the gynozooecium (as they do in *Plagioecia*), and the margins of the gynozooecium are not diffuse with deep embayments formed by autozooecia (as in *Mesonopora*).

RANGE. Aalenian to ?Recent.

Hyporosopora constricta sp. nov. Figs 38, 50–51

HOLOTYPE. BM(NH) D55232, Little Coxwell Pit, Pitt Colln.

PARATYPES. BM(NH) D55097, Little Coxwell Pit, Pitt Colln; D55230, Little Coxwell Pit, Gaster Colln; D55231, Little Coxwell Pit, Thomas Colln.

NAME. 'Constricted', referring to the autozooecial apertures.

DESCRIPTION. Zoaria are thin, discoidal (bereniciform), typically small, sometimes lobate, with a narrow distal fringe of basal lamina and one tier of zooecia visible at the growing edge (Fig. 51B). The ancestrula is overgrown by latter zooecia.

Autozooecia are slender, with peristomes well raised (up to 0·3 mm high; Fig. 51A), apertures longitudinally elliptical and constricted medially by groups of blunt mural spines growing inwards from the sides of the aperture at about the height of the colony surface (Fig. 50B). Frontal walls are transversely wrinkled with sparse teardrop-shaped pseudopores pointed distally, about 800–1000 per mm^2. Occluded autozooecia are occasionally present, their terminal diaphragms level with the colony surface and bearing sporadic, irregularly-shaped pseudopores (Fig. 50C).

Gynozooecia are subtriangular, and deeply indented by the surrounding autozooecia (Figs 38, 51C); the ooeciostome is strongly reflexed proximally, the ooeciopore considerably smaller than an autozooecial aperture.

MEASUREMENTS. LAM, mean 0·12 mm; TAM, mean 0·06 mm; LPM, mean 0·14 mm; TPM, mean 0·10 mm; FWL, 0·60–0·70 mm; FWW, 0·13–0·15 mm; GDL, 0·50–0·60 mm; GW, 0·70–0·90 mm; LOPM, 0·05–0·06 mm; TOPM, 0·06–0·08 mm; LOSM, 0·08 mm; TOSM, 0·09–0·11 mm.

REMARKS. This species is distinguished from previously described bereniciform tubuliporines by the presence of groups of mural spines (intrazooecial spines) forming a medial constriction to the autozooecial aperture. Although these structures are clearly visible in the well-preserved type material, they may not be recognizable in specimens of inferior preservation.

Available specimens encrust brachiopods and sponges.

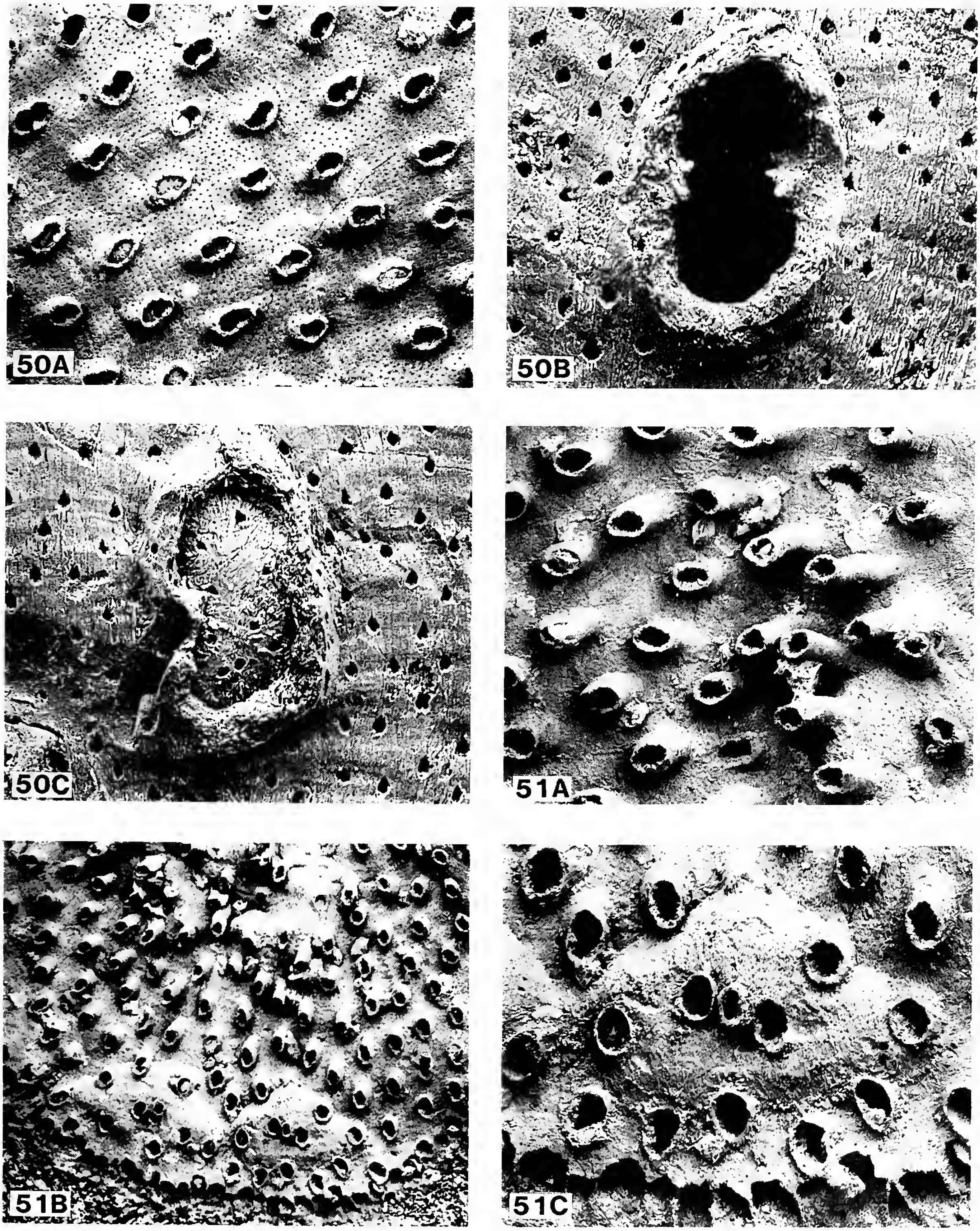
Hyporosopora larwoodi sp. nov. Figs 42, 52–56

HOLOTYPE. BM(NH) D55096, *ex* Durham University Colln.

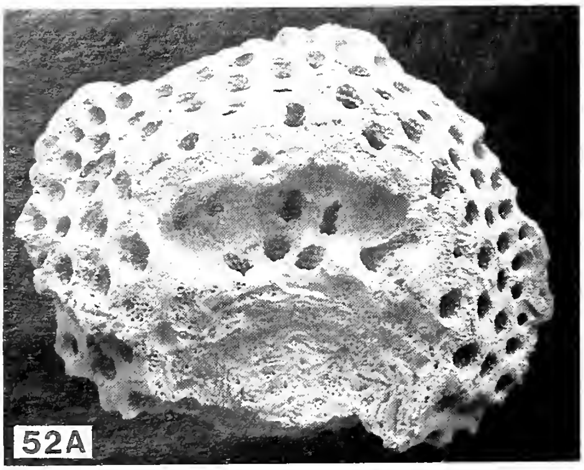
PARATYPES. BM(NH) D55097–8, D57938, Little Coxwell Pit, Elliott Colln; D55221–4, Little Coxwell Pit, Thomas Colln; D55227, Little Coxwell Pit, Pitt Colln; D55228, Little Coxwell Pit, Whiteley Colln; D55229, Bowler's Pit, Gaster Colln; D57597, Little Coxwell Pit, Pitt Colln. USNM 69000 (with the holotype of *Oncousoecia coarctata* (Canu & Bassler))

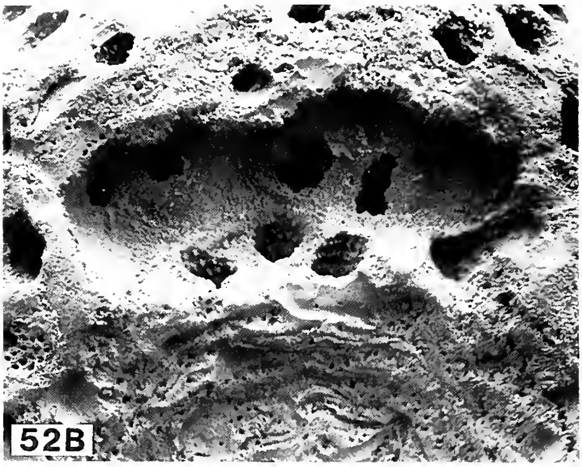
NAME. In recognition of the scientific contributions of bryozoologist Dr Gilbert P. Larwood (University of Durham).

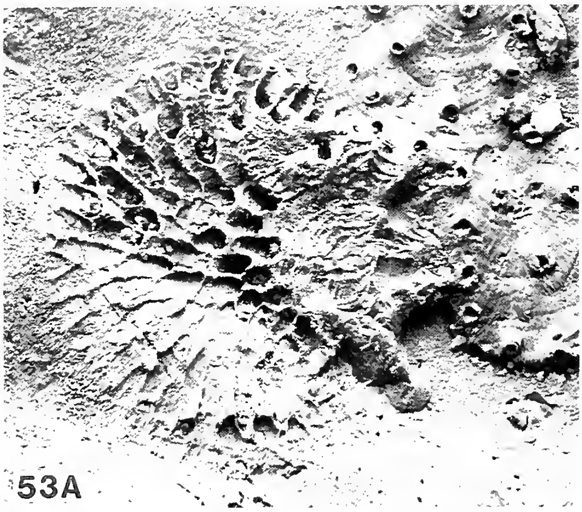
DESCRIPTION. Zoaria adnate, small (usually less than 3 mm in diameter), and bereniciform, circular (Fig. 55) or fan-shaped

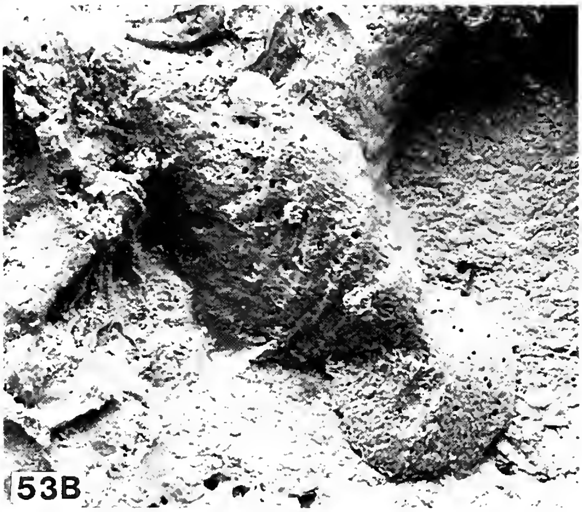


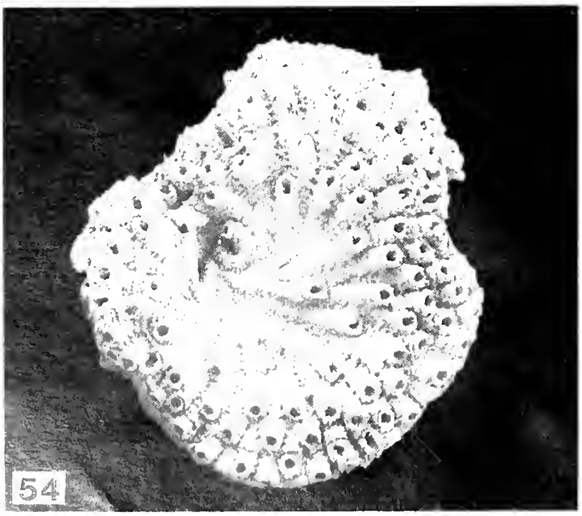
Figs 50–51 *Hyporosopora constricta* sp. nov. Fig. 50, BM(NH) D55097; 50A, autozooecia, × 38; 50B, autozooecial aperture constricted by groups of mural spines, × 270; 50C, autozooecial aperture with terminal diaphragm, × 255. Fig. 51, BM(NH) D55232, **holotype**; 51A, utozooecia with long peristomes, × 41; 51B, × 23; 51C, gynozooecium and ooeciopore (distal direction is downwards), × 54; see also Fig. 38.

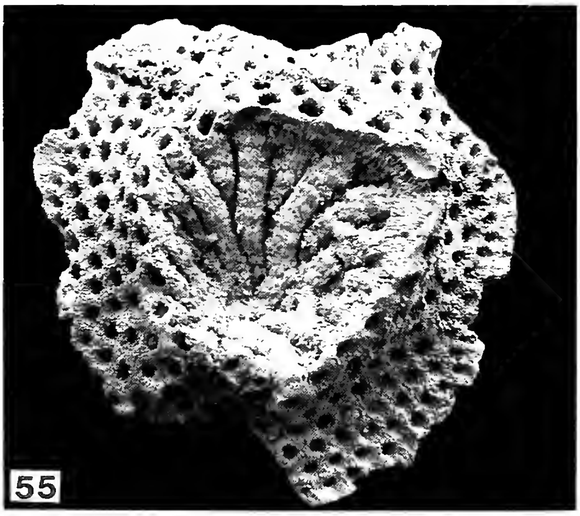

52A


52B


53A


53B


54


55

Figs 52–55 *Hyporosopora larwoodi* sp. nov. Fig. 52, BM(NH) D55099; 52A, broken, free colony, × 36; 52B, fractured gynozooecium, × 69; see also Fig. 42. Fig. 53, USNM 69000, colony encrusting the same substrate as the holotype of *Oncousoecia coarctata* (Canu & Bassler); 53A, abraded fan-shaped colony overgrowing *O. coarctata*, × 30; 53B, ancestrula, × 115. Fig. 54, BM(NH) D55098, free colony with concentration of autozooecial apertures close to the growth margin, × 26. Fig. 55, BM(NH) D57938, small, free colony with thick growth margin, × 38.

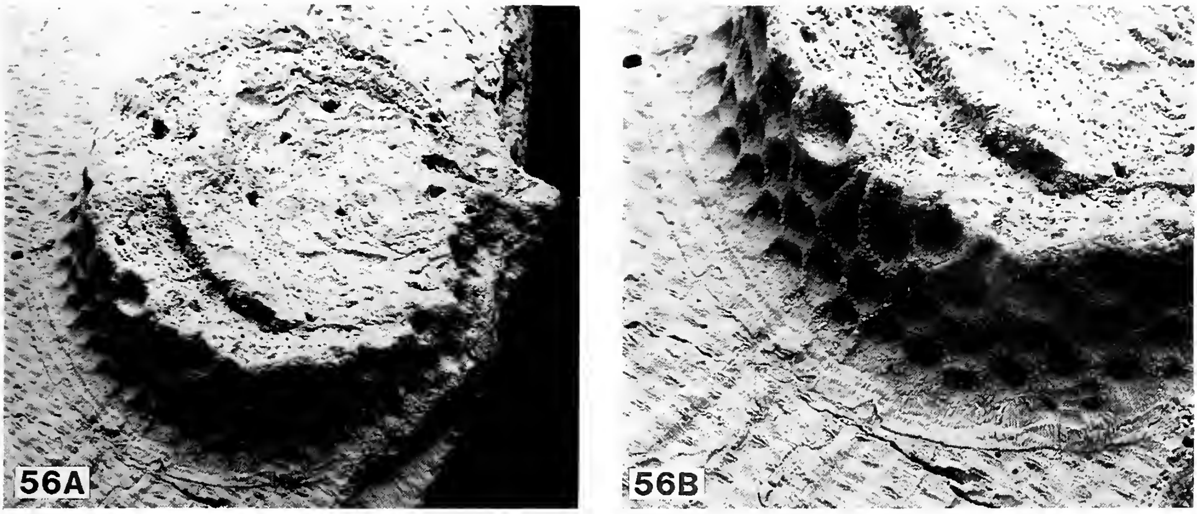


Fig. 56 *Hyporosopora larwoodi* sp. nov., BM(NH) D55096, **holotype**; 56A, oblique view showing thick growth margin and absence of apertures on the frontal surface of the colony, × 29; 56B, growth margin, × 60.

(Fig. 53A) in outline. Fan-shaped peripheral subcolonies may be developed from the main colony. In some colonies (Figs 55, 56), zooecia open only at the thick colony growing edge which reveals several tiers of zooecia. The pseudoporous frontal surface of the colony is devoid of apertures in these colonies and may be rugose with closely-spaced transverse wrinkles (Fig. 56A), with or without longitudinal ridges (Fig. 55) corresponding to the frontal walls of individual zooecia. In other colonies, zooecial apertures are present on the frontal surface, typically sparsely distributed in the depressed proximal part of the colony but closely spaced near the edge of the colony (Fig. 54). The distal fringe of the basal lamina extends up to 0·1 mm away from the budding zone.

Autozooecia opening on frontal surfaces of colonies intersect the surface at an acute angle and have circular or transversely elongate apertures with thick rims. Blade-like mural spines have been observed within fractured autozooecia.

The ancestrula has a protoecium about 0·21 mm in diameter (Fig. 53B).

Gynozooecia (Figs 42, 52) have transversely elliptical frontal walls (broken in all available specimens) and terminal, transversely elongate ooeciopores smaller than the autozooecial apertures.

Measurements. TAM, *c.* 0·11 mm; FWW, *c.* 0·18 mm; GDL, 0·40 mm; GW, 1·00 mm; TOPM, 0·08 mm; LOPM, 0·05 mm.

Remarks. This species is characterized by the small but thick colonies whose frontal surfaces either lack apertures or have apertures concentrated in a band close to the periphery of the colony. The zooecia make a shallow angle with the colony surface and it seems likely that slight variations in this angle determine whether zooecia open on the frontal surface of the colony or only at the thick growing edge of the colony. The latter condition gives a morphology resembling the Palaeozoic genus *Flabellotrypa* (see Brood 1975). Zooecial frontal wall length is extremely variable; the shortest zooecia are only 0·20 mm long, whereas incomplete zooecia (whose distal parts are still at the growing edge) may exceed 1·4 mm in length. No previously described species from the Cretaceous has this characteristic colony morphology.

H. larwoodi is relatively common in the Faringdon Sponge Gravel and can be found as small colonies encrusting a wide variety of substrates, or in sediment samples as detached colonies (Figs 52, 54–55) which apparently grew on perishable substrates.

Hyporosopora mantelli sp. nov. Figs 40, 57–59

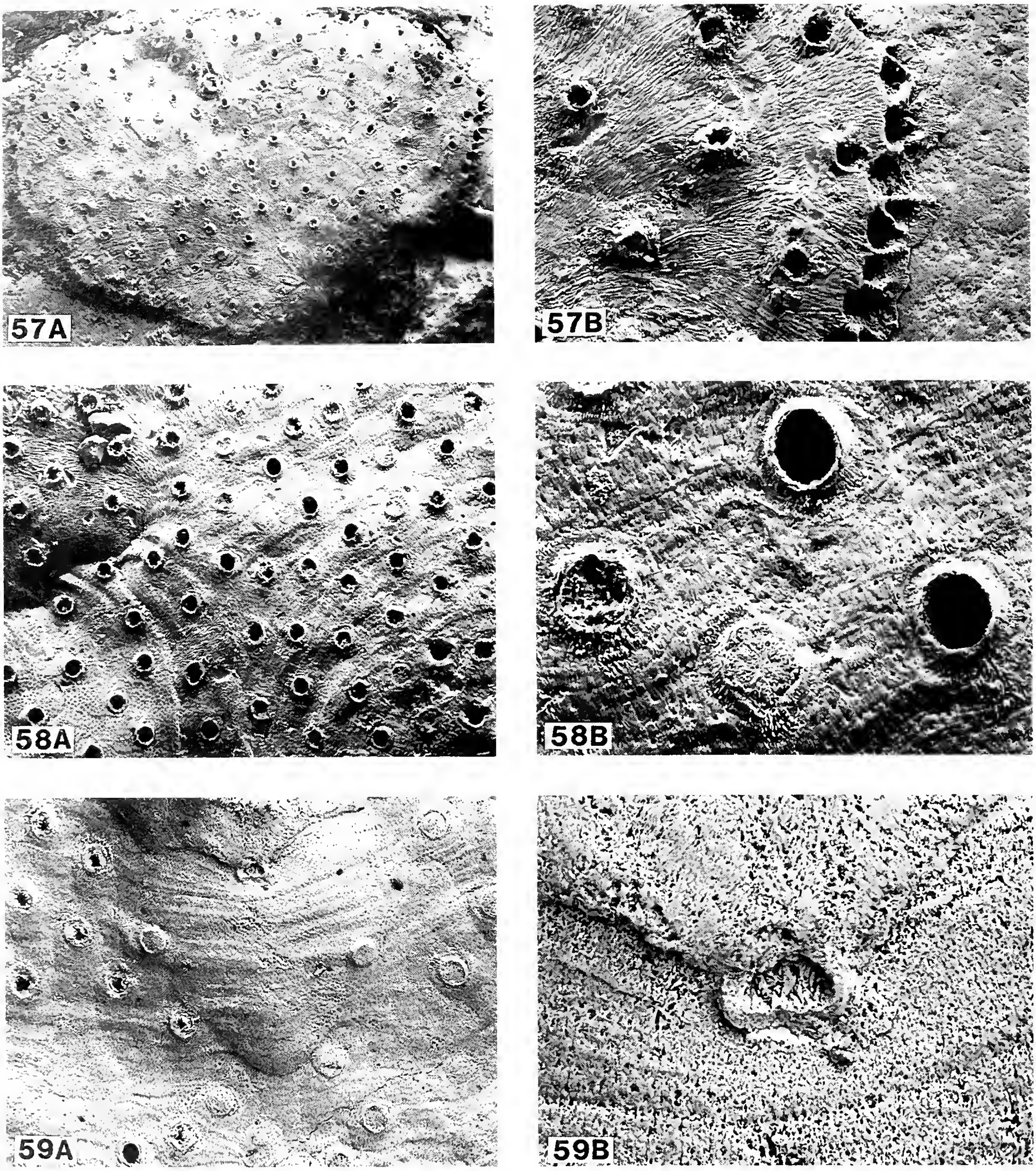
1883 ?*Reptomultisparsa haimeana* de Loriol; Keeping: 137.
1899 *Reptomultisparsa haimei* (de Loriol); Gregory: 117; fig. 5.
1926 *Trigonoecia haimei* (de Loriol); Canu & Bassler: 39 (*partim*); pl. 1, figs 10–12 only.

Holotype. USNM 69886a, figd by Canu & Bassler (1926: pl. 1, fig. 12).

Paratypes. BM(NH) 10265 (figd by Gregory 1899: fig. 5), Mantell Colln; 50781, Morris Colln; D55072, D55127, D55129, D55131, Little Coxwell Pit, Gaster Colln; D55073, Little Coxwell Pit, Whiteley Colln; D55128, Gaster Colln; D55130, Little Coxwell Pit, Pitt Colln; D55428, Wicklesham Pit, Wilson Colln. SM B27889–91, encrusting a piece of bone and labelled '*Diastopora oceanica*'; B27959, labelled '*Ceriopora polymorpha*'. USNM 69886b (figd by Canu & Bassler 1926, pl. 1: fig. 10 as *Trigonoecia haimei*).

Name. For Gideon Mantell, the famous 19th Century fossil collector who collected one of the paratypes.

Description. Zoarium adnate, initially unilamellar (Fig. 57A) and subcircular (bereniciform), becoming multilamellar by the addition of subcolonies which begin as subcircular overgrowths, apparently produced by eruptive frontal budding. Multilamellar colonies may attain a considerable size; specimen BM(NH) 10265 has ten or more layers and covers most of a cup-shaped sponge 8 cm in diameter. Zoarial layers are very thin (*c.* 0·25 mm) and only one tier of buds is



Figs 57–59 *Hyporosopora mantelli* sp. nov. Fig. 57, BM(NH) 50781; 57A, × 17; 57B, growth margin with single tier of zooecial buds, × 65. Fig. 58, BM(NH) D55072; 58A, × 32; 58B, autozooecial apertures, one with a terminal diaphragm, × 141. Fig. 59, USNM 69886a, **holotype**; 59A, gynozooecium, × 46; 59B, ooeciopore, × 200; see also Fig. 40.

normally visible at the growing edge (Fig. 57B). The distal fringe of the basal lamina is not extensive. Zoarial surfaces are flat but may be crossed by irregular transverse wrinkles of low amplitude (Fig. 58A). Colonies have a characteristically shiny appearance when viewed with an optical microscope.

Autozooecia are immersed, small, slender, and have rounded, slightly dilated distal ends. Apertures are very small, circular or longitudinally elongate, widely spaced, and lack significant peristomes (Fig. 58B). Sparsely pseudoporous terminal diaphragms may occur. Pseudopores are subcircular and occur at a density of about 2000 per mm^2. The ancestrula is overgrown by later zooecia.

Gynozooecia are rare, their distal frontal walls are of low profile, subtriangular in outline (Figs 40, 59A), a little wider than long, with lateral lobes extending a little distal of the ooeciopore. The ooeciopore is transversely elongate (Fig. 59B).

MEASUREMENTS (determined from 10 autozooecia and 1 gynozooecium in the holotype). LAM, 0·08–0·09 mm; TAM, 0·06–0·09 mm; FWL, 0·45–0·72 mm; FWW, 0·15–0·21 mm; GTL, 1·32 mm; GDL, 0·93 mm; GW, 1·22 mm; LOPM, 0·05 mm; TOPM, 0·08 mm.

REMARKS. This new species was first described from Faringdon as *Reptomultisparsa haimei* de Loriol by Gregory (1899), who gave no reason for changing the species name from de Loriol's *haimeana* to *haimei*. The figured type specimen of *R. haimeana* (MHNG 29635, from the Neocomian of Salève) has been examined and found to differ from the Faringdon species in the considerably larger size of the zooecia (TAM = 0·12 mm, cf. 0·04–0·06 mm). A second de Loriol species, *Berenicea pulchella* (figured type MHNG 29625, which is poorly preserved and has slightly smaller zooecia), may be a synonym of *R. haimeana* de Loriol.

Canu & Bassler (1926) described supposed *Trigonoecia haimeana* (de Loriol) from both Switzerland (Ste Croix) and Faringdon. Their Ste Croix material (including USNM 69885, depicted in their pl. 1, fig. 9) has more prominent zooecia with a closer spacing of the apertures than the Faringdon specimens and is regarded as a different species.

Gregory (1899) incorrectly gave the apertural diameter of *H. mantelli* as 0·10 mm, and erroneously described the zoarial layers as thick, possibly because he studied a worn part of the solitary specimen (BM(NH) 10265) which was available to him.

H. mantelli is commonly found encrusting sponges but can also be found on other substrates, especially pebbles.

Genus ***MESONOPORA*** Canu & Bassler, 1929

TYPE SPECIES. *Mesonopora typica* Canu & Bassler, 1929 (= *Berenicea concatenata* Reuss, 1867, *fide* Walter, 1970: 132); Middle Jurassic, Poland.

REMARKS. *Mesonopora* is a genus of bereniciform plagioeciids in which the gynozooecium is strongly indented at its margins by autozooecia but, unlike *Plagioecia*, is not pierced by autozooecia (see Taylor & Sequieros 1982).

RANGE. Bathonian to ?Recent.

Mesonopora fecunda (Vine, 1885) Figs 39, 60–61

?1868 *Reptomultisparsa tenella* de Loriol: 61; pl. 5, figs 15–16.
1885 *Diastopora fecunda* Vine: 18.
1889 *Diastopora fecunda* Vine; Vine: 266.
?1891 *Diastopora fecunda* Vine; Vine: 379.
1899 *Reptomultisparsa congesta* (Reuss); Gregory: 118 (*partim*); pl. 6, fig. 5 only.
1989 *Mesonopora tenella* (de Loriol); Walter: 134; text-fig. 15; pl. 7, figs 2–5; pl. 8, figs 1–6; pl. 9, figs 5–9.

MATERIAL. BM(NH) D55090–1, Little Coxwell Pit, Whiteley Colln; D55155 (several colonies encrusting a sponge), Treacher Colln (*ex* University of Reading Collection); D55156, Little Coxwell Pit, Pitt Colln.

DESCRIPTION. Zoarium encrusting, discoidal bereniciform (Fig. 60B, C), thick (*c.* 0·8 mm), with a deep growth margin showing 3 to 8 tiers of zooecial buds (Fig. 60D). In one specimen the growth margin is raised free of the substrate. Discoidal peripheral subcolonies (Fig. 60A), up to 4 mm in diameter, arise at the growing edge and overlap parent subcolonies, giving a compound colony of offset discs. The ancestrula is overgrown by later zooecia.

Autozooecia are slender, moderately large, with distally convex, poorly-defined frontal walls and small, closely-spaced, longitudinally elliptical apertures without significant peristomes. Terminal diaphragms, which may occlude the ontogenetically older zooecia, are sparsely pseudoporous and are situated at or slightly above frontal wall level. In good preservation the frontal walls are seen to be crossed by irregular, sinous, transverse ridges (Fig. 61A). Pseudopores are usually present only between the ridges, in a density of approximately 1300 per mm^2. Tubercle-like mural spines are visible in some zooecial buds (Fig. 61B).

Gynozooecia (Figs 39, 60B) are large, very broad and crescent-shaped, their margins indented by autozooecia. The ooeciopore cannot be identified with certainty in the abraded material available.

MEASUREMENTS. TAM, 0·04–0·06 mm; FWW, 0·07–0·10 mm; GDL, *c.* 1·00 mm; GW, *c.* 4·00 mm.

REMARKS. The type specimen of *Mesonopora fecunda* Vine is BM(NH) B4452 from the Cambridge Greensand (Cenomanian). Apparently conspecific specimens from Faringdon share the discoidal offset subcolonies of the type and have similar zooecial dimensions. However, determination of the Faringdon material as *Mesonopora fecunda* must remain provisional until larger suites of better-preserved specimens from Faringdon and Cambridge become available.

It is possible that the Faringdon species is the same as *Reptomultisparsa tenella* de Loriol, but the type material of this species is missing from the collections of the MHNG.

Although this species is here assigned to *Mesonopora*, the occurrence of marginal discoidal subcolonies invites comparison with *Plagioecia patina* (Lamarck), the Recent type species of *Plagioecia* (see Hayward & Ryland 1985).

This is a rare species at Faringdon. Of the poorly-preserved colonies in the BM(NH) collections, three encrust sponges and one a branch fragment of *Meliceritites gracilis*.

Genus ***UNITUBIGERA*** d'Orbigny, 1853

TYPE SPECIES. *Unitubigera discus* d'Orbigny, 1853, by subsequent designation of Bassler, 1935; Neocomian of Ste Croix.

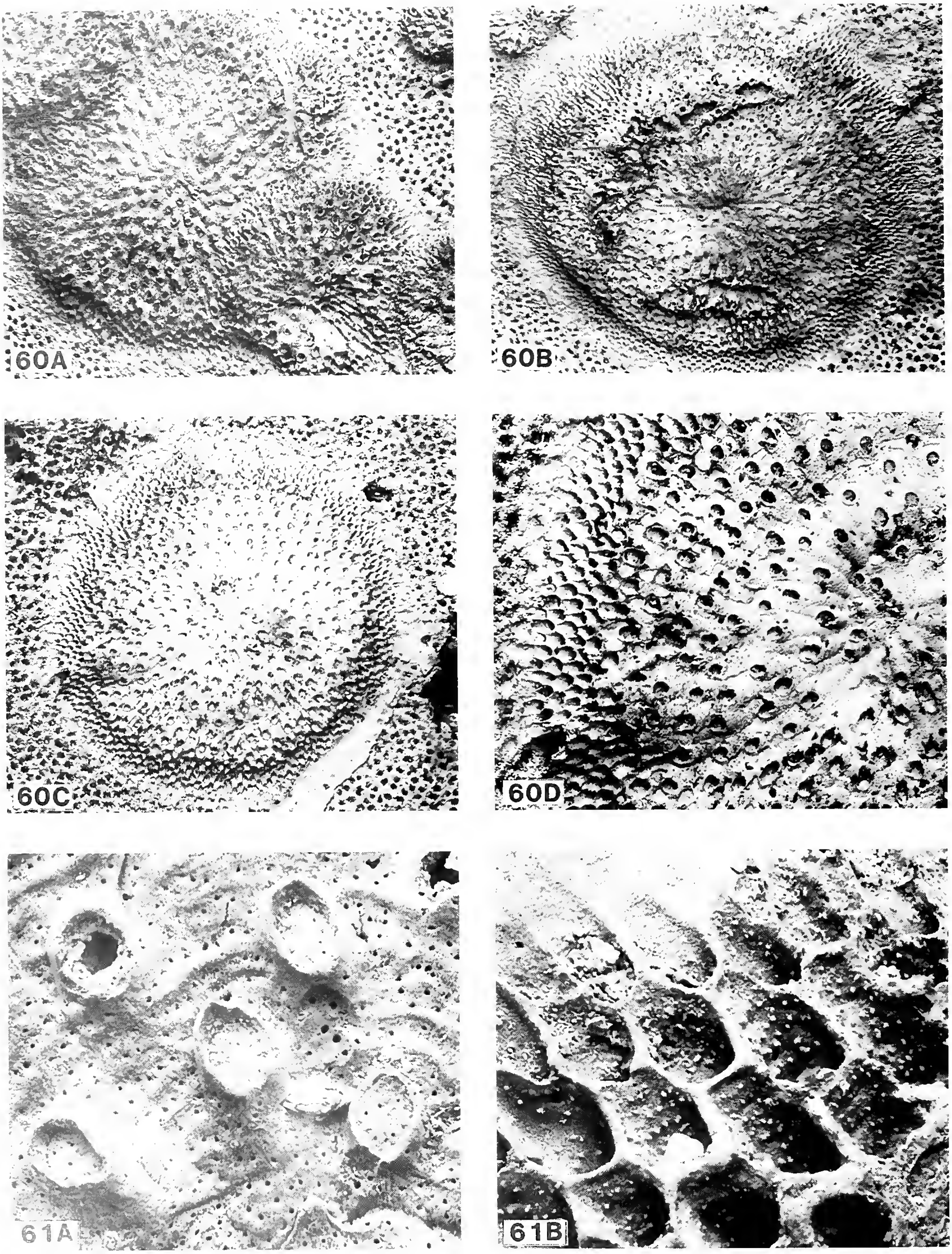
REMARKS. Bereniciform tubuloporines with apertures arranged uniserially in connate, radial rows are placed in the genus *Unitubigera*. Walter (1987*b*) has redescribed the type species and provided a revised diagnosis for *Unitubigera*.

RANGE. Uncertain, possibly Valanginian to Miocene.

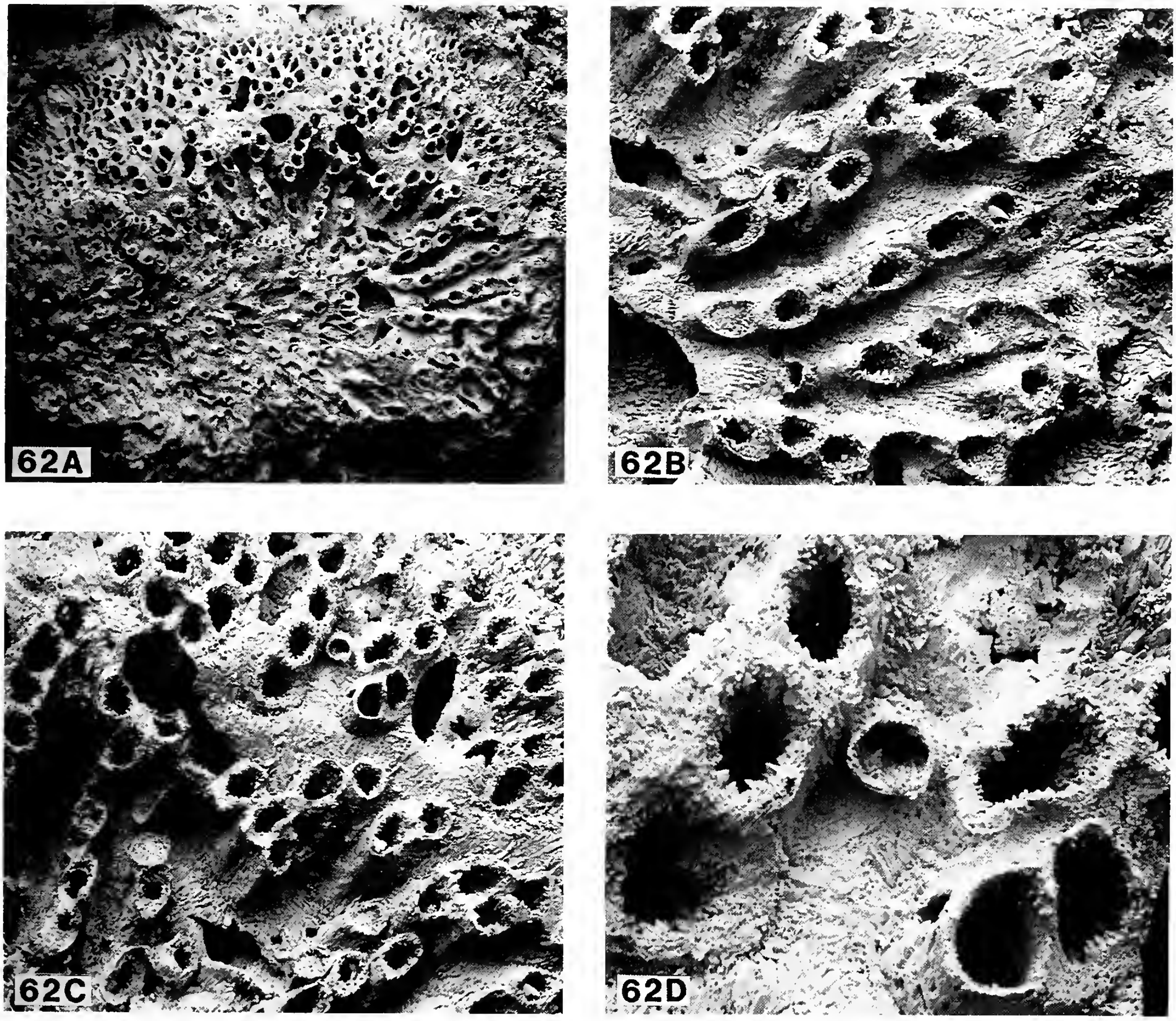
Unitubigera sp. Fig. 62

MATERIAL. BM(NH) D55112, Little Coxwell Pit, Gaster Colln; D55116, Little Coxwell Pit, Pitt Colln.

DESCRIPTION. Zoarium encrusting (Fig. 62A), discoidal, approximately circular in outline, 6–8 mm in diameter. Several generations of zooecial buds are visible at the growing edge.



Figs 60–61 *Mesonopora fecunda* (Vine). Fig. 60, BM(NH) D55155, several colonies encrusting a sponge. 60A, colony with peripheral subcolony, × 10; 60B, colony with abraded gynozooecia, × 12; 60C, discoidal colony showing thick growth margin, × 10; 60D, detail of the colony shown in 60C, × 23; see also Fig. 39. Fig. 61, BM(NH) D55090; 61A, autozooecia with terminal diaphragms and transversely ridged frontal walls, × 171; 61B, zooecial buds with tubercle-like mural spines, × 171.



ig. 62 *Unitubigera* sp., BM(NH) D55116; 62A, partly overgrown colony, × 11; 62B, radial rows of autozooecial apertures, × 41; 62C, broken gynozooecium, × 33; 62D, ooeciopore, × 116.

Autozooecial apertures are longitudinally elongate and rranged uniserially in radial rows with successive apertures arely connate (Fig. 62B). Peristomes are inclined at a low ngle to the colony surface.

Gynozooecia (Fig. 62C) have distal frontal walls which are iffuse, transversely elongate and indented at their edges by utozooecial apertures. Ooeciopores (Fig. 62D) are located etween rows of autozooecia and are transversely elongate, he ooeciostome being reflexed proximally.

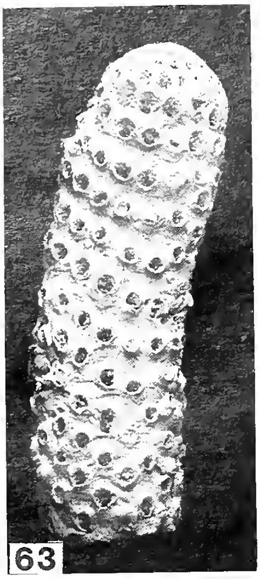
EASUREMENTS. TAM, 0·07–0·10 mm; TPM, 0·10–0·17 mm; WW, 0·15–0·17 mm; GDL, 0·40–0·70 mm; GW, 0·60–2·00 m; LOPM, 0·05–0·07 mm; TOPM, 0·09–0·10 mm.

EMARKS. This is a rare species in the Faringdon Sponge ravel. Both of the available specimens encrust sponges and oth have gynozooecia. Their preservation, however, is poor. hey may belong to the species *Unitubigera discus* d'Orbigny 853, originally described from the Valanginian of Ste Croix nd later revised by Walter (1972, 1987*b*). However, a robable specimen of *U. discus* from the Lower Tealby lay (Hauterivian) of Nettleton (BM(NH) D52791) has significantly larger autozooecial apertures than the material from Faringdon.

Unitubigera and the similar genus *Actinopora* have been recorded in error from Faringdon on at least two occasions. A specimen in the Davey Collection (OUM K 53) labelled *Unitubigera papyracea* is presumably the specimen Davey records in his species lists (1877: 7 and 1905: 28). This specimen is actually a worn *Idmonea radiolitorum* partially covered by a colony of *Reptomultisparsa*. Specimens labelled as *Actinopora* in the BGS Collections (Tablet D 32/2, specimens 43761 and 43762) are *Reptoclausa hagenowi*, as pointed out by Gregory (1909*b*: 239). These could well be the specimens recorded by Sharpe (1854: 189) as *Actinopora*. True *Actinopora*, distinguished from *Unitubigera* by the multiserial (often biserial) arrangement of the connate zooecial apertures, appears to be absent from Faringdon.

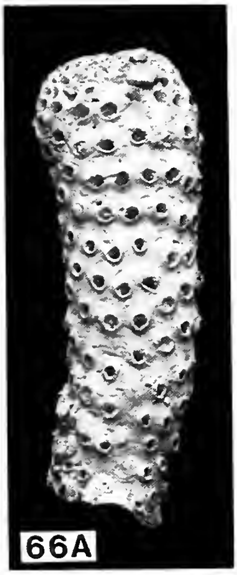
Genus ***CARDIOECIA*** Canu & Bassler, 1922

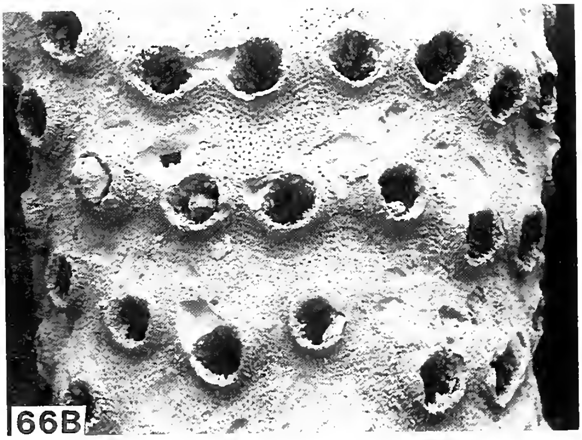
TYPE SPECIES. *Bidiastopora neocomiensis* d'Orbigny, 1853, by original designation; Neocomian of Ste Croix, Switzerland.


63

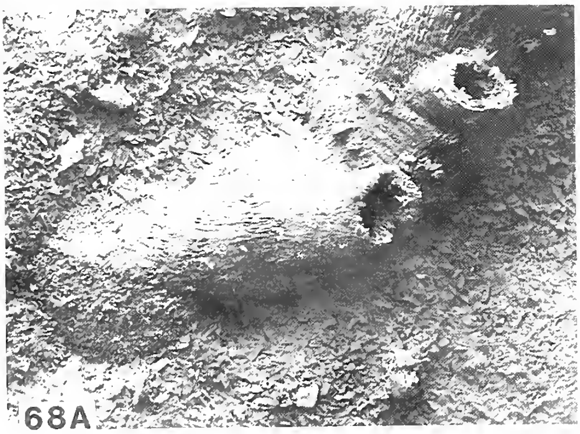

64

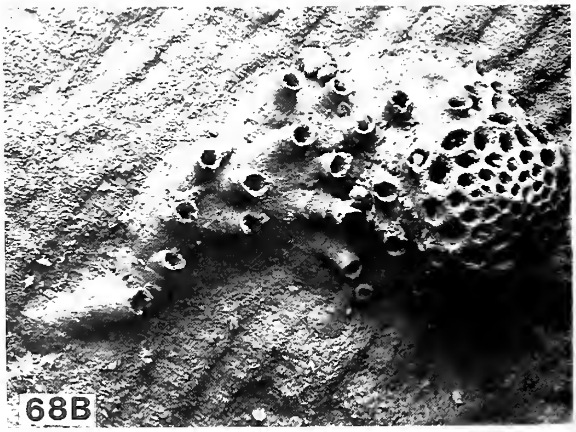

65


66A


66B


67


68A


68B

Figs 63–68 *Cardioecia neocomiensis* (d'Orbigny). Fig. 63, USNM 69893c, × 13. Fig. 64, USNM 69893d, × 10. Fig. 65, USNM 69898, holotype of *C. pauper* Canu & Bassler, × 12. Fig. 66, BM(NH) D55081; 66A, × 10; 66B, autozooecia, × 41. Fig. 67, BM(NH) D55074, broken gynozooecium, × 23. Fig. 68, BM(NH) D53698; 68A, ancestrula, × 47; 68B, colony base with short erect stem, × 15.

Remarks. *Cardioecia* is a plagioeciid characterized by erect vinculariiform branches which have a short median budding lamina. Possible extant species of the genus are known (Harmelin 1976), but at least some of them lack the probosciniform bases present in the type species.

As the type species of *Notoplagioecia* Canu & Bassler, 1922 (*N. farringdonensis* Canu & Bassler, 1922) is considered to be a junior synonym of the type species of *Cardioecia*, the genus *Notoplagioecia* is here placed in synonymy with *Cardioecia*.

Range. Valanginian to ?Recent.

Cardioecia neocomiensis (d'Orbigny, 1853) Figs 63–69

1853 *Bidiastopora neocomiensis* d'Orbigny: 800; pl. 784, figs 9–11.
1922 *Cardioecia (Bidiastopora) neocomiensis* (d'Orbigny) Canu & Bassler: 19; pl. 4, fig. 3.
1922 *Notoplagioecia farringdonensis* Canu & Bassler: 30; pl. 1, fig. 18.
?non 1926 *Cardioecia neocomiensis* (d'Orbigny); Canu & Bassler: 40; pl. 2, figs 1–7; fig. 19A–B.
non 1926 *Cardioecia neocomiensis parvula* Canu & Bassler: 42; pl. 2, fig. 8.
?1926 *Cardioecia neocomiensis entalophoroides* Canu & Bassler: 42; pl. 2, figs 9–10.
1926 *Cardioecia faringdonensis* Canu & Bassler: 44; pl. 3, figs 9–15; fig. 19E–G.
1926 *Cardioecia pauper* Canu & Bassler: 44; pl. 5, figs 1–2.
1926 *Notoplagioecia faringdonensis* [sic] Canu & Bassler: 48; pl. 5, figs 3–5; fig. 22.
?1965 *Cardioecia neocomiensis* (d'Orbigny); Cotillon & Walter: 934; pl. 40, fig. 7.
1966 *Mesenteripora neocomiensis* (d'Orbigny) Walter: 898; pl. 26, figs 9–10.
?1966 *Mesenteripora campicheana* (d'Orbigny); Walter: 898; pl. 26, figs 11–12.
1967 *Mesenteripora sanctacrucensis* nom. nov., Walter: 56.
1971 *Cardioecia neocomiensis* (d'Orbigny); Hillmer: 55; pl. 6, figs 1–5; text-figs 14–15.
1971 *'Cardioecia' faringdonensis* Canu & Bassler; Hillmer: 58; pl. 6, figs 7–11; text-fig. 16.
1972 *Mesenteripora sanctacrucensis* Walter; Walter: 313 [?*partim*]; pl. 21, figs 8–9.
1975 *Entalophora faringdonensis* (Canu & Bassler); Walter *et al.*: 99; pl. 8, figs 8–10.
1985 *Mesenteripora sanctacrucensis* Walter; Walter: 16; pl. 5, figs 1–7, pl. 6, figs 3–7 (non figs 1–2); pl. 9, fig. 12 (non figs 13–15).

Material. BM(NH) D7465 (colony base encrusting a pebble), Cunnington Colln; D7980 (colony base encrusting a pebble), Treacher Colln; D38853, D52196 (7 colony bases), D55074 3), D55075 (2), D55076, D55077 (2), D55078–81, D55136, Little Coxwell Pit, Pitt Colln; D53698 (colony base), D57645, Little Coxwell Pit, Davis Colln; D55132, Bowler's Pit, Pitt Colln; D55133 (2), Bowler's Pit, Gaster Colln; D55134 (4), Little Coxwell Pit, Gaster Colln; D55135 (sample), D55137 3), Little Coxwell Pit, Thomas Colln; D55138 (sample), Cleevely Colln. USNM 69893 (5 + thin sections), syntypes of *Cardioecia faringdonensis* Canu & Bassler; 69898, holotype of *Cardioecia pauper* Canu & Bassler; 68718 (2), syntypes of *Notoplagioecia farringdonensis* Canu & Bassler.

Description. Zoarium dendroid with slightly compressed branches (Figs 63–66), averaging about 2–3 mm in diameter, circular to elliptical in transverse section, bifurcating more-or-less in the plane of compression, successive bifurcations subparallel. Zooecia are budded from a short median lamina (Fig. 69), which is orientated parallel to the plane of branch compression, and open around the entire perimeter of the branch. Branch growth tips are bluntly conical. The encrusting colony base (Fig. 68) is probosciniform, generally curved, and lacks bifurcations. With a single possible exception, each base gives rise to only one erect stem; cf. Walter (1985) who figures (pl. 5, fig. 2) the base of a colony from the Valanginian of the Jura which apparently bifurcates and gives rise to several erect stems.

Autozooecia are moderately large and arranged in irregular verticels (Fig. 66B) or in approximate quincunx, about 12 zooecia in a circumference of the branch. Frontal walls are flat to slightly convex, about twice as long as wide, with circular pseudopores at a density of about 1200 per mm^2. Apertures usually have low rims, although moderately well developed peristomes occur in a few specimens (e.g. peristomes 0·5 mm long are present in autozooecia on the base of D53698). Autozooecial apertures are subcircular, large, and occasionally occluded by terminal diaphragms. The ancestrula (Fig. 68A) is large (1·2 mm long) with a very wide protoecium (0·5 mm or more).

Gynozooecia (Fig. 67) have subtriangular, well-inflated distal frontal walls indented slightly by autozooecial apertures, and have small, transversely elongate ooeciopores.

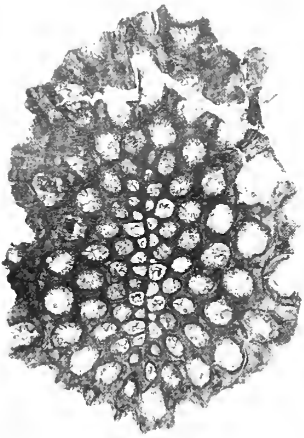
Measurements. TAM, 0·10–0·16 mm; TPM, 0·20–0·28 mm; FWL, *c.* 0·65 mm; FWW, *c.* 0·35 mm; GTL, 1·20–2·00 mm; GW, 0·90–1·20 mm; TOSM, 0·20 mm; LOSM, 0·13 mm.

Remarks. *Cardioecia neocomiensis* has a long synonomy which reflects the wide distribution of the species in the Valanginian to Aptian of Europe.

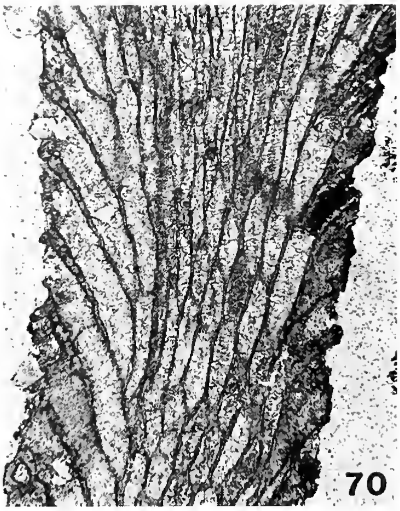
Canu & Bassler (1922, 1926) described three new species from Faringdon: *Notoplagioecia farringdonensis, Cardioecia faringdonensis*, and *C. pauper*. These were founded on very slight differences and are all regarded as junior synonyms of *C. neocomiensis* (d'Orbigny, 1853). In general, specimens of *C. neocomiensis* from Faringdon have slightly broader branches and thicker peristomes than specimens from argillaceous facies of the Neocomian (e.g. BM(NH) D53146 from the Hauterivian of Lincolnshire). These variations are regarded as ecophenotypic responses of no significance at species level; Flor (1972) found similar branch width variations in the vinculariiform cyclostomes *Spiropora verticellata* and *Entalophora proboscoidea*.

The species name *sanctacrucensis* was introduced by Walter (1967) for *Mesenteripora [Bidiastopora] neocomiensis* (d'Orbigny, 1853: 800; pl. 784, figs 9–11), to avoid hononymy with *M. [Mesenteripora] neocomiensis* (d'Orbigny, 1853: 808; pl. 756, figs 7–9). We regard the new name as superfluous, the former species having been transferred previously to *Cardioecia* by Canu & Bassler (1922).

C. neocomiensis is one of the most common species present at Faringdon. The rather robust branches are an adundant component of sediment samples, and the encrusting colony bases are also comparatively common, some detached from their substrates, but others encrusting shell material, sponges, other bryozoans or pebbles.



69



70

Figs 69–70 Thin sections. Fig. 69, *Cardioecia neocomiensis* (d'Orbigny), USNM 69893f, syntype of *C. faringdonensis* Canu & Bassler, thick transverse section showing budding lamina, × 29. Fig. 70, *Ceata granulata* (Canu & Bassler), BM(NH) D55141, oblique longitudinal section showing shallow angle of intersection between zooecia on the left and colony surface, × 32.

Genus *CEATA* Strand, 1928

TYPE SPECIES. *Cea rustica* d'Orbigny, 1854, by subsequent designation of Bassler, 1935; Senonian of Vendôme, France.

REMARKS. *Ceata* was proposed by Strand (1928) to replace *Cea* d'Orbigny, 1854, a junior homonym of a hymenopteran genus. It is seemingly a plagioeciid with narrow bifoliate erect branches and trumpet-shaped zooecial tubes which intersect the colony surface at an acute angle. There is some doubt as to whether the type species of this genus has pseudoporous frontal walls of the kind which are visible in well-preserved specimens of *Ceata granulata* (Canu & Bassler) from Faringdon. If not, the Faringdon species may have to be reassigned.

RANGE. Barremian to Senonian.

Ceata granulata (Canu & Bassler, 1926) Figs 70–74

1926 *Cea granulata* Canu & Bassler: 49; pl. 5, figs 6–14; text-fig. 23A–B.
non 1975 *Cea granulata* (Canu & Bassler); Walter *et al*: 108; pl. 9, figs 14–15 [=*Poriceata ardescensis* Walter, 1983].
1981 *Ceata granulata* (Canu & Bassler) Voigt: fig. 1h.
1983 *Ceata granulata* (Canu & Bassler); Walter: pl. 1, figs 1–2.

LECTOTYPE. USNM 69899c, the specimen figured by Canu & Bassler (1926: pl. 5, figs 13–14) is here chosen as the lectotype.

PARALECTOTYPES. USNM 69899a (Canu & Bassler 1926: pl. 5, figs 9–10), 69899b (pl. 5, figs 7–8), 69899d (pl. 5, figs 11–12). There is also a thin section but this bears little resemblance to the section shown by Canu & Bassler in their text-figure 23.

OTHER MATERIAL. BM(NH) D55082 (2), D55086, D55140, D55141 (4 thin sections), D55142 (4), D55143 (sample), Little Coxwell Pit, Thomas Colln; D55083–4, D55139, D55144 (sample), Little Coxwell Pit, Pitt Colln; D55085, ? locality, Pitt Colln; D55145, Little Coxwell Pit, Davis Colln; D55146 (6), ?Little Coxwell Pit, Cleevely Colln; D55147, Curry Colln.

DESCRIPTION. Zoarium erect, consisting of compressed branches which bifurcate in the plane of the compression, though with successive bifurcations somewhat subparallel owing to torsion of the branches. A median budding lamina occupies the centre of the branches which are 1–2 by 0·8–1·0 mm in diameter. Ill-defined maculae with low densities of zooecial apertures have been observed (cf. *Heterohaplooecia* Voigt & Viaud, 1983, and *Plagioecia spissa*, p. 90).

Autozooecia are long trumpet-shaped tubes which intersect the colony surface at a low angle (Fig. 70). In well-preserved specimens (Figs 71, 73) autozooecial frontal walls ('facettes' of Canu & Bassler, 1926) are present which are pseudoporous (*c.* 1800 pseudopores per mm^2) and apparently very thin. Apertures are circular in zooecia with frontal walls (Fig. 73B), closely packed, and have a slightly raised rim ('salient peristome'). In the majority of specimens, however, autozooecial frontal walls are absent (probably owing to mechanical abrasion but possibly primary) and the zooecia have 'false' apertures (Fig. 72B) which are polygonal (often hexagonal or pentagonal) and about 0·15 mm in diameter.

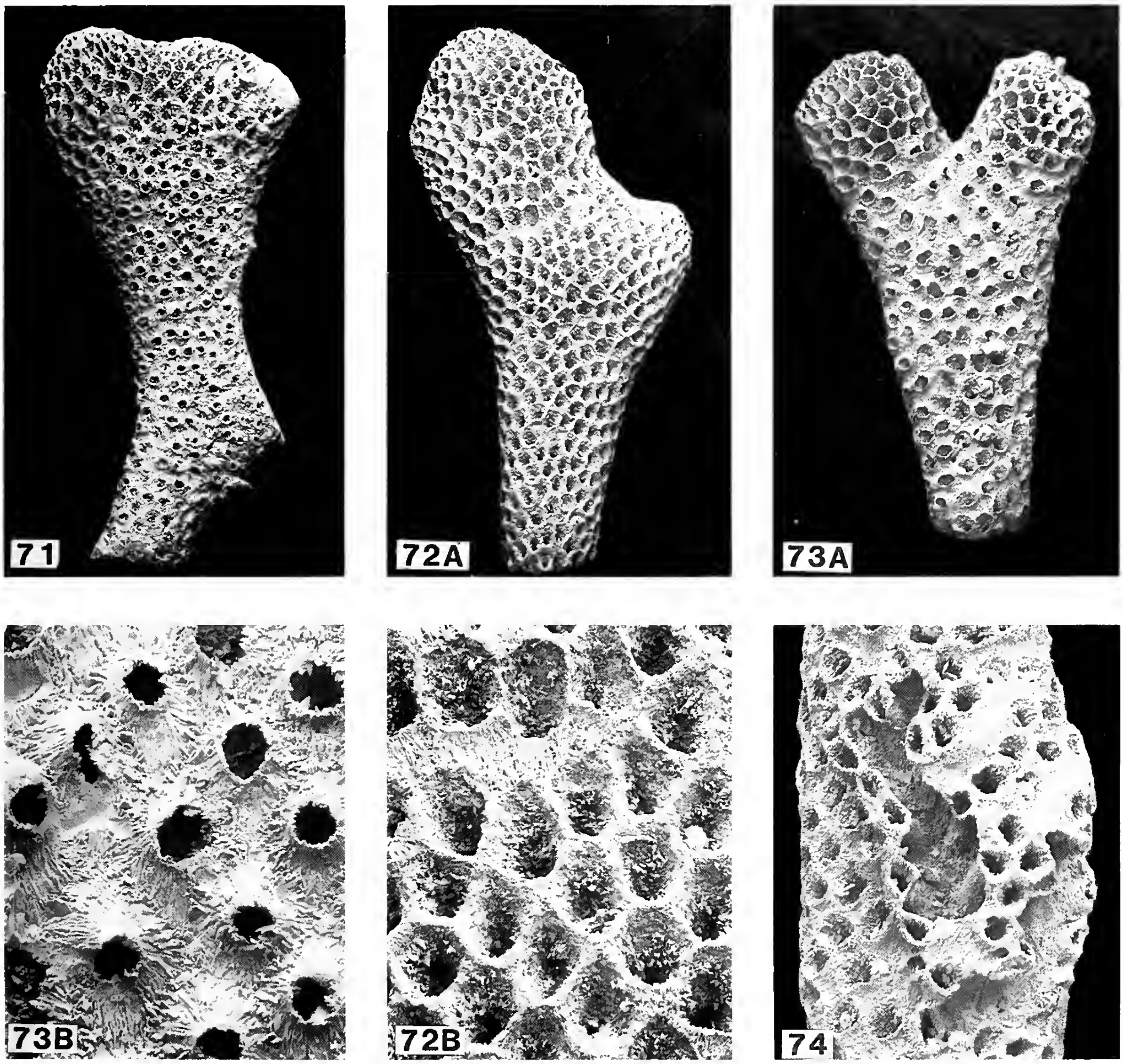
Gynozooecia (Fig. 74) are uncommon and all known examples are damaged. The bulbous distal part of the gynozooecium has two digitate lateral lobes strongly indented by surrounding autozooecia, which extend well distally of the median ooeciopore. The ooeciopore is apparently transversely elongate and small.

MEASUREMENTS. TAM, 0·08 mm; GDL, *c.* 2·3 mm; GW, *c.* 1·0 mm; TOPM, 0·04 mm.

REMARKS. Although branch fragments of this species are abundant at Faringdon, the colony base is unknown. The great majority of specimens are devoid of their zooecial frontal walls. Specimens are most easily confused with *Cardioecia neocomiensis* but are generally less robust.

Genus *MESENTERIPORA* Blainville, 1830

TYPE SPECIES. *Mesenteripora michelini* Blainville, 1830, by original designation; Bathonian of Normandy, France.



Figs 71–74 *Ceata granulata* (Canu & Bassler). Fig. 71, USNM 69899c, **lectotype** (herein selected), with autozooecial frontal walls intact, × 10. Fig. 72, USNM 69899a; 72A, branch with autozooecial frontal walls missing, × 11; 72B, obliquely orientated autozooecia lacking frontal walls, × 53. Fig. 73, BM(NH) D55086; 73A, bifurcating branch, × 12; 73B, circular autozooecial apertures, × 57. Fig. 74, BM(NH) D55084, broken gynozooecium, × 30.

Remarks. *Mesenteripora* is a plagioeciid genus with erect, foliaceous colonies which are bilamellar, the zooecia budding from both sides of a median budding lamina. In the type species, colonies have tightly folded sinuous fronds, and the gynozooecium is subtriangular in outline (see Walter 1970). Neocomian species of the genus have been revised by Walter (1985).

Range. Pliensbachian to Recent.

?*Mesenteripora campicheana* (d'Orbigny, 1853) Fig. 75

1853 *Bidiastopora campicheana* d'Orbigny: 800; pl. 784, figs 6–8.

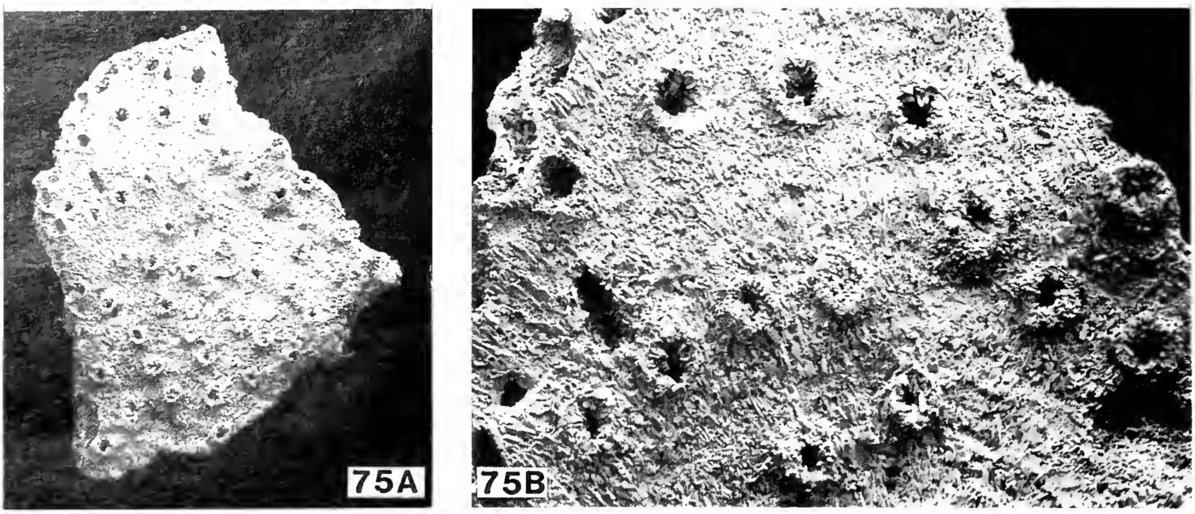
1985 *Mesenteripora campicheana* (d'Orbigny) Walter: 10; pl. 1, figs 1–9; pl. 9, figs 6–7.

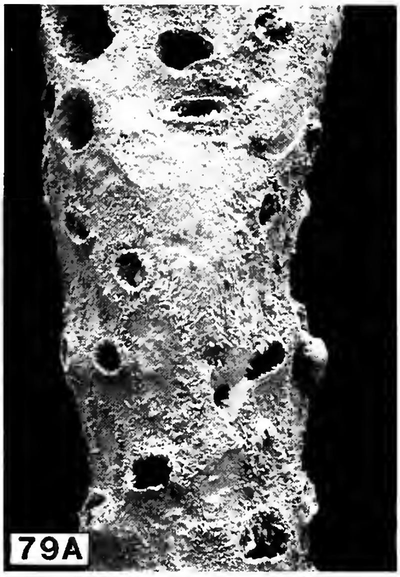
Material. BM(NH) D55441, Little Coxwell Pit, Davis Colln.

Description. A single poorly-preserved fragment (2×3 mm) of a thin bilamellar frond about 0·3 mm in thickness (Fig. 75A). The autozooecia are immersed, and have apertures which are circular to longitudinally elongate with a slightly raised peristome (Fig. 75B). No gynozooecia are preserved; in specimens described by Walter (1985), the gynozooecia are boomerang-shaped with lateral lobes extending distally of the ooeciopore.

Measurements. TAM, mean 0·08 mm; TPM, mean 0·15 mm.

Remarks. The absence of gynozooecia precludes certain determination of this specimen which is, however, worthy of





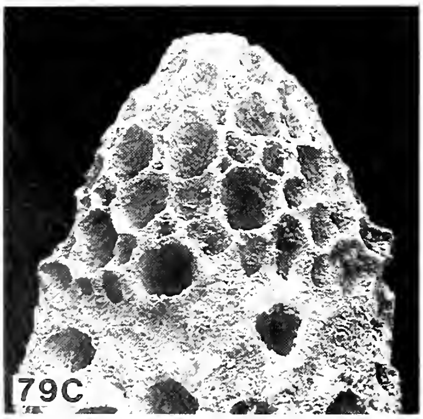


Fig. 75 *?Mesenteripora campicheana* (d'Orbigny), BM(NH) D55441; 75A, fragment of bifoliate frond, × 22; 75B, autozooecia, × 60.

Figs 76–80 *Entalophoroecia quadripartita* (Canu & Bassler). Fig. 76, USNM 69852b, paralectotype, × 24. Fig. 77, BM(NH) D55092, × 32. Fig. 78, BM(NH) D55093b, branch fragment with worn gynozooecium, × 22. Fig. 79, BM(NH) D55163; 79A, gynozooecium, × 53; 79B, ooeciopore, × 134; 79C, growth tip (small buds are probably kenozooecia), × 60. Fig. 80, BM(NH) D55093a, fractured branch, × 90.

note in being the only foliaceous tubuloporine recorded from Faringdon.

Genus *ENTALOPHOROECIA* Harmelin 1974*b*

TYPE SPECIES. *Tubulipora deflexa* Couch, 1844, by original designation; Recent.

REMARKS. *Entalophoroecia* was proposed to accommodate some living tubuloporine species (see Harmelin 1974b, 1976; Hayward & Ryland 1985) of a type previously assigned to *Entalophora* Lamouroux but differing from this genus (type species *Entalophora cellarioides* Lamouroux from the Bathonian, see Walter 1970) in not having an axial canal. Colonies of the type species of *Entalophoroecia* possess extensive, probosciniform encrusting bases and complexly interlobed gynozooids with circular ooeciopores on the erect branches.

RANGE. Cretaceous to Recent (this range is highly tentative pending re-evaluation of the diverse species of vinculariiform cyclostomes found in Mesozoic and Cenozoic sediments).

Entalophoroecia quadripartita (Canu & Bassler, 1926)

Figs 76–80

1926 *Clinopora quadripartita* Canu & Bassler: 12; pl. 29, figs 8–11.

LECTOTYPE. USNM 69852a, figd by Canu & Bassler (1926: pl. 29, figs 8, 10, 11), is here chosen as lectotype.

PARALECTOTYPE. USNM 69852b, figd by Canu & Bassler (1926: pl. 29, fig. 9). Only the distal part of this specimen remains; the specimen as figured is considered by A. H. Cheetham (personal communication) to be possibly parts of two specimens glued together.

OTHER MATERIAL. BM(NH) D55092, D55166 (2), Davis Colln; D55123, D55165 (4), Little Coxwell Pit, Davis Colln; D55093 (6), D55157 (sample), D55158 (sample), D55167 (3), D55169 (10), Little Coxwell Pit, Elliott Colln; D55159 (sample), D55160 (sample), D55161 (6), D55162, D55163, D55164 (12), Little Coxwell Pit, Thomas Colln.

DESCRIPTION. Zoarium vinculariiform, consisting of narrow (0·3–1 mm diameter) bifurcating branches (Figs 76–78) which may have dilated portions. Branch growth tips are tall cones (Fig. 79C). The colony base is unknown.

Autozooecia are small and slender, their frontal walls bordered by a slightly raised wall and bearing pseudopores at a density of 1300–1900 per mm^2. Apertures are circular, slightly transversely or slightly longitudinally elongate and have short preserved peristomes. In a branch circumference there are generally 6–8 zooecia, increasing to 10–12 in dilated branches. Aperture spacing and arrangement is highly variable.

Kenozooecia, small and of varying shape, are often abundant and are interspersed irregularly between the autozooecia. They may be visible at growth tips as small buds (Fig. 79C).

Gynozooecia (Figs 78–79), usually preserved broken, have a V-shaped distal frontal wall which includes two lateral lobes extending well distally of the median ooeciopore. The ooeciopore is transversely elongate and slit-like (Fig. 79B).

MEASUREMENTS. TAM, 0·06–0·10 mm; TPM, 0·10–0·14 mm; FWW, mean 0·14 mm; TOSM, 0·20 mm; LOSM, 0·06 mm; TOPM, 0·17 mm; LOPM, 0·04 mm.

REMARKS. Canu & Bassler (1926) assigned this species to *Clinopora* Marsson. The type species of this Upper Cretaceous genus, *C. lineata* (Beisel), has the entire branch surface covered with narrow kenozooecia which form lineations parallel to the growth direction. In *E. quadripartita*, however, autozooecial frontal walls are well developed and kenozooecia are scattered irregularly among the autozooecia; assignment of the Faringdon species to *Clinopora* is therefore incorrect.

Although *Entalophoroecia* Harmelin is a more appropriate genus for the reception of this species, some reservations remain in view of the ooeciopore which is circular in the type species of *Entalophoroecia* but distinctly transverse in *E. quadripartita*.

E. quadripartita resembles *Entalophora vassiacensis* d'Orbigny, 1853, redescribed by Walter (1977) from the Aptian of the Gard (France), in general morphology and particularly in the shape of the gynozooecium. Further study may reveal the two species to be synonymous.

The two Neocomian species *Dichospiropora neocomiensis* (d'Orbigny, 1853) and *Bicoronipora reticuloides* (Canu & Bassler, 1926) have colony forms and gynozooecia similar to those of *E. quadripartita* (see Walter 1987*a*). However, *D. neocomiensis* differs from *E. quadripartita* in having the autozooecial apertures arranged in transverse rings, and *B. reticuloides* in having a narrow axial canal within the branches.

Branch fragments of *E. quadripartita* are very common at Faringdon and it is surprising that all authors prior to Canu & Bassler (1926) overlooked the species. It is readily distinguished from all other Faringdon tubuloporine species except *Collapora hillmeri* by the narrowness of the branches. Unequivocal discrimination between *E. quadripartita* and *C. hillmeri* requires the presence of gynozooecia which have lobes extending distally of the ooeciopore only in the former species.

Family **ELEIDAE** d'Orbigny, 1853
(= MELICERITITIDAE Pergens, 1889)

Genus *MELICERITITES* Roemer, 1840

TYPE SPECIES. *Ceriopora gracilis* Goldfuss, 1826, by subsequent designation of Gregory, 1899; Cenomanian of Essen, West Germany.

REMARKS. Melicerititids are unique among cyclostomes in possessing zooids with hinged opercula closing the aperture (see Levinsen 1912). These are calcified structures which are often preserved *in situ*; when missing, the past presence of an operculum can be inferred from the straight proximal edge of the aperture which formed the hinge line of the operculum. In many species polymorphic zooids – eleozooids (Taylor 1985) – with enlarged opercula are developed.

Meliceritites is the only eleid genus known in the Aptian. Species of *Meliceritites* have vinculariiform colonies with autozooecia opening around the entire perimeter of the branches (cf. *Meliceritella*), a single-walled organization (cf. *Foricula*), and eleozooecia either absent or greatly outnumbered by the autozooecia (cf. *Atagma*).

RANGE. Barremian to Maastrichtian.

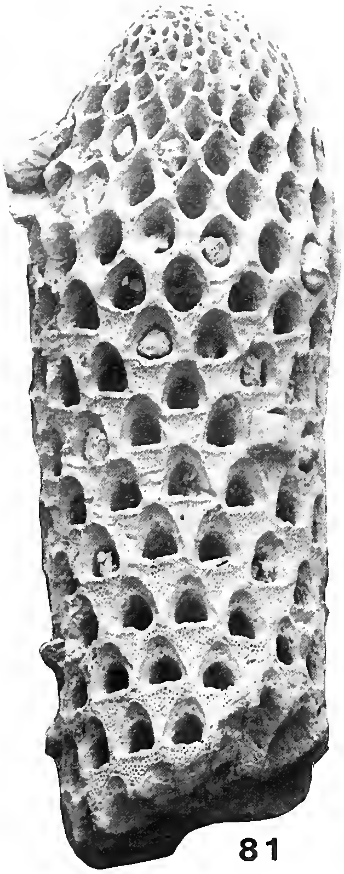


Fig. 81 *Meliceritites gracilis* (Goldfuss), BM(NH) D55288, branch with growth tip, × 30; see also Fig. 82.

Meliceritites gracilis (Goldfuss, 1827) Figs 81–84

1827 *Ceriopora gracilis* Goldfuss: 35; pl. 10, fig. 11a–c.
1840–1 *Meliceritites (Ceriopora) gracilis* (Goldfuss) Roemer: 18; pl. 5, fig. 13.
?1871 *Meliceritites gracilis* (Goldfuss); Simonowitsch: 66.
non 1887 *Meliceritites gracilis* (Goldfuss); Marsson: 46; pl. 4, fig. 8 [=*M. gothica* Levinsen].
non 1897 *Meliceritites gracilis* (Goldfuss); Canu: 752; pl. 22, figs 1–2.
1899 *Meliceritites gracilis* (Goldfuss); Gregory: 324; fig. 38.
1912 *Meliceritites gracilis* (Goldfuss); Levinsen: 28; figs a, b on p. 29.
1922 *Meliceritites gracilis* (Goldfuss); Canu & Bassler: 83; pl. 13, figs 1–4.
1975 *Meliceritites semiclausa* (Michelin); Walter *et al.*: 109; pl. 10, figs 5–6; text-fig. 8.
1981 *Meliceritites gracilis* (Goldfuss); Voigt: 445; fig. 2j.

MATERIAL. BM(NH) D55287, Little Coxwell Pit, Curry Colln; D55288–9, Little Coxwell Pit, Elliott Colln; D55290–1, Little Coxwell Pit, Whiteley Colln; D55292, Cleevely Colln; D55293–4, Davis Colln.

DESCRIPTION. Colonies are dendroid with moderately thick (1–1·5 mm), bifurcating vinculariiform branches (Fig. 81) which may develop overgrowths through branch collision. Growth tips are rounded conical in shape.

Autozooecia are generally arranged in well-defined transverse rows (Fig. 82), and are rounded diamond-shaped to subhexagonal in frontal outline with pseudoporous frontal walls of relatively small area. Apertures are closely-spaced, large, arched and significantly higher than wide. There is no true opercular shelf, but apertures are flared and may possess a deep distal ledge (Fig. 84A). Opercula (Fig. 84B) are seldom found *in situ*. Apertures are very often occluded by non-pseudoporous diaphragms (Fig. 83), located at the level of flaring, some of which have a central depression and pore.

Gynozooecia are unknown in Faringdon specimens; however, specimens from the U. Barremian of southern France and the Cenomanian of Germany have gynozooecia with bulbous distal frontal walls, longitudinally elliptical to subtriangular in outline, a transversely elongate ooeciopore and an atrial ring.

Eleozooecia are absent.

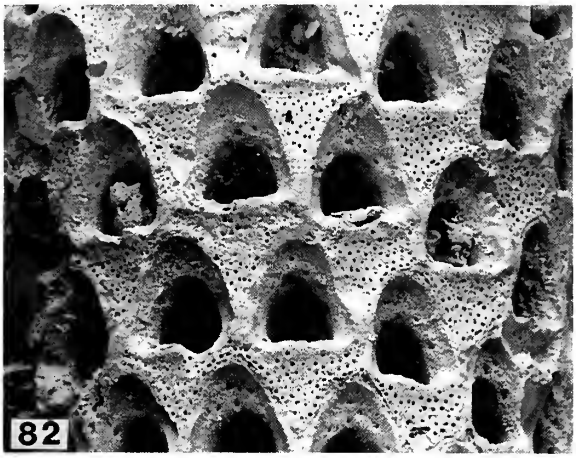
MEASUREMENTS (based on determinations of 10 autozooecia from BM(NH) D55288). FWL, 0·33–0·50 mm; FWW, 0·24–0·29 mm; LAM, 0·21–0·26 mm; TAM, 0·17–0·20 mm.

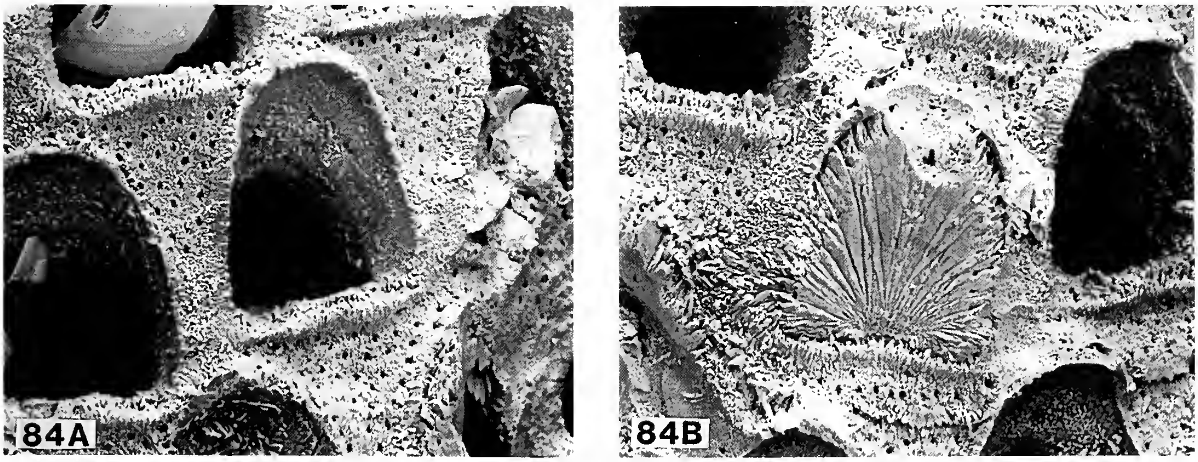
REMARKS. This species has not been previously recorded from Faringdon and is considerably rarer than the three other melicerititids. It is distinguished by the shape of the large autozooecial apertures which are significantly higher than wide.

The type locality for *M. gracilis* is the Cenomanian of Essen, West Germany. The species appears to range down into the Upper Barremian, making it one of the oldest known melicerititids. However, populations of differing age are not absolutely identical. Some, though not all, of the specimens from Essen possess autozooecia with platforms extending inwards from the hinge line and perpendicular to the frontal wall (see the 'salpinginid tubuliporate' figured by Boardman *et al.* 1983: fig. 141, 5a–c). Curved, asymmetrical apertures are also a feature of many Essen specimens. Specimens from the Barremian of Nord Serre de Tourre (France) may have tubercles close to the proximolateral borders of the autozooecial apertures. There is also variation in the precise location and obliquity of diaphragms, the area of frontal walls and the dimensions of the autozooecia. Taking this variation into account, it is possible that *Meliceritites upwarensis* Keeping, described from the Aptian of Upware (holotype SM B26098), which closely resembles *M. gracilis* but has larger autozooecia (LAM 0·26–0·29 mm; TAM 0·18–0·23 mm), is a junior synonym of *M. gracilis*.

Meliceritites dendroidea (Keeping, 1883) Figs 85–91

?1853 *Multelea gracilis* d'Orbigny [sic; (Goldfuss)]; d'Orbigny: 645; pl. 739, figs 1–3.
1883 *Entalophora dendroidea* Keeping: 138; pl. 7, fig. 12a, b.
1899 *Meliceritites semiclausa* (Michelin); Gregory: 328 (*partim*); pl. 14, fig. 3 only.
1926 *Lobosoecia semiclausa* (Michelin); Canu & Bassler: 63; pl. 14, figs 12–13.
1926 *Meliceritites semiclausa* Gregory [sic; (Michelin)]; Canu & Bassler: 66; pl. 11, figs 12–13.





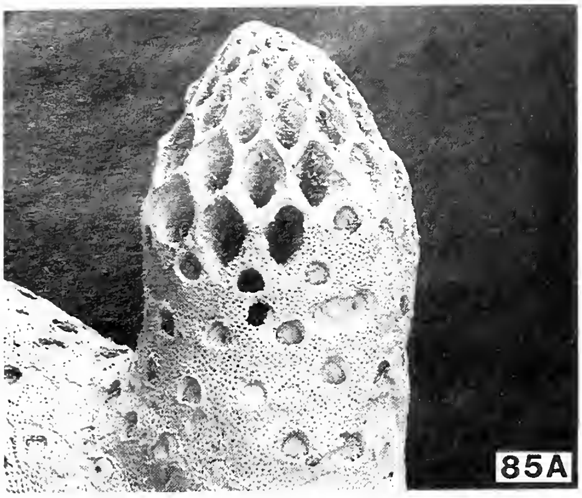
Figs 82–84 *Meliceritites gracilis* (Goldfuss). Fig. 82, BM(NH) D55288, autozooecia, × 69; see also Fig. 81. Fig. 83, BM(NH) D55287, terminal diaphragm covering autozooecial aperture, × 130. Fig. 84, D57392; 84A, open autozooecial aperture in a slightly oblique view, × 180; 84B, operculum, × 185.

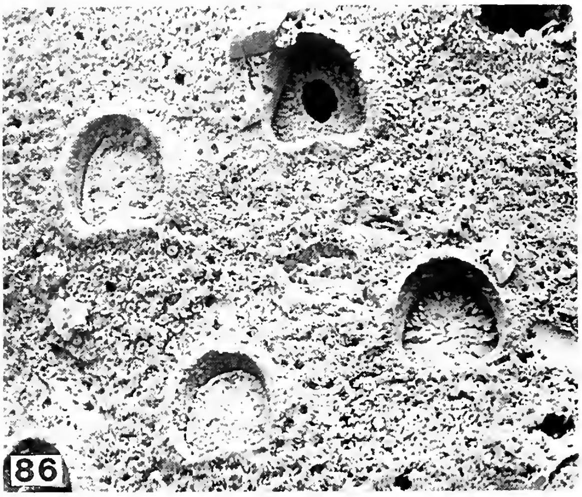
non 1974 *Meliceritites semiclausa* (Michelin); Masse & Walter: 192; pl. 36, figs 4–5, 9.
non 1975 *Meliceritites semiclausa* (Michelin); Walter *et al.*: 109; pl. 10, figs 5–6; text-fig. 8.
?1977 *Meliceritites semiclausa* (Michelin); Walter: 328; pl. 1, figs 5, 10.
?1979 *Meliceritites semiclausa* (Michelin); Walter & Clavel: 823; pl. 1, figs 1–2.

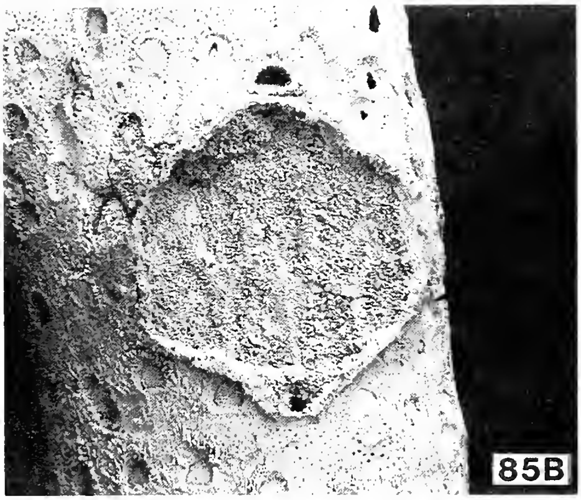
MATERIAL. BM(NH) 50781, Morris Colln; 60539, Cunnington Colln (figd by Gregory 1899: pl. 14, fig. 3, who erroneously gave the horizon and locality as Upper Greensand, Warminster); D15051, Treacher Colln; D52153 (sample), D52189–90 (samples), D57706–7 (SEM stub), Little Coxwell Pit, Pitt Colln; D55173 (sample), Thomas Colln; D55174, D55350 (sample), Little Coxwell Pit, Gaster Colln; D55176 (sample), D57648 (sample), Davis Colln; D55177–78 (samples), D55271, D55273 (sample), D55349 (sample), Little Coxwell Pit, Thomas Colln; D55268, Wicklesham Pit (Red Gravels), Taylor Colln; D55269, Little Coxwell Pit, Laurie Colln; D55270 (sample), Little Coxwell Pit, Cleevely Colln; D55272 (sample), Little Coxwell Pit, Curry Colln; D55285 (sample), D57389, Little Coxwell Pit, Elliott Colln.

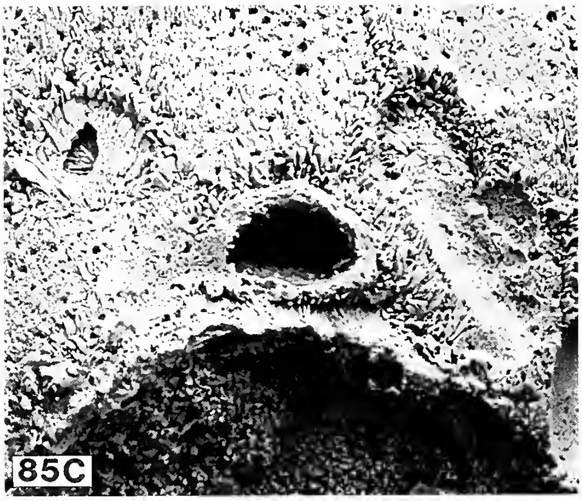
DESCRIPTION. Colonies are dendroid (Fig. 90) with narrow (0·72–1·17 mm), vinculariiform branches which bifurcate infrequently (internode length 1·4 mm to more than 8·0 mm) and are often slightly sinuous. Branches may anastomose and the resultant concave attachment scars are commonly found in fragmented material. Growth tips have a rounded conical shape (Fig. 85A) and are sometimes occluded. Colony bases may be extensive, giving rise to more than one erect branch. Overgrowths (Figs 87–88) are uncommon in Faringdon specimens (cf. specimens from the Lower Greensand of Upware), except close to the colony base (Fig. 91) where they are apparently formed as a result of frontal budding.

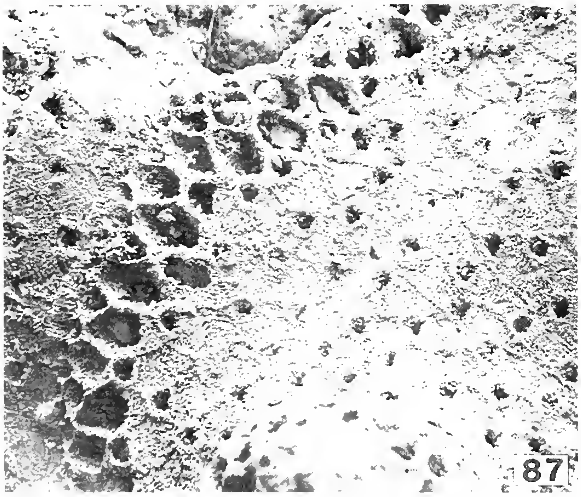
Autozooecia are generally arranged in well-defined transverse rows, and have subhexagonal frontal outlines, their distal parts rounded to accommodate the aperture, with interzooecial walls usually standing a little above the level of the slightly convex, pseudoporous frontal walls. Apertures (Fig. 86) are very small, hemi-elliptical, about as long as wide, and well-rounded distally. A slight distal and lateral apertural rim is present, the hinge line is gently convex without distinct hinge teeth, and there is no appreciable operculum shelf. Diaphragms (Fig. 86) are commonly found just inward of the aperture and vary from sparsely

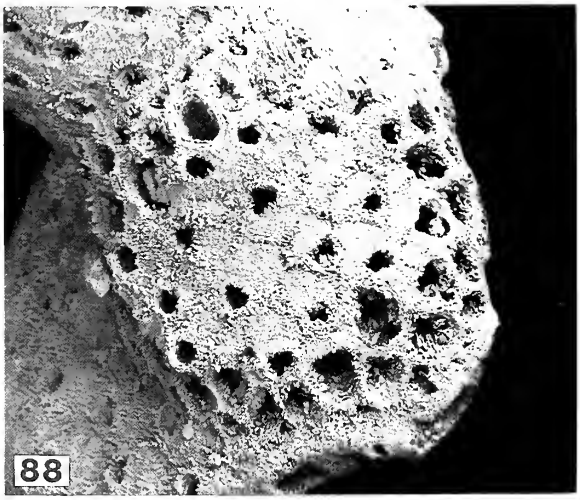












Figs 85–88 *Meliceritites dendroidea* (Keeping). Fig. 85, BM(NH) D57389; 85A, growth tip, × 42; 85B, gynozooecium with abraded frontal wall, × 62; 85C, ooeciopore, × 218. Fig. 86, BM(NH) 60539, terminal diaphragms (one of which is bored) occluding autozooecial apertures, × 147. Fig. 87, BM(NH) 50781, colony base, × 40. Fig. 88, BM(NH) D57391, frontally-budded overgrowth near colony base, × 55.

Fig. 89 *Meliceritites dendroidea* (Keeping), BM(NH) D52153, broken gynozooecium, × 69.

pseudoporous to non-pseudoporous, occasionally with a central depression and pore. Opercula are frequently found *in situ*; worn examples have 10–12 pits arranged in a crescent parallel to the lateral and distal edges of the operculum. The inner surfaces of dissected opercula appear to lack distinct sclerites but have a raised marginal shelf.

Eleozooecia have not been observed in Faringdon specimens; however, a specimen from the Aptian Bargate Stone of Kent possesses eleozooecia with apertures of a similar shape to the autozooecia but about twice the size.

Gynozooecia are moderately common. The bulbous distal part of the frontal wall has a longitudinally elliptical to pear-shaped outline (Figs 85B, 89), often with a parallel-sided initial portion leading from the hemi-elliptical parental aperture. Autozooecia and kenozooecia bordering the gynozooecium are often raised. Interzooecial walls of occluded autozooecia are prominent on the floor of abraded gynozooecia (Fig. 85B), but an atrial ring has not been observed. The ooeciopore, situated a little distal of the bulbous part of the gynozooecium, is transversely elliptical (Fig. 85C); in one example it is apparently occluded by a diaphragm.

MEASUREMENTS (autozooecial dimensions from 10 determinations of zooecia in one colony; gynozooecial dimensions from measurements of 6 gynozooecia). FWL, 0·32–0·39 mm; FWW, 0·18–0·23 mm; LAM, 0·08–0·09 mm; TAM, 0·08–0·09 mm; GTL, 1·11–1·58 mm; GDL, 0·92–1·35 mm; GW, 0·75–0·93 mm; LOPM, 0·05 mm; TOPM, 0·08–0·09 mm.

REMARKS. *Meliceritites dendroidea* is a very common species at Faringdon and can be distinguished from the other melicerititids by the small size of the apertures and the narrow diameter of the branches.

The species is usually incorrectly cited as *Meliceritites semiclausa* (Michelin), a species from the Cenomanian of Le Mans which has larger autozooecia, abundant eleozooecia with funnel-shaped apertures, and branches with narrow axial canals.

Faringdon specimens of *Meliceritites dendroidea* (Keeping) have slightly smaller autozooecia than the holotype (SM B26086) from the Lower Greensand of Upware, but very few autozooecia can be measured in this poorly-preserved specimen and those that are measurable all come from an overgrowth close to the colony base. It is possible that the *Multelea gracilis* (Michelin, *non* Goldfuss) of d'Orbigny (1853), described from the Albian of Grandpré, is a synonym of *Meliceritites dendroidea*. However, autozooecia measured from specimens in the d'Orbigny Collection (MNHN 6022) have larger frontal walls than either Upware or Faringdon specimens.

Meliceritites cunningtoni (Gregory, 1899) Figs 92–96

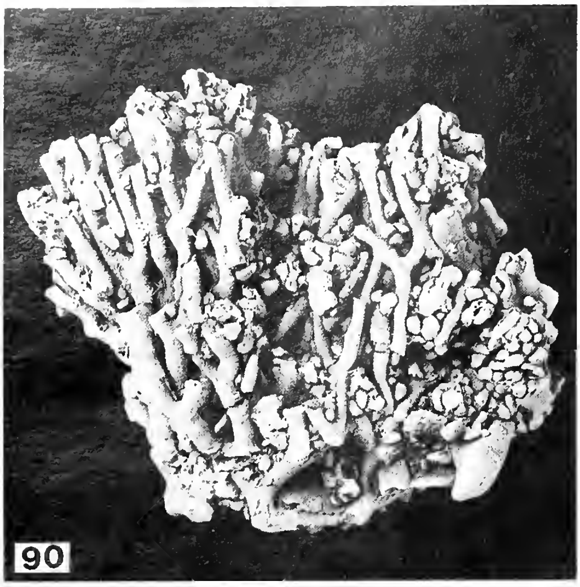
1899 *Nodelea cunningtoni* Gregory : 308; text-figs 35–36.
1926 *Meliceritites cunningtoni* (Gregory) Canu & Bassler: 65; pl. 13, figs 1–8.
1981 *Meliceritites cunningtoni* (Gregory); Voigt: 441; fig. 1e.

LECTOTYPE. BM(NH) D5137, Cunnington Colln, figured by Gregory (1899: text-fig. 35) is here selected as the lectotype. Faringdon Sponge Gravel, Faringdon.

PARALECTOTYPES. BM(NH) D5131, D5132, D5137, Faringdon, Cunnington Colln. The remaining specimens (syntypes) listed by Gregory (1899: 309) are either worn and indeterminate or comprise mixed samples of vinculariiform cyclostomes.

OTHER MATERIAL. BM(NH) D52191 (sample), D55258 (sample), D55259 (sample), D55260–1, D57390, D57702 (SEM stub), Little Coxwell Pit, Pitt Colln; D55169 (sample), Little Coxwell Pit, ?colln; D55170 (sample), D55172 (sample), Little Coxwell Pit, Thomas Colln; D55171 (sample), D57386, D57649 (sample), Davis Colln; D55262 (sample), Little Coxwell Pit, Gaster Colln; D55263 (sample), Little Coxwell Pit, Thomas Colln; D55264 (sample), Cleevely Colln; D57703 (SEM stub), Little Coxwell Pit, ?Colln. USNM 69917, 7 fragments mounted on a card, figd by Canu & Bassler (1926: pl. 13, figs 1–8).

DESCRIPTION. Colonies are dendroid with relatively thick (1·45–2·0 mm), straight or slightly curved, vinculariiform branches (Fig. 92A) which bifurcate at irregular intervals (internode lengths of 0·36 mm to over 14 mm have been observed), successive bifurcations generally occurring in planes at 90°. The colony base has not been observed. Occasional overgrowths seem to be the result of branch collisions. Branch growth tips are rounded dome-shaped or



Figs 90–91 *Meliceritites dendroidea* (Keeping), optical photographs. Fig. 90, BM(NH) D55268, well-preserved bushy colony, × 1·9. Fig. 91, BM(NH) 50781, colony base (lower right) encrusting a pebble together with various other species, × 1·8.

high rounded cones (Fig. 92A); sometimes the immature zooecia at the growth tip are occluded by pseudoporous terminal diaphragms at a level slightly proximal of the outer ends of their interzooidal walls.

Autozooecia, generally arranged in well-ordered transverse rows (Fig. 92B), are subhexagonal in frontal outline and have small frontal walls and large, closely-spaced apertures which are more-or-less hexagonally packed. Apertures (Fig. 92D) are flared, hemielliptical, a little wider than high, well-rounded distally, and have slightly convex hinge lines. Rarely a concentric inner rim occurs within the aperture, indicating intramural budding (Fig. 92B). Opercula (Fig. 95) are frequently preserved *in situ*; they have a microstructure of coarse crystallites in a typically melicerititid fan-like arrangement, and a crescent of pits close to the free edges. The inner side of opercula, revealed by dissecting out individual opercula or observing abraded *in situ* opercula, has a pair of thick, apparently hollow, inward-sloping sclerites continuous with a knob-like process which extends proximally of the hinge line. Zooecia commonly have only the proximal part of the operculum preserved (Fig. 96), a style of preservation which is rarely found in species of melicerititids and suggests a strong articulation between the hinge line and operculum. Apertures may be occluded by sparsely to densely pseudoporous diaphragms situated proximally of the outer edge of the aperture, sloping distally outwards, often irregular and sometimes possessing a central depression; such diaphragms may be observed beneath the operculum in zooecia with fractured opercula (Fig. 92C).

Gynozooecia (Figs 93–94) are rare, small, and have a subtriangular surface outline, about as broad as long, with a bulbous distal frontal wall which is seldom preserved. The ooeciopore, located distally of the dilated part of the gynozooecium, is small (0·07 mm in diameter), circular and borne on a proximally-reflexed ooeciostome (Fig. 93). An atrial ring (see Levinsen 1912) has not been observed. Abraded gynozooecia reveal the prominent hexagonal interzooidal walls of the zooecia beneath the floor of the gynozooecium (Fig. 94).

Measurements (autozooecial dimensions from ten determinations on the lectotype; gynozooecial dimensions from three gynozooecia in separate colonies). FWL, 0·41–0·50 mm; FWW, 0·27–0·33 mm; LAM, 0·05–0·18 mm; TAM, 0·17–0·21 mm; GTL, 1·20–1·38 mm; GDL, 1·05–1·23 mm; GW, 1·11–1·32 mm.

Remarks. This species is abundant at Faringdon but is unknown elsewhere. It is distinguished from the three other Faringdon melicerititids by the larger size of the apertures and the greater diameter of the branches. The apertures are also very closely spaced, and the frontal walls reduced in area. The occurrence of a process extending proximally of the hinge line on the inner side of the operculum is seemingly unique among melicerititid species.

Canu & Bassler (1926: pl. 13, figs 4–5) illustrate apparent eleozooids ('eleocellaria') in *M. cunningtoni*. These are in fact abraded autozooecia in which remnants of the hinge lines resemble partially-preserved pivotal bars of cheilostome avicularia, the analogues of melicerititid eleozooids (see Taylor 1985). True eleozooids are absent from *M. cunningtoni* and Faringdon populations of all melicerititid species.

Meliceritites transversa Canu & Bassler, 1926

Figs 97–101

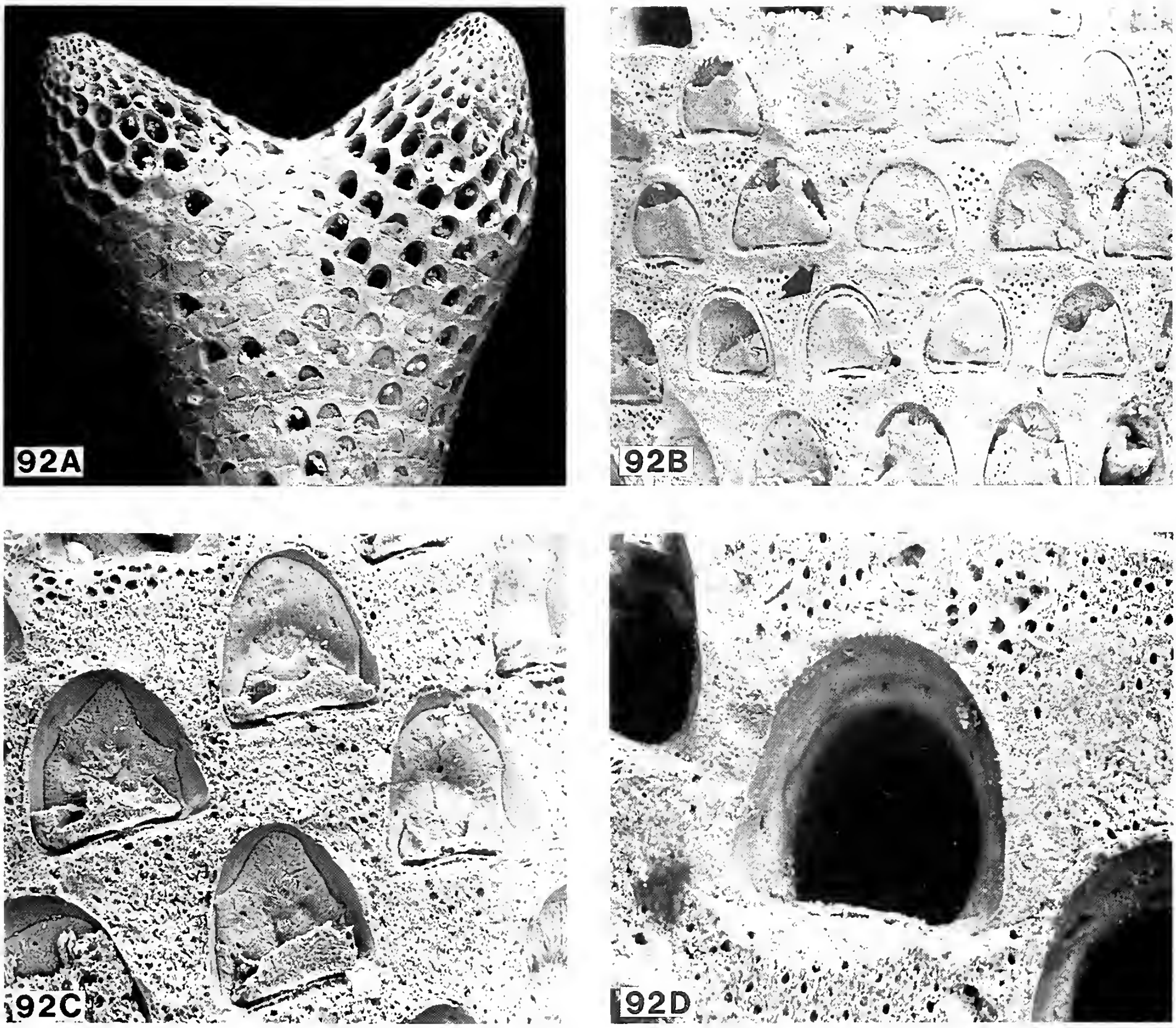
1926 *Meliceritites transversa* Canu & Bassler: 64; pl. 12, figs 1–12.

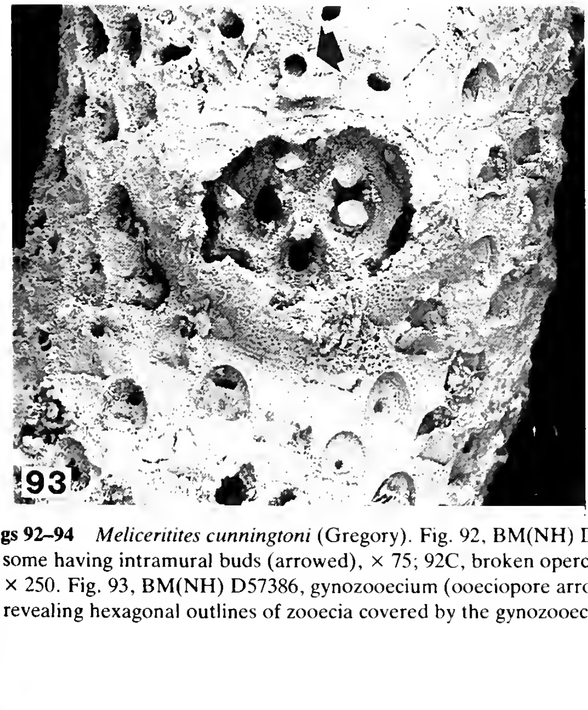
1981 *Meliceritites haimeana* (d'Orbigny); Voigt: 441; fig. 1f.

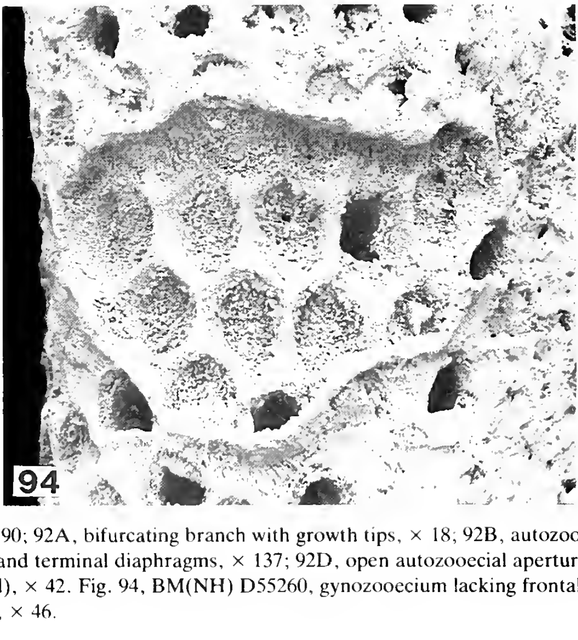
Lectotype. USNM 69916a, figd by Canu & Bassler (1926: pl. 12, figs 2, 3, 6) is here designated as lectotype.

Paralectotypes. USNM 69916b-i, the remaining specimens on the card of syntypes.

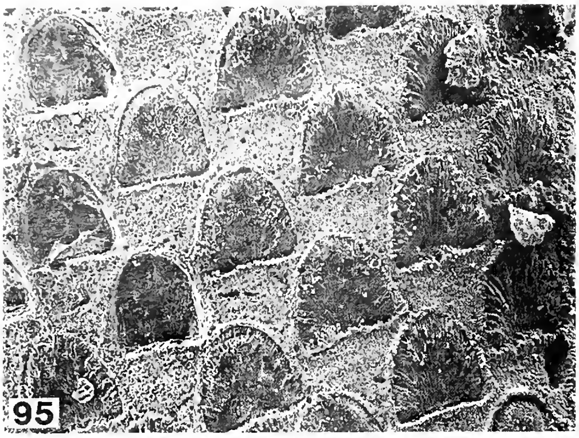
Other material. BM(NH) D52154 (sample), D52156 (sample), D55275 (sample), D55281–2, D55284, D57704–5

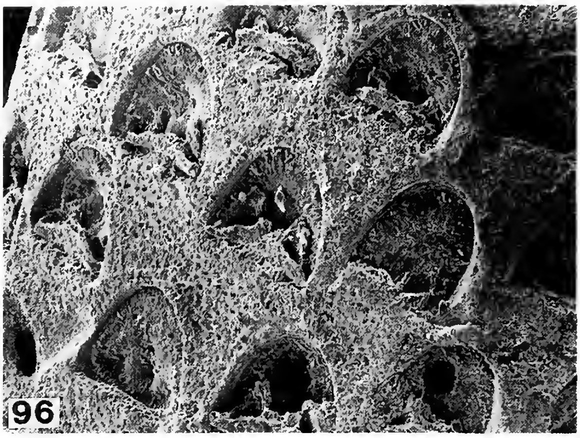




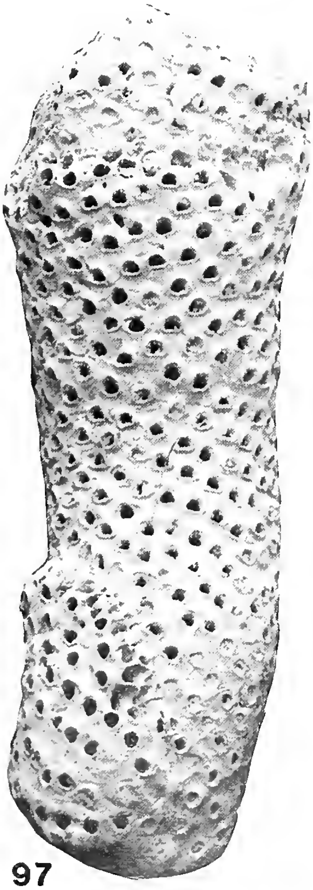


Figs 92–94 *Meliceritites cunningtoni* (Gregory). Fig. 92, BM(NH) D57390; 92A, bifurcating branch with growth tips, × 18; 92B, autozooecia, some having intramural buds (arrowed), × 75; 92C, broken opercula and terminal diaphragms, × 137; 92D, open autozooecial aperture, × 250. Fig. 93, BM(NH) D57386, gynozooecium (ooeciopore arrowed), × 42. Fig. 94, BM(NH) D55260, gynozooecium lacking frontal wall revealing hexagonal outlines of zooecia covered by the gynozooecium, × 46.





Figs 95–96 *Meliceritites cunningtoni* (Gregory), secondary electron images of coated specimens. Fig. 95, BM(NH) D57703, operculate autozooecia, × 52. Fig. 96, BM(NH) D57702, oblique view of autozooecia with fractured opercula showing apparently hollow sclerites, × 78.



97

Fig. 97 *Meliceritites transversa* Canu & Bassler, USNM 69916b, paralectotype, × 17.

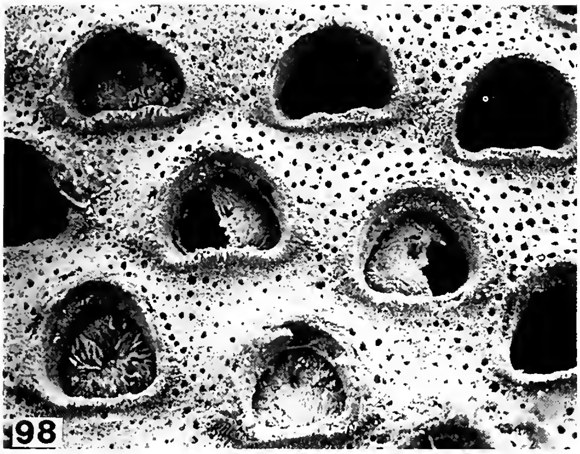
(SEM stub), Little Coxwell Pit, Pitt Colln; D55175, D55182–4 (samples), D55283, D57387, Little Coxwell Pit, Gaster Colln; D55185–7 (samples), D55279 (sample), D57388, Little Coxwell Pit, Thomas Colln; D55191–2, Bowler's Pit, Pitt Colln; D55276–7 (sample), Little Coxwell Pit, Curry Colln; D55278 (sample), D55286, Little Coxwell Pit, Elliott Colln; D55280, Cleevely Colln.

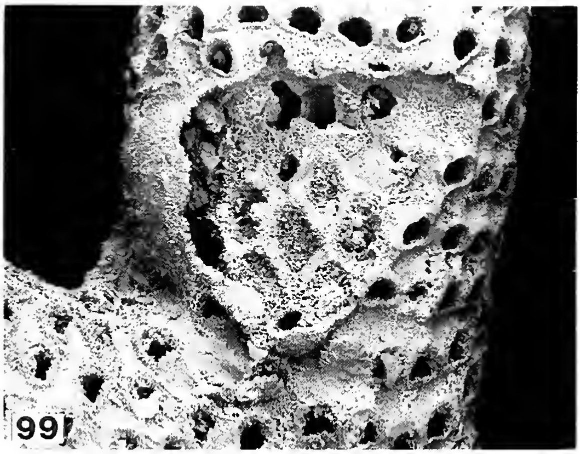
DESCRIPTION. Colonies are dendroid with moderately thick (0·9–1·6 mm) vinculariiform branches (Fig. 97) which bifurcate generally at intervals of 3–6·5 mm and sometimes abruptly become thinner following a bifurcation. Branch growth tips are rounded to conical. Overgrowths are common; some apparently arose from the colony base, but others arose on the surface of the erect branches. Overgrowths form by frontal budding (Fig. 101), successive overgrowths sometimes having their origins directly above one another. The colony base (Fig. 100) is bereniciform, gives rise to a single erect branch, and may have an occluded growth margin (Fig. 100B) and occasional kenozooecia.

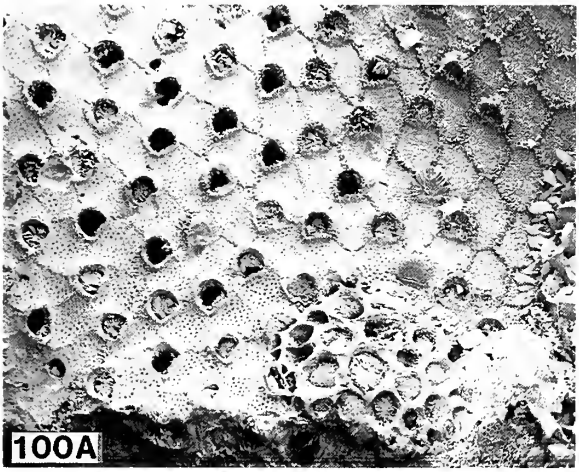
Autozooecia are usually arranged in well-defined transverse rows, and have a subhexagonal frontal outline with the interzooecial walls standing up slightly above the level of the pseudoporous frontal wall. Autozooecia in overgrowths and on the colony base are longer and narrower than those in erect branches (compare Figs 100A and 98). Apertures are moderately large, usually slightly broader than high, hemi-elliptical, well-rounded distally, and have a distinct, thickened apertural rim and a hinge line with two prominent teeth (Fig. 98). Terminal diaphragms are sometimes present proximally of the apertural rim; they vary from densely pseudoporous to non-pseudoporous, and may possess a central depression and pore (Fig. 98). The opercular shelf is absent or extremely slight. Opercula are very rarely preserved *in situ*; the only observed examples (Fig. 100C) are recrystallized but appear to have a crescent of pits, as is typical for melicerititids.

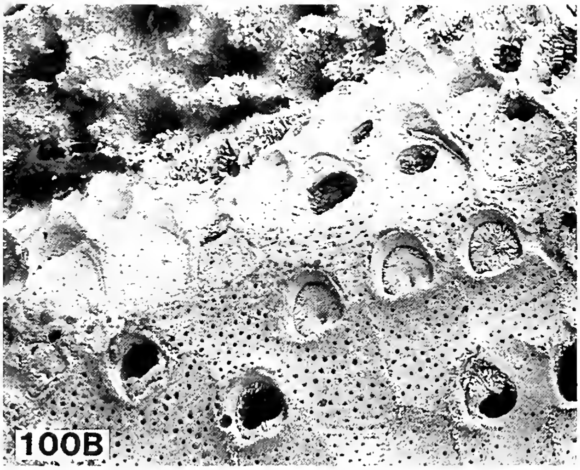
Gynozooecia (Fig. 99) are rare but when present occur in multiples. The bulbous distal frontal wall has a subtriangular outline shape, broader than long. Interzooecial walls of occluded zooecia are prominent on the floor of gynozooecia whose roofs have been removed. The ooeciopore is situated slightly distally of the dilated part of the gynozooecium, and is small and transversely elongate. An atrial ring does not seem to occur.

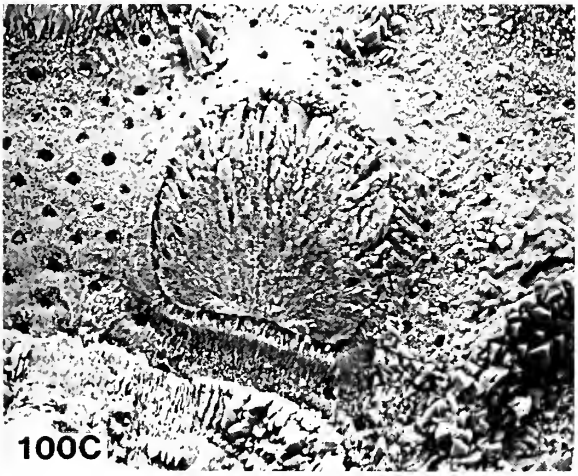
MEASUREMENTS (autozooecial dimensions from ten determinations of zooecia from an erect branch and ten determinations of zooecia in an overgrowth in one colony; gynozooecial dimensions from four gynozooecia in two colonies). FWL, 0·30–0·39 mm; FWW, 0·17–0·26 mm; LAM, 0·09–0·12 mm; TAM, 0·11–0·14 mm; GTL, 0·92–1·20 mm; GDL, 0·81–1·10 mm; GW, 1·13–1·50 mm; LOPM, 0·05 mm; TOPM, 0·09 mm.

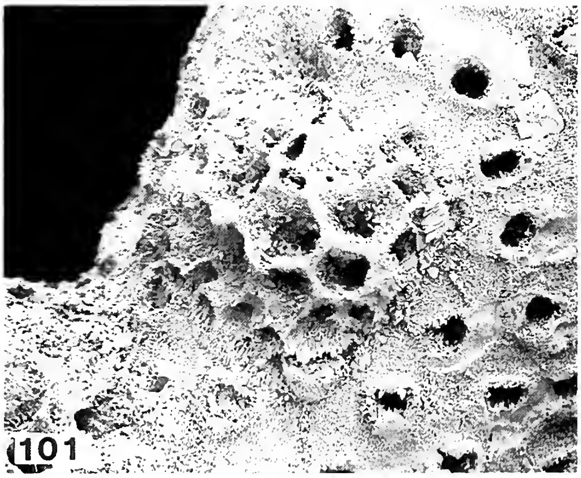












Figs 98–101 *Meliceritites transversa* Canu & Bassler. Fig. 98, BM(NH) D55284, autozooecia some of which have terminal diaphragms with a central depression and pore, × 115. Fig. 99, BM(NH) D57387, broken gynozooecium, × 44. Fig. 100, BM(NH) D55175, colony base; 100A, basal autozooecia and abortive frontally-budded overgrowth (bottom right), × 40; 100B, occluded growth margin, × 89; 100C, operculum, × 350. Fig. 101, BM(NH) D57388, small frontally-budded overgrowth, × 65.

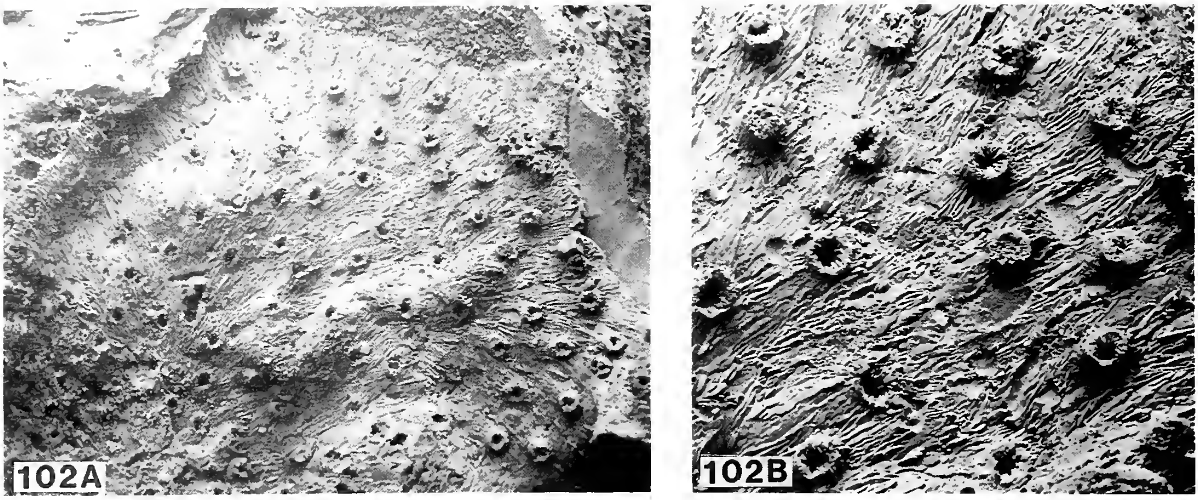


Fig. 102 *'Berenicea' filifera* Canu & Bassler, USNM 69848, holotype; 102A, × 15; 102B, coarsely preserved autozooecia, × 29.

Remarks. Branch fragments of *M. transversa* are abundant at Faringdon. Zooecial size and branch diameter are intermediate between the two other common Faringdon melicerititids, *M. dendroidea* and *M. cunningtoni*. The species is readily distinguished from the much rarer *M. gracilis* by the well-rounded apertures.

M. transversa has previously been regarded (Walter & Busnardo 1971; Walter *et al.* 1975) as a junior synonym of *M. haimeana* (d'Orbigny), and Voigt (1981) has figured a Faringdon specimen under this latter name. However, the synonymy is not well supported. The specimens of *M. haimeana* figured by d'Orbigny (1853: pl. 617, figs 11-14) are either indeterminate or appear much more like *M. dendroidea* than *M. transversa*. Unfortunately, d'Orbigny's type specimens (MNHN d'Orbigny Colln 6021) are missing from the tablet to which they were originally attached. The type locality is given as Grandpré, an Albian locality no longer available. *M. transversa* has not been recorded at this stratigraphical level elsewhere.

Family **incertae sedis**

Genus '***BERENICEA***' Lamouroux, 1821

Following Taylor & Sequieros (1982), the generic designation '*Berenicea*' is used informally for species of bereniciform tubuloporines in which the gynozooecium is unknown (*Berenicea* Lamouroux, 1821 is a *nomen dubium*). Reassignment of at least some of these species is anticipated after discovery of their gynozooecia.

'Berenicea' filifera Canu & Bassler, 1926 Fig. 102

1926 *Berenicea filifera* Canu & Bassler : 11; pl. 29, figs 3–4.

Holotype. USNM 69848, figd by Canu & Bassler (1926: pl. 29, figs 3–4).

Description. The zoarium is thin and unilamellar, bereniciform, with an irregular outline.

Autozooecial apertures are of moderate size, circular or slightly longitudinally elongate, very widely spaced in irregular quincunx, with thick, slightly raised peristomes up to 0·3 mm high where preserved in a hollow. Frontal walls are immersed.

Measurements (from Canu & Bassler 1926). TAM, 0·12–0·13 mm; TPM, 0·17 mm; FWW, 0·24–0·30 mm.

Remarks. The only available specimen of this rare species is the holotype which encrusts a sponge. The species resembles '*Berenicea*' *faringdonensis* but has more widely spaced apertures.

Canu & Bassler (1926: 11) describe the frontal walls as 'ornamented with small salient interrupted longitudinal *threads*'. Under the SEM these are seen to be the edges of the calcite crystals which form the recrystallized frontal walls.

'Berenicea' faringdonensis Canu & Bassler, 1926 Figs 103–104

1926 *Berenicea faringdonensis* Canu & Bassler: 11; pl. 29, figs 5–6.

Holotype. USNM 69847, figd by Canu & Bassler (1926: pl. 29, figs 5–6).

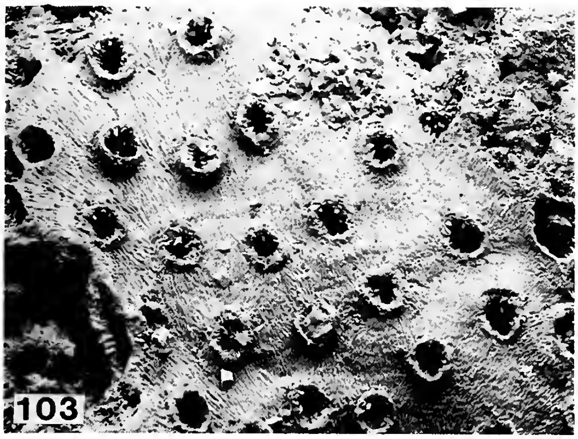
Other material. BM(NH) D55070 Bowler's Pit, Pitt Colln; D55106 (with *Plagioecia orbifera* and Stomatoporid sp. 2), Little Coxwell Pit, Gaster Colln; D55125, Bowler's Pit, Gaster Colln; D55126, Little Coxwell Pit, Thomas Colln.

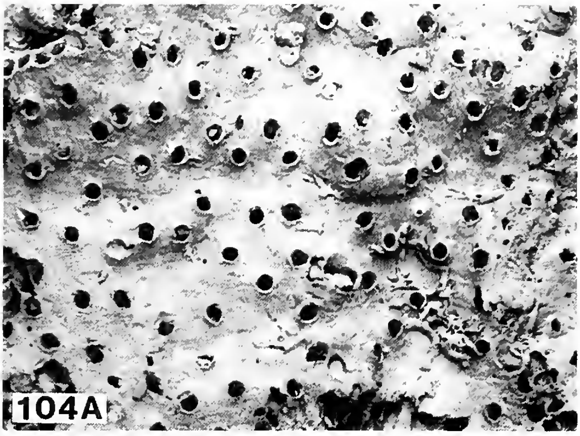
Description. Zoarium adnate, bereniciform and often large but thin. Intact growth margins have not been observed; the only available specimens are damaged remnants of large colonies.

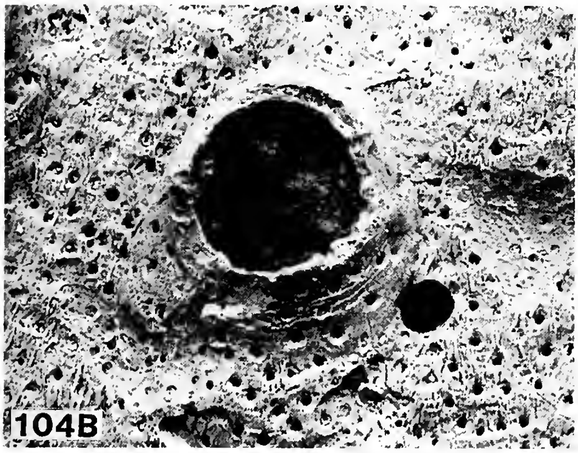
Autozooecia are large and possess longitudinally elongate or circular apertures which are sometimes occluded by pseudoporous terminal diaphragms on top of short, distally-tapering peristomes. The zooecia are immersed, their slender frontal walls being only very gently convex, though zooecial boundaries may be marked by slight but conspicuous furrows. Pseudopores are circular.

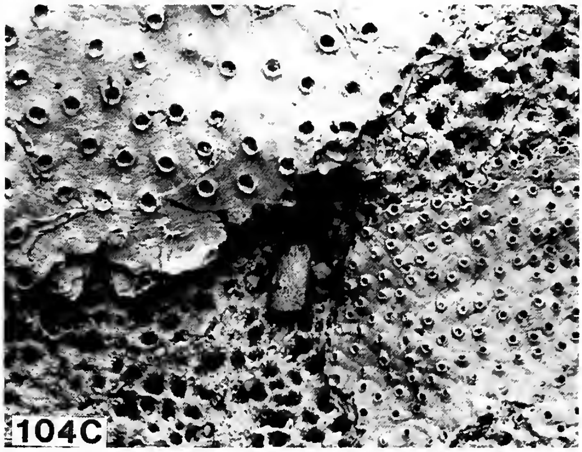
Kenozooecia may be developed.

Indisputable gynozooecia are unknown. However, a single









Figs 103–104 *'Berenicea' faringdonensis* Canu & Bassler. Fig. 103, USNM 69847, holotype, × 25. Fig. 104, BM(NH) D55106; 104A, × 14; 104B, autozooecial aperture with small boring to the bottom right, × 150; 104C, colony encrusting a sponge and growing towards a colony of *Plagioecia orbifera* (Canu & Bassler), × 17.

doubtful gynozooecium observed in BM(NH) D55070 seems o have a *Hyporosopora*-like, transversely elongated frontal wall.

MEASUREMENTS. LAM, 0·15–0·17 mm; TAM, 0·14–0·15 mm; FWL, 0·84–1·20 mm; FWW, 0·21–0·24 mm.

REMARKS. All available specimens encrust sponges (Fig. 104C). The relatively flat colony surface serves to distinguish his species from *'Berenicea' grandipora* which has similarly arge zooecia.

Specimen BM(NH) D55106 is bored by numerous small (*c.* 0·04 mm) holes which are arranged without regular pattern but usually restricted to one per zooecium (Fig. 104B). It is empting to speculate that these were made by a predator.

Berenicea' grandipora Canu & Bassler, 1926

Figs 105–106

926 *Berenicea grandipora* Canu & Bassler: 11; pl. 28, figs 2–3.

HOLOTYPE. USNM 69846, figd by Canu & Bassler (1926: pl. 28, figs 2–3).

OTHER MATERIAL. BM(NH) D55069, D55071, Little Coxwell Pit, Gaster Colln.

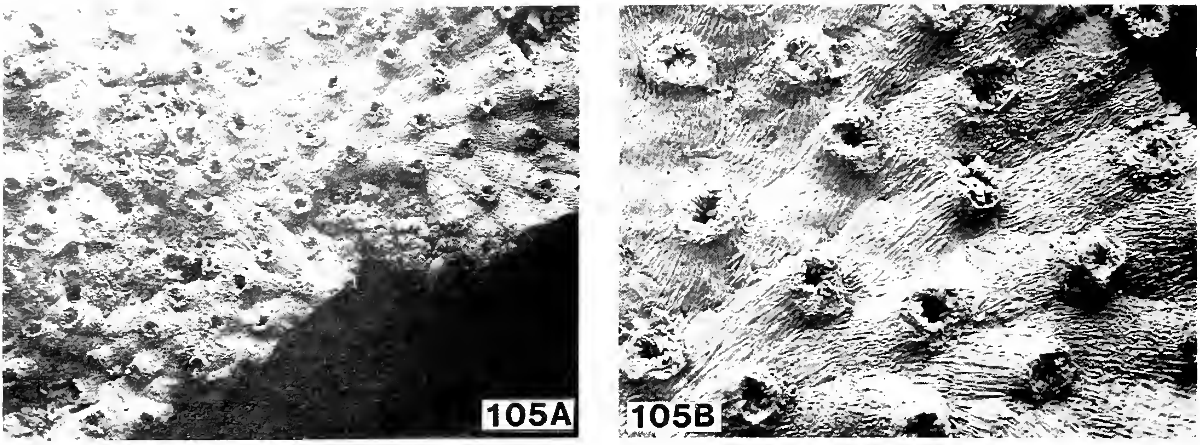
DESCRIPTION. Zoarium adnate, irregular in outline, typically fan-shaped bereniciform (Figs 105A, 106A), and thin, with only one generation of zooecial buds visible at the growth margin.

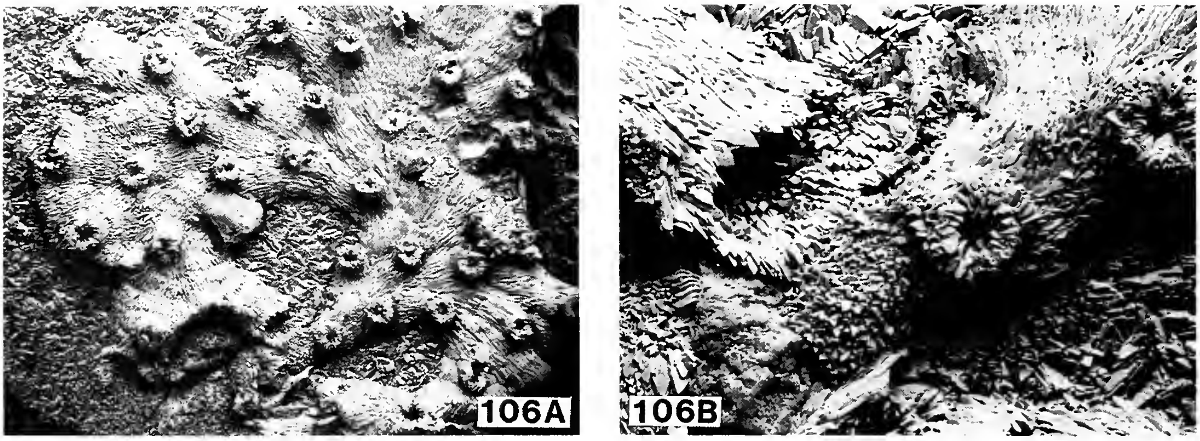
Autozooecia are large with convex frontal walls visible throughout their length (Fig. 105B). Maximum frontal wall width is often attained mid-length, giving the zooecia a flask shape. Apertures are large, though appreciably smaller than the maximum width of the frontal wall, circular or slightly transversely elliptical, and lacking significant preserved peristomes. Possible terminal diaphragms have been observed in the poorly-preserved holotype.

The ancestrula (Fig. 106B) is short (length inclusive of the protoecium 0·54 mm), and has a relatively narrow protoecium and a large aperture (*c.* 0·14 mm).

A possible partially-formed gynozooecium is present at the growing edge of BM(NH) D55069 (Fig. 106A), but is too incomplete to furnish useful information.

MEASUREMENTS. LAM, 0·17–0·20 mm; TAM, 0·15–0·18 mm; FWL, 0·90–1·19 mm; FWW, 0·27–0·35 mm.





Figs 105–106 *'Berenicea' grandipora* Canu & Bassler. Fig. 105, USNM 69846, holotype; 105A, × 8; 105B, autozooecia, × 30. Fig. 106, BM(NH) D55069; 106A, small, lobate colony, × 16; 106B, poorly-preserved ancestrula, × 70.

REMARKS. Zooecial dimensions are very similar in *'B.' grandipora* and *'B.' faringdonensis*. Canu & Bassler (1926) differentiated these two species firstly by the respectively regular or irregular arrangement of the apertures, but this is not borne out by their figures or by the type specimens. However, Canu & Bassler's second differentiating character, the respectively visible and immersed zooecia, provides a valid distinction. *'B.' grandipora* also differs from *'B.' faringdonensis* in the flask-shaped zooecia, the tendency for the autozooecial apertures to be transversely rather

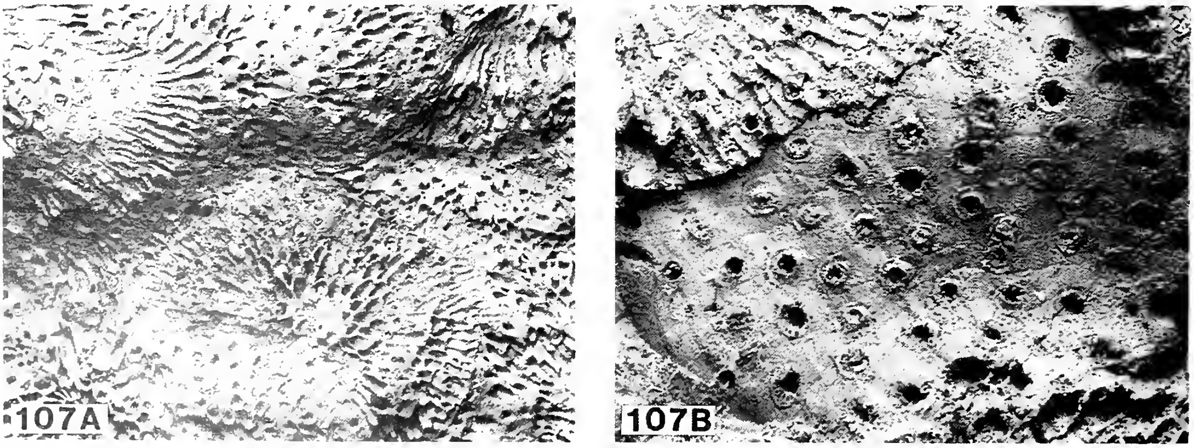
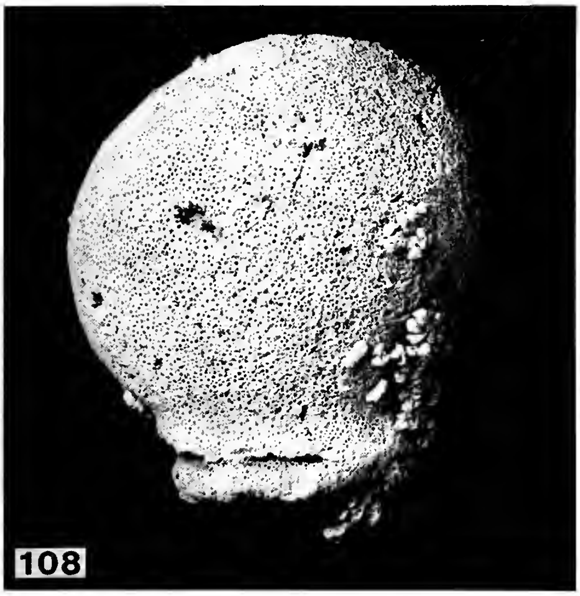
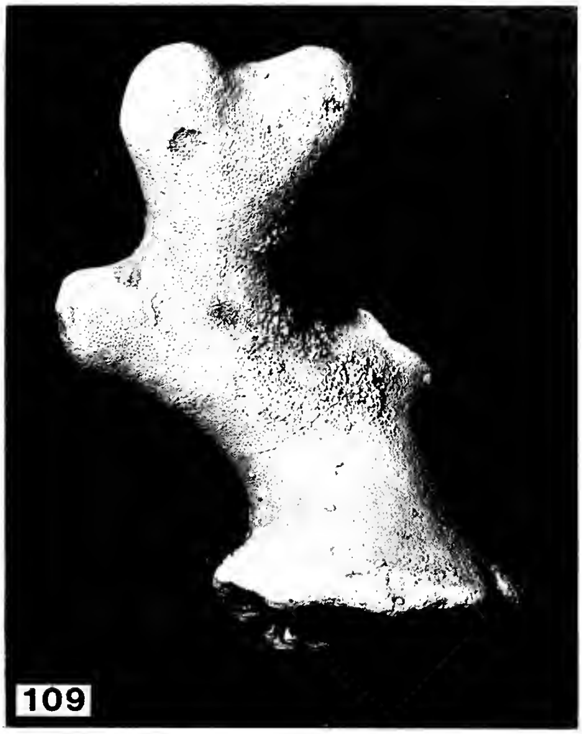
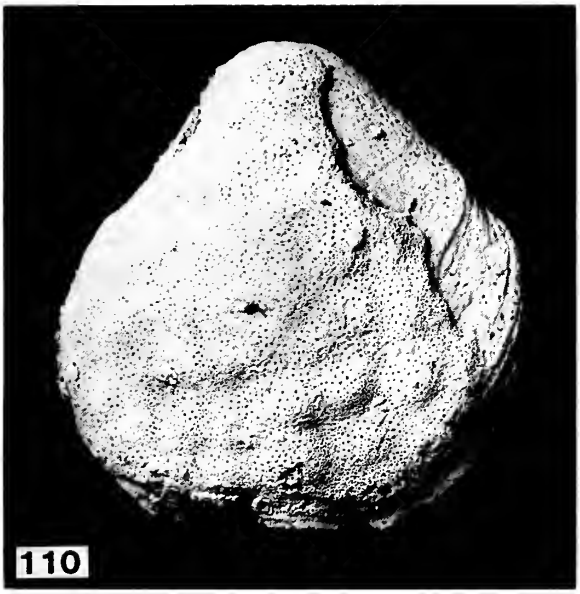
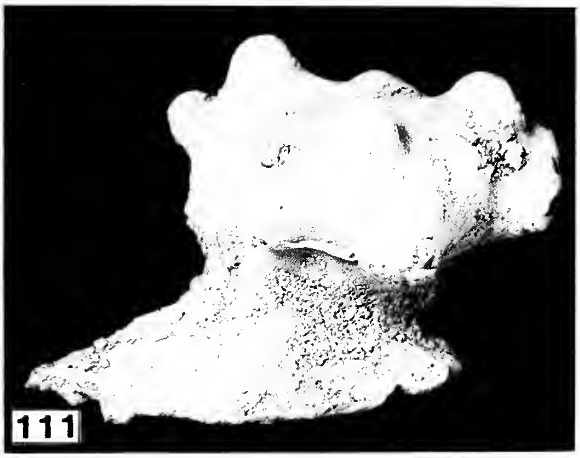


Fig. 107 *'Berenicea'* cf. *sowerbyi* (Lonsdale). BM(NH) D55347; 107A, abraded subcolonies, × 11; 107B, autozooecia (distal is to the left), × 28.


108


109


110


111

Figs 108–111 Optical photographs of some cerioporine species. Fig. 108, *Heteropora clavata, sensu* Gregory (?*non* Kade), BM(NH) D55208, × 5·5. Fig. 109, *Heteropora keepingi* Gregory, BM(NH) D7169, × 2·8. Fig. 110, *Seminodicrescis variolata* (Gregory), BM(NH) D55299, colony encrusting a brachiopod, × 4·4. Fig. 111, *Ceriopora farringdonensis* Gregory, BM(NH) D7290, × 2·3.

than longitudinally elongate, and the lobate form of the colonies.

'Berenicea' cf. **sowerbyi** (Lonsdale, *in* Dixon 1850)

Fig. 107

?1971 *Reptomultisparsa* sp.; Hillmer: 46; pl. 3, fig. 7.

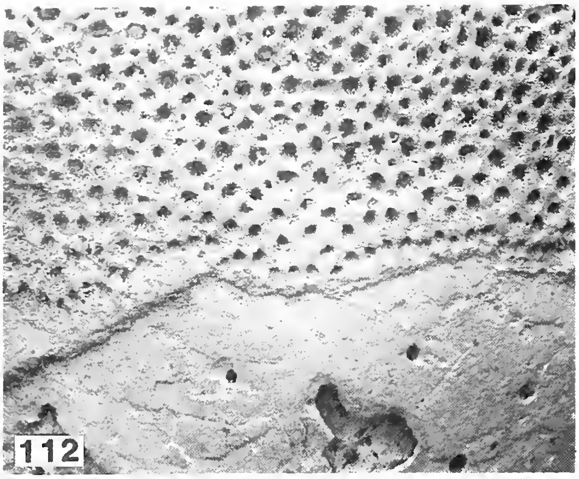
Material. BM(NH) D55347, Bowler's Pit, Gaster Colln.

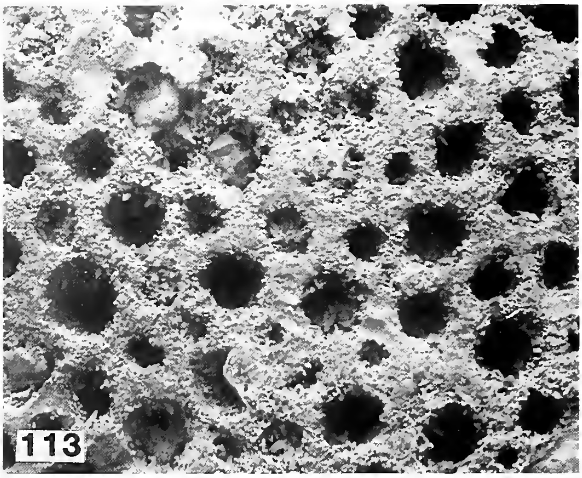
Description. Colony encrusting, multilamellar, composed of numerous subcolonies arranged in a *Cellulipora*-like configuration. The subcolonies are subcircular in outline (Fig. 107B) and variable in size but often 5–6 mm in diameter. Only one tier of zooecial buds is normally visible at the growth margins of the thin subcolonies. New subcolonies appear to originate by eruptive frontal budding from the centres of established subcolonies.

Autozooecia (Fig. 107B) have well-defined frontal walls which taper proximally and are well-rounded distally. Apertures are circular, and preserved peristomes are thin and low.

Measurements. TAM, 0·09–0·10 mm; TPM, 0·12–0·16 mm; FWL, 0·40–0·60 mm; FWW, 0·18–0·22 mm.

Remarks. Although the solitary available specimen, which encrusts a sponge, is mostly worn, the better-preserved parts resemble an Upper Cretaceous specimen (BM(NH) D2991)





Figs 112–113 *Heteropora clavata, sensu* Gregory (?*non* Kade). Fig. 112, BM(NH) D41378, overgrowth, × 30. Fig. 113, BM(NH) D55209, autozooecia and kenozooecia, × 95.

described as *Reptomultisparsa sowerbyi* (Lonsdale) by Gregory (1899). However, the zooecial dimensions of this Chalk bryozoan are smaller than in the Faringdon specimen. Lonsdale's (*in* Dixon 1850) type of *Diastopora sowerbyi* is unfortunately missing. The Faringdon specimen also resembles a colony figured by Hillmer (1971) from the Hauterivian of Germany as *Reptomultisparsa* sp. on account of the multilamellar growth-form.

Suborder **CERIOPORINA** von Hagenow, 1851
Family **HETEROPORIDAE** Waters, 1880

Genus ***HETEROPORA*** Blainville, 1830

Type species. *Ceriopora cryptopora* Goldfuss, 1826, designated by Gregory (1896); Maastrichtian of Maastricht, Netherlands.

Remarks. Numerous Jurassic to Recent cerioporine species have been referred by various authors to Blainville's (1830) genus *Heteropora*. Most possess dendroid branching colonies and well-defined zooecial dimorphism with autozooecial apertures surrounded by smaller kenozooecial apertures. This concept of the genus is, however, erroneous. Nye (1976) studied specimens of the type species, *H. cryptopora* (Goldfuss) from the Maastrichtian, and found no evidence of zooecial dimorphism. Furthermore, instead of having dendroid branches with endozones and exozones, colonies are bulbous and constructed of a series of overgrowths.

The correct generic assignment of dendroid, dimorphic cerioporines previously referred to *Heteropora* remains unclear. For the one such species (*Heteropora keepingi* Gregory) from the Faringdon Sponge Gravel the genus name *Heteropora* is therefore used tentatively. However, a second Faringdon species, *H. clavata, sensu* Gregory 1909*b*, may be more closely related to the type species.

Range. In the broad taxonomic sense, Aalenian to Recent.

Heteropora clavata*, *sensu Gregory 1909*b*, ?*non* Kade, 1852. Figs 108, 112–113

?non 1852 *Heteropora clavata* Kade: 32
1909*b* *Heteropora clavata* Kade; Gregory: 64.
1909*a* *Heteropora clavata* Kade; Gregory: 192; fig. 51.

Material. BM(NH) D7294 (2 pieces and 1 thin section), Caleb Evans Colln (figd Gregory 1909*a*: fig. 51); D41378–9, D55209, D55210 (3 thin sections only), D55220, Little Coxwell Pit, Thomas Colln; D52187 (3 pieces and one acetate peel, comprising two specimens), Little Coxwell Pit, Pitt Colln; D55208, Little Coxwell Pit, Gaster Colln; D57583, Cleevely Colln; D57584, Little Coxwell Pit, Ware Colln.

Description. Zoarium club-shaped or subspherical (Fig. 108) with a slightly expanded base, up to 22 mm high by 15 mm wide. Overgrowths may arise on the 'head' and grow down the 'stalk' of the zoarium (Fig. 112). Maculae are apparently absent.

Zooecia are weakly dimorphic, circular to subcircular autozooecial apertures being surrounded by smaller kenozooecial apertures (Fig. 113). Some of the autozooecial apertures are occluded by diaphragms situated a little proximal of the apertural rim. Mural spines have not been observed but available material is not well preserved.

In thin sections the zoarium can be seen to consist of a succession of capping overgrowths with poorly-defined endozones. Zooecial walls are thick in endozones and exozones, indistictly laminated, sometimes moniliform in the exozone. Diaphragms, slightly aborally convex, may occur at intervals slightly greater than the width of the zooecial tubes and are commonly situated at different levels in adjacent zooecia. A single brood-chamber has been seen in section; it is covered by zooecia from the same overgrowth, and is 1·2 mm wide by 0·3 mm high, has an uneven floor of occluded zooecia, and a smooth roof supported by a few zooecia or septa, or both, which pass through the chamber.

Measurements. TAM, 0·08–0·10 mm; KAM, 0·03–0·06 mm.

Remarks. Kade's species *Heteropora clavata*, based on a drift specimen of uncertain age, was not figured in his original publication and cannot be recognized with certainty from the description. Professor E. Voigt (personal communication 1984) expressed doubt that the Faringdon species was conspecific with Kade's species. Gregory (1909*a*) suggested that Kade's name should be ignored because it is a *nomen nudum*,

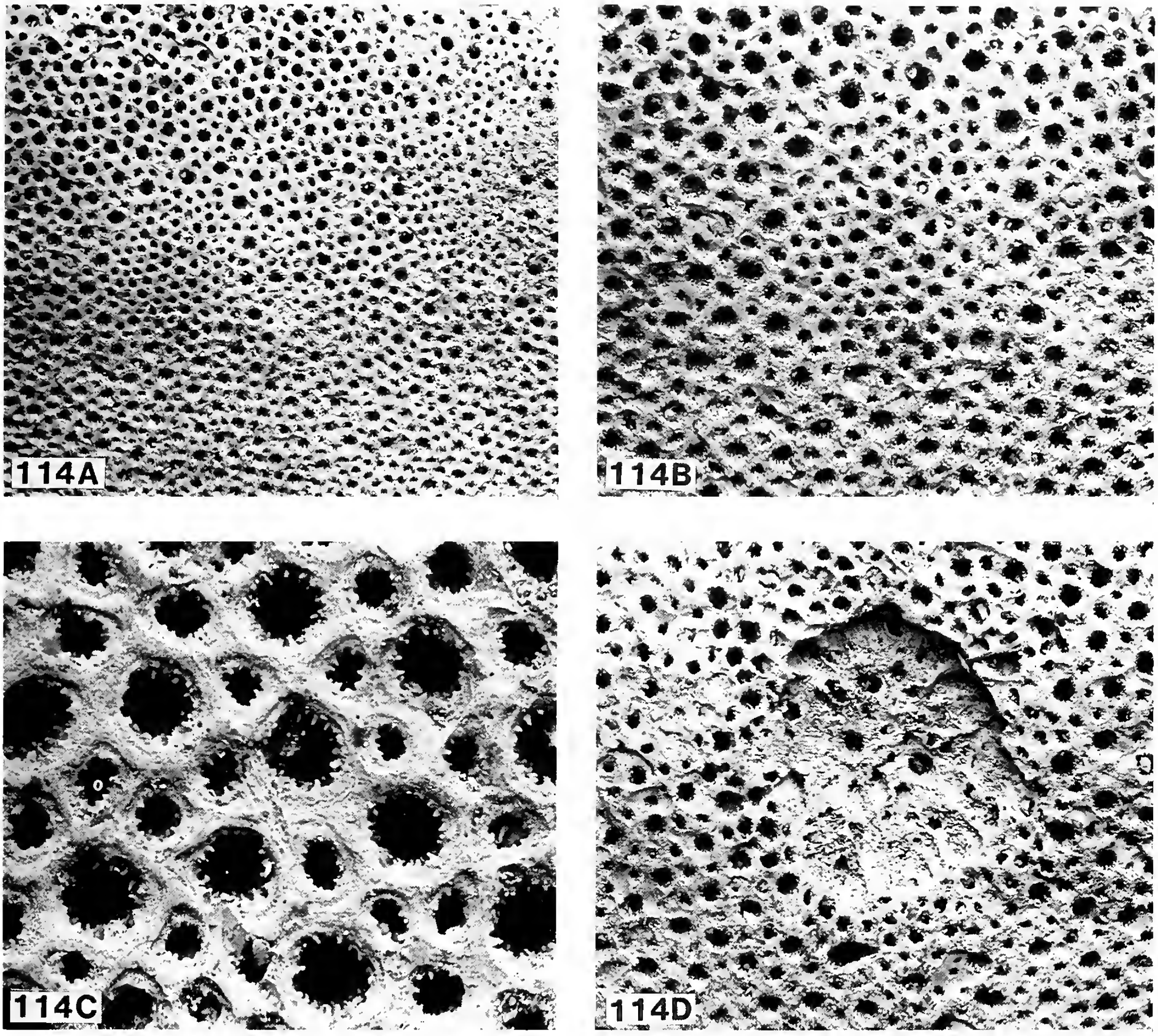


Fig. 114 *Heteropora keepingi* Gregory, BM(NH) D7292a, **lectotype** (herein selected); 114A, colony surface, × 21; 114B, maculum composed of kenozooecia, × 39; 114C, autozooecia and kenozooecia in intermacular area, × 130; 114D, worn brood chamber, × 38.

but went on to set up a Faringdon specimen, BM(NH) D7294, as the 'type' of the species. This specimen has no validity as the type of *H. clavata*; even if Kade's original material was shown to be lost, the Faringdon specimen cannot serve as a neotype because it comes from a widely different locality. Therefore, the correct name for the Faringdon species remains unclear, and it is herein referred to as *Heteropora clavata, sensu* Gregory, ?*non* Kade. We refrain from renaming it, pending more detailed study of better material.

This species can be distinguished from *H. keepingi* Gregory by the clavate colony-form, lack of maculae, apparent absence of mural spines and the multilayered structure of the colony, visible especially in thin sections.

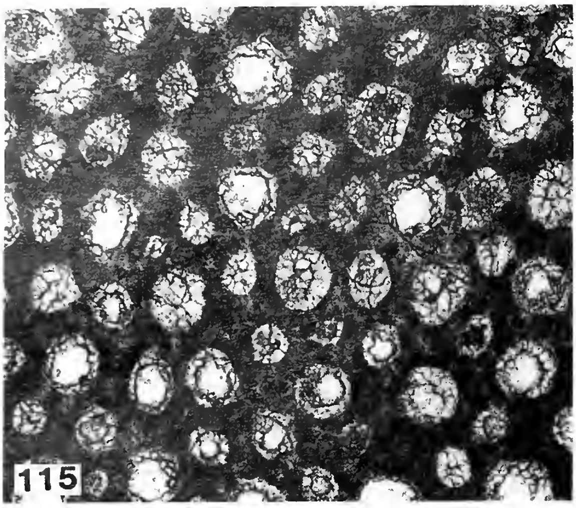
Heteropora keepingi Gregory, 1909*b* Figs 109, 114–116

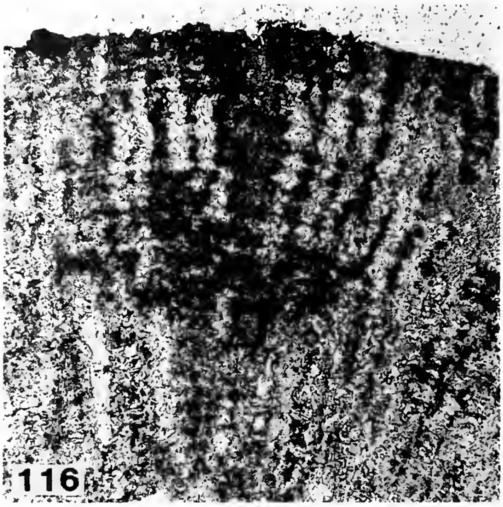
1909*b* *Heteropora keepingi* Gregory: 64.
1909*a* *Heteropora keepingi* Gregory; Gregory: 190; pl. 5, figs 7–8; fig. 50.
?1926 *Ceriopora dimorphocella* Canu & Bassler: 29; pl. 24, figs 1–6; pl. 31, figs 7–8; fig. 14.
?1926 *Heteropora nummularia* Canu & Bassler: 13; pl. 20, figs 6–8.

LECTOTYPE. BM(NH) D7292a, Faringdon, Cunnington Colln (figd Gregory, 1909*a*: pl. 5, fig. 7), is here chosen as lectotype.

PARALECTOTYPES. BM(NH) D7169 (of the four specimens mentioned by Gregory (1909*a*: 191) three remain), Faringdon, Ellis Colln; B118 (specimen and thin section), Lower Greensand, ?Isle of Wight (figd Gregory, 1909*a*: pl. 5, fig. 8; fig. 50).

OTHER MATERIAL. BM(NH) D7292b–c (these specimens were not listed by Gregory 1909*a* and, unlike D7292a, cannot be regarded as types), Cunnington Colln; D55215 (2 thin sections), D55216 (4 thin sections), D55218, D55219, Little Coxwell Pit, Thomas Colln; D55122, Little Coxwell Pit, Davis Colln. USNM 69872 (syntypes of *Ceriopora dimorphocella* comprising 1 thin section, 4 specimens and 3 remnants).





Figs 115–116 *Heteropora keepingi* Gregory, thin sections. Fig. 115, USNM 69872, syntype of *Ceriopora dimorphocella* Canu & Bassler, tangential section, × 74. Fig. 116, BM(NH) D55216, transverse section of exozone showing strongly moniliform zooecia, × 33.

Description. Zoaria (Fig. 109) are dendroid with thick branches, 8–15 mm in diameter, which bifurcate at intervals. Distal branch growth tips are blunt and rounded. Maculae, marked by concentrations of kenozooecia (Fig. 114B), are spaced about 3–4 mm apart on the zoarial surface. Zoarial bases are expanded but not extensive.

Autozooecial apertures are subcircular to polygonal, small, and surrounded by smaller, more angular kenozooecial apertures (Fig. 114C). Mural spines may be visible within both autozooecial and kenozooecial apertures; they are densely concentrated, taper distally, have rounded ends and are up to about 0·01 mm long.

Brood chambers (Fig. 114D) are visible as shallow depressions, approximately 2 mm in diameter, on the colony surface in the positions of maculae. Intact roofs have not been observed in hand specimens. Most of the autozooecia and kenozooecia below the chamber are occluded by a calcified layer forming the floor of the chamber.

Thin sections show the coaxial endozone (5 mm in diameter in D55216) and exozone, with moderately thick zooecial walls in the endozone and thick, distinctly moniliform walls in the exozone (Fig. 116). Diaphragms are absent or rare, and have aborally convex diaphragms. Brood chambers have not been observed in section.

Measurements. TAM, mean 0·10 mm; KAM, mean 0·04 mm.

Remarks. *Heteropora nummularia* Canu & Bassler, 1926, described from Faringdon, is represented by a single, worn specimen (USNM 69853). This is a flat, discoidal colony sharing with *H. keepingi* a similar arrangement of autozooecial and kenozooecial apertures which are, however, generally smaller in *H. nummularia* though variable in size. *H. nummularia* may be the early encrusting stage of *H. keepingi* before development of erect branches. *Ceriopora dimorphocella* Canu & Bassler (Fig. 115) seems also to be a junior synonym of *H. keepingi*.

H. keepingi can be confused with *Ceriopora farringdonensis* Gregory (see below) which, although normally more massive, can on occasions have a similar dendroid colony-form. Externally the two species can be distinguished by the lack of well-developed zooecial dimorphism and maculae in *C. farringdonensis*. In thin section the exozonal walls of *H. keepingi* are more distinctly moniliform, endozonal walls are thicker, diaphragms are less common, and the zooecial tubes have a smaller diameter.

Genus *CERIOPORA* Goldfuss, 1826

Type species. *Ceriopora micropora* Goldfuss, 1826, by subsequent designation of Gregory (1896); U. Cretaceous, locality uncertain (see Nye 1976: 56).

Remarks. The type species of *Ceriopora* has been revised by Nye (1976), who gives a history of the concept of the genus. The name is generally applied to heteroporid species with massive, globular or subramose colony-forms, and lacking clearly defined dimorphism of the zooecia. Differences between *Ceriopora*, *Reptonodicava* d'Orbigny (see Nye 1976: 139), and *Ripisoecia* Canu & Bassler (see Walter, 1970) seem slight and clarification of the relationships between these genera will demand detailed morphological investigations of a wide range of species.

Range. ?Aalenian to ?Pliocene.

Ceriopora farringdonensis Gregory, 1909*b* Figs 111, 117

1909*b* *Ceriopora farringdonensis* Gregory: 63.
1909*a* *Ceriopora farringdonensis* Gregory; Gregory: 161; pl. 5, figs 1–4; fig. 42.

Holotype. BM(NH) 10298 (specimen and 1 thin section), Mantell Colln, figd Gregory (1909*a*: pl. 5, figs 1-2). No specimens are mentioned by number in the original description of this species (Gregory 1909*b*), but this specimen is stated as the type in the later paper by Gregory (1909*a*).

Other material. BM(NH) 10237, 10302, Mantell Colln; D3144 (uncut specimen, thin section and 2 remnants; thin section figd Gregory 1909*a*: fig. 42), Brown Colln; D7290

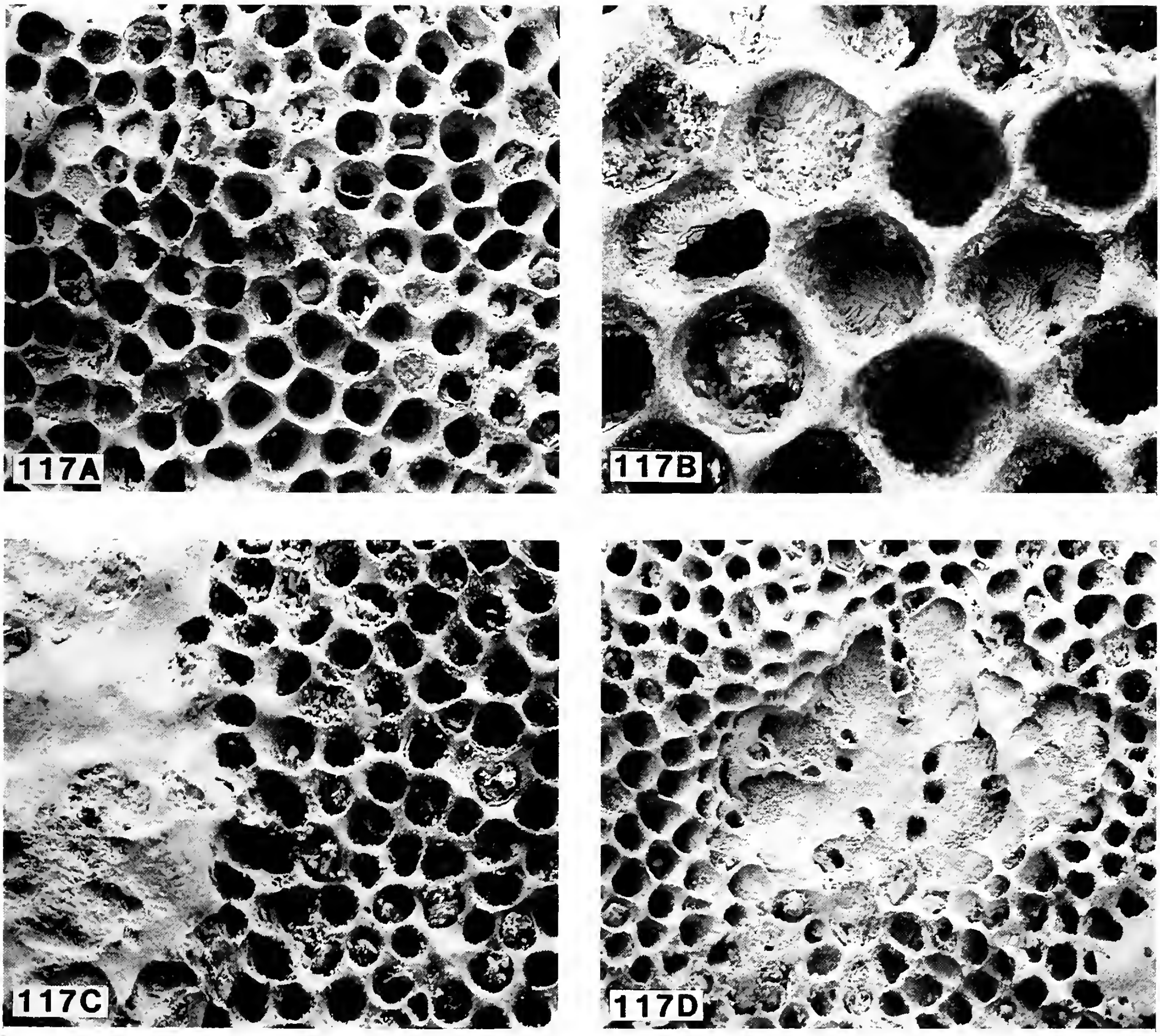


Fig. 117 *Ceriopora farringdonensis* Gregory, BM(NH) 10298, holotype; 117A, × 48; 117B, autozooecia, some with diaphragms, × 148; 117C, edge of overgrowth, × 36; 117D, incomplete brood chamber, × 32.

(reregistered from 55111; figd Gregory 1909*a*: pl. 5, fig. 3), Cunnington Colln; D7291 (figd Gregory 1909*a*: pl. 5, fig. 4), Sharp Colln; D37735, Ellis Colln (one of four specimens mentioned by Gregory (1909*a*: 191) as *Heteropora keepingi*, and re-registered from D7169); D57587, Little Coxwell Pit, Whiteley Colln; D57588–9 and D57590 (3 thin sections), Little Coxwell Pit, Pitt Colln; D57585, Little Coxwell Pit, Wise Colln; D57586, Wright Colln; D57591–2, Little Coxwell Pit, Davis Colln.

DESCRIPTION. Zoarium of variable form: massive, pedunculate with tuberous lobes (Fig. 111) or dendroid; massive zoaria are up to 50 mm across, branches of dendroid zoaria up to 27 mm in diameter. Overgrowths are commonly developed; the calcareous laminae (Fig. 117C) which occlude apertures over parts of colony surfaces appear related to intrazoarial overgrowths. Maculae are not generally visible although irregularly arranged monticule-like elevations may occur (Fig. 117A).

Zooecial apertures are monomorphic but very variable in size, and are subcircular to polygonal in shape. Diaphragms may occur a little beneath the level of the colony surface (Fig. 117B).

Brood chambers are preserved as depressions, 2–3 mm across, on the surface of zoaria. Autozooecia, linked by septum-like radial walls, apparently pierce brood chambers (Fig. 117D). Complete roofs have not been observed in hand specimen, and the ooeciopore is consequently unknown.

In section, branches of dendroid zoaria have thin-walled endozones and coaxial exozones. Zooecial walls in the exozone are moniliform and have an apparently granular microstructure with occasional dark patches. Brood chambers are seen to have thin, pseudoporous roofs, and their chambers (up to 3 mm wide by 0·5 mm high) are crossed by occasional zooecia and septa-like walls. Subterminal diaphragms commonly occur in zooecia beneath brood chambers and are situated a little proximally of the floor of the brood chamber.

MEASUREMENTS. TAM, 0·07–0·13 mm.

REMARKS. Although this species is fairly common at Faringdon and there are good specimens in most collections, Canu & Bassler (1926) apparently had no specimens and did not mention it. The distinction between *C. farringdonensis* and *H. keepingi* is discussed above (p. 118).

Genus *TETROCYCLOECIA* Canu, 1917

TYPE SPECIES. *Tetrocycloecia dichotoma* Canu, 1917, = *Ceriopora dichotoma* Goldfuss 1827, *sensu* Reuss, 1848, by original designation; Miocene, Eisenstadt, Austria.

REMARKS. The emendation of the genus name *Tetrocycloecia* to *Tretocycloecia* by Canu & Bassler (1920) has been followed by most subsequent authors, but Nye (1976) gives reasons for regarding this as unjustified, and the original spelling is used here.

Tillier (1975) and Nye (1976) have revised the type species of this genus, which in external morphology is very similar to *T. multiporosa* described below from Faringdon. However, *T. multiporosa* has kenozooecial apertures which are more funnel-shaped than in *T. dichotoma*. Furthermore, the clearly-differentiated ooeciopore is far smaller than the autozooecial apertures in *T. multiporosa*, whereas it is indistinct and may be the same size as an autozooecial aperture in *T. dichotoma*. Further detailed study is necessary to resolve whether the two species are really congeneric.

T. multiporosa may also be related to *Sparsicavea* d'Orbigny, 1853 (type species *S. carantina* d'Orbigny from the Turonian). Gynozooecial morphology, and autozooecial and kenozooecial arrangement are similar, although the walls of the kenozooecia tend to be raised into prominent surficial ridges in *Sparsicavea*.

RANGE. Aptian to Miocene.

Tetrocycloecia multiporosa Canu & Bassler, 1926

Figs 118–123

?1853 *Sparsicavea irregularis* d'Orbigny: 949; pl. 617, figs 5–7.

1926 *Tretocycloecia (?) multiporosa* Canu & Bassler: 83; pl. 16, figs 5–8.

1926 *Tretocycloecia densa* Canu & Bassler: 83; pl. 16, figs 9–14.

1926 *Sparsicavea irregularis* d'Orbigny; Canu & Bassler: 91; pl. 15, figs 11–14.

LECTOTYPE. USNM 69939b, figd Canu & Bassler (1926: pl. 16, fig. 5 (right-hand branch), and fig. 6), is here selected as the lectotype.

PARALECTOTYPES. USNM 69939a, figd Canu & Bassler (1926: pl. 16, fig. 5 (left-hand branch), and figs 7–8).

OTHER MATERIAL. BM(NH) D52158 (sample), D52224 (6), D52225 (sample), D55193 (sample), D55194 (2), D55196, D57718, Little Coxwell Pit, Pitt Colln; D55212, Bowler's Pit, Pitt Colln; D55195 (sample), D55206–7, D57717, Little Coxwell Pit, Gaster Colln; D55197 (2), Cleevely Colln; D57650 (10), Davis Colln; D55198 (2), Bowler's Pit, Thomas Colln; D55199, D55200 (6), D55201 (9), D55203, D55205 (2), D55213 (6), D55214 (sample), D57714–6 (thin sections), Little Coxwell Pit, Thomas Colln. USNM 69940 (4 syntypes of *T. densa* Canu & Bassler, 1926).

118

Fig. 118 *Tetrocycloecia multiporosa* Canu & Bassler, USNM 69939b, **lectotype** (herein selected), branch fragment with gynozooecium, × 23; see also Fig. 119.

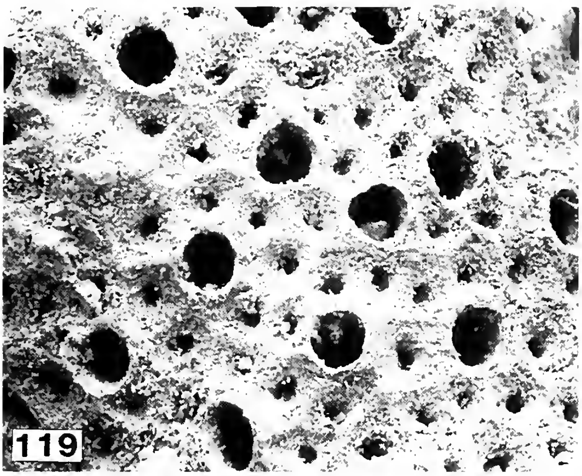
DESCRIPTION. Zoarium dendroid, vinculariiform (Fig. 118), with branches of moderate diameter (1–1·5 mm) which bifurcate and anastomose frequently. The colony base is a small conical expansion bearing a high concentration of kenozooecia.

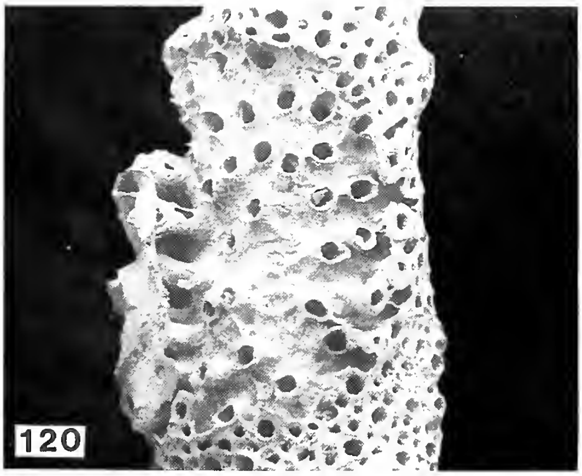
Autozooecial apertures are small, circular, with a slightly protuberant rim, and are surrounded by kenozooecia (Fig. 119).

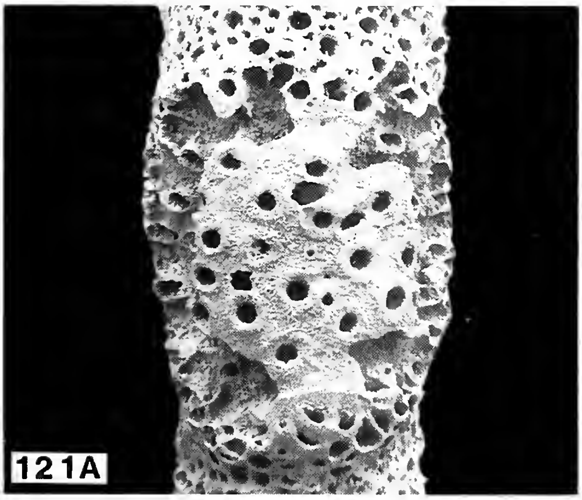
Kenozooecial apertures are very small, circular, funnel-shaped and depressed beneath the level of the colony surface, and polygonal in frontal outline.

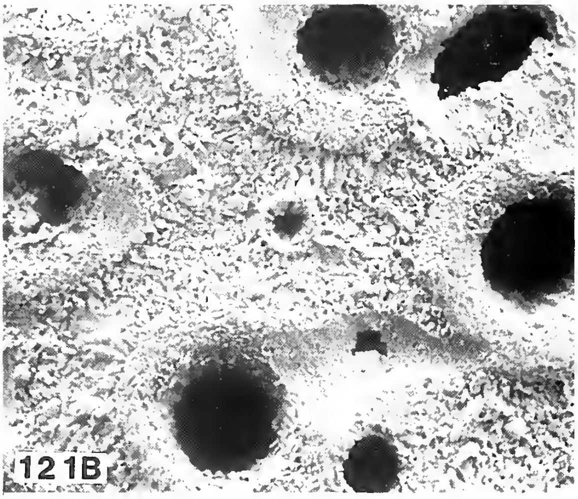
Gynozooecia are common but are usually preserved with little or none of the frontal wall intact (Fig. 120). They are roughly circular in outline, and may be bulbous in relief, causing a localized swelling of the branch. The gynozooecial roof is a pseudoporous exterior wall which is penetrated by numerous autozooecia with thick apertural rims (Fig. 121A). Broken gynozooecia reveal that vertical internal walls as well as these autozooecia support the roof. The floor of the gynozooecium is formed of polygonal kenozooecial apertures occluded by a calcified lamina bearing very short mural spines; there may be a central funnel-like opening which is presumed to lead into the proximal part of the fertile zooecium. The rarely preserved ooeciopore (Fig. 121B) is situated in the centre of the gynozooecial roof, and is circular and very small, considerably smaller than an autozooecial aperture. The ooeciostome is slight.

In thin section, the endozone is seen to occupy about ⅔ of

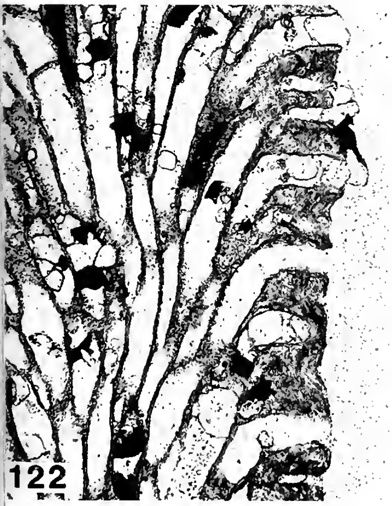

119

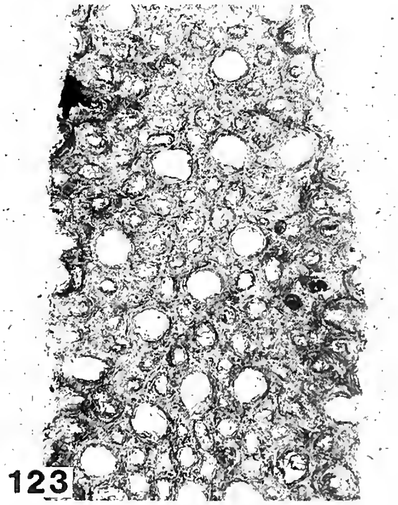

120


121A


121B

Figs 119–121 *Tetrocycloecia multiporosa* Canu & Bassler. Fig. 119, USNM 69939b, **lectotype**, autozooecia and kenozooecia, × 102; see also Fig. 118. Fig. 120, BM(NH) D57717, broken gynozooecium, × 30. Fig. 121, BM(NH) D55207; 121A, gynozooecium with relatively complete frontal wall, × 28; 121B, ooeciopore (centre), × 164.


122


123

Figs 122–123 *Tetrocycloecia multiporosa* Canu & Bassler, thin sections. Fig. 122, BM(NH) D57714, oblique longitudinal section, × 55. Fig. 123, BM(NH) D55715, shallow tangential section, × 55.

the branch diameter, and is surrounded by an exozone in which zooecial walls thicken abruptly (Fig. 122). The kenozooecia appear to be budded around the endozonal–exozonal boundary. Zooecial walls are parallel-sided (i.e. not moniliform) and show well-developed rounded laminations in longitudinal section in the exozone. Some of the autozooecia are partitioned by thin diaphragms in the endozone. Most diaphragms are orally flexed where they meet the zooecial walls (basal diaphragms), but some near the outside of the endozone are aborally flexed.

Measurements (ranges of mean values from four colonies, except for ooeciopore). TAM, 0·07–0·08 mm; TPM, 0·11–0·13 mm; KAM, 0·03–0·05 mm; width of kenozooecial frontal surface area, 0·10 mm; GDL, 0·60–2·00 mm; GW, 0·90–1·50 mm; LOPM, 0·03 mm; TOPM, 0·03 mm.

Remarks. Canu & Bassler (1926) used three separate species names for material from Faringdon which is here described as *T. multiporosa*. One of these species, *Sparsicavea irregulare* d'Orbigny, originally described from the Albian of the Ardennes, is difficult to intëpret from d'Orbigny's figures and description, but may possibly be a senior synonym of *T. multiporosa*. *T. densa* Canu & Bassler was distinguished from *T. multiporosa* by the smaller size of the kenozooecia ('mesopores'). This difference is, however, gradational and seems related to the ontogenetic stage of the kenozooecia.

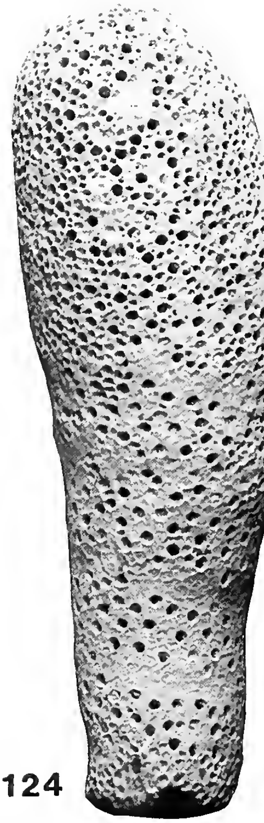
Genus *CLAUSA* d'Orbigny, 1853

Type species. *Ceriopora heteropora* d'Orbigny, 1850, by subsequent designation of Gregory, 1899; Cenomanian of France.

Remarks. The vinculariiform branches of species of *Clausa* are characterized by the presence of numerous polygonal kenozooecia, sometimes occluded by terminal diaphragms, surrounding the circular, open apertures of the autozooecia. These kenozooecia have often been referred to as 'dactylethrae', and Gregory (1896) used their occurrence to define a cyclostome suborder, Dactylethrata, which was retained by Bassler (1953) in the 'Treatise'. However, dactylethrae as understood by Gregory (1896) comprise at least two non-homologous structures: occluded kenozooecia as in *Clausa*, and autozooecia occluded during late ontogeny as in *Terebellaria*. There appears to be no sound basis for recognizing the Dactylethrata, some genera of which are apparently tubuloporines (e.g. *Reticulipora*, *Terebellaria*) and others cerioporines (e.g. *Clausa*, *Reptomulticlausa*).

Although gynozooecia have been described in the type species of *Clausa*, none have been found in the Faringdon species *Clausa zonifera*. In *C. heteropora*, gynozooecia have a strongly digitate outline (Walter *et al.* 1975) and appear to be roofed with exterior wall. Together with the absence of calcified exterior frontal walls in the autozooecia, this implies classification of *Clausa* with the cerioporines as currently understood. There is a good resemblance in external morphology between *Clausa* and some Recent heteroporids (e.g. *Heteropora pelliculata*, see Borg 1933: pl. 3, fig. 4) in which occluded kenozooecia surround circular autozooecial apertures. Therefore, *Clausa* is here assigned to the Heteroporidae with the caveat that more research is required, particularly on internal morphology.

Range. Aptian to ?Recent. Extension of the range of *Clausa* from the Cretaceous into the Recent rests on the synonymy (Brood 1972), which requires confirmation, of the living genus *Bientalophora* Borg, 1944 with *Clausa*.



124

Fig. 124 *Clausa zonifera* Canu & Bassler, USNM 69935d, **lectotype** (herein selected), × 14.

Clausa zonifera Canu & Bassler, 1926 Figs 124–127

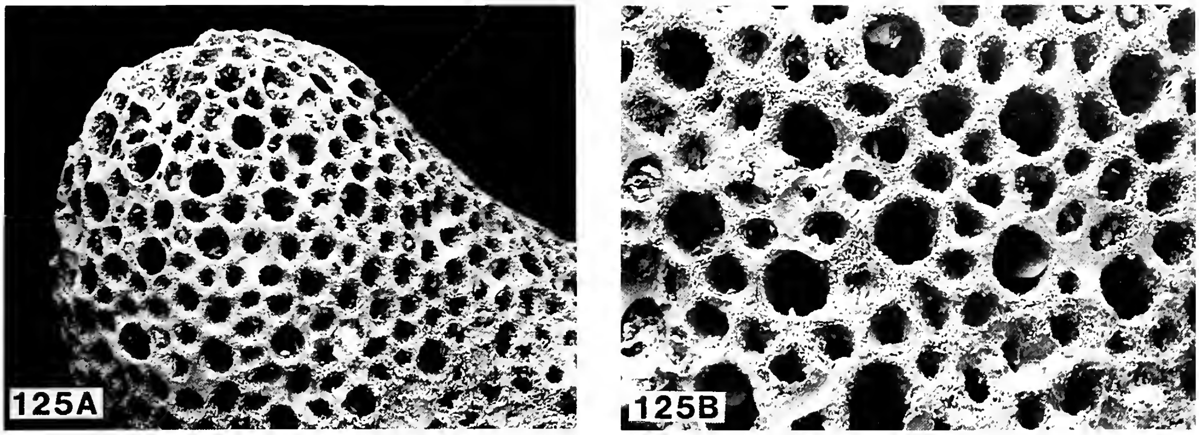
1926 *Clausa zonifera* Canu & Bassler: 80; pl. 17, figs 8–11; pl. 31, fig. 9.

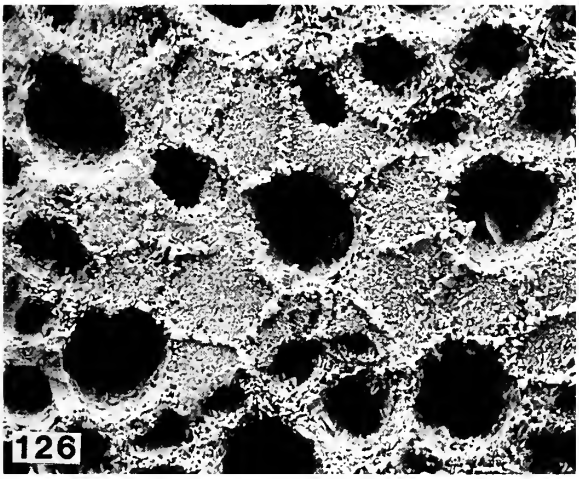
Lectotype. USNM 69935d, figd by Canu & Bassler (1926: pl. 17, figs 10–11), is here chosen as the lectotype.

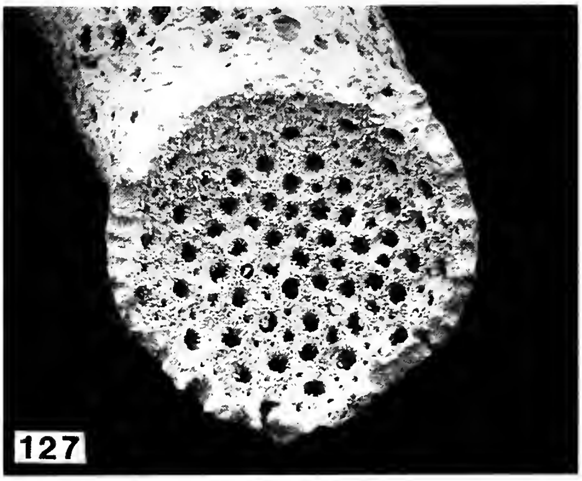
Paralectotypes. USNM 69935a-c, e-g, and one thin section.

Other material. BM(NH) D52148 (sample), D52183 (sample), D55087–9, D57729 (3 thin sections and remnant), D57735, Little Coxwell Pit, Pitt Colln; D52129–39 (sample), D52150 (6), D52153 (sample), D57719–20, Little Coxwell Pit, Thomas Colln; D52148 (sample), D55149 (2), Little Coxwell Pit, Gaster Colln; D55151 (sample), D55152 (2), Bowler's Pit, Gaster Colln; D55154 (sample), Bowler's Pit, ?colln; D57651 (5), Davis Colln.

Description. Zoaria erect, dendroid, with cylindrical branches (averaging 2·5 mm diameter, range 1·5–3 mm) which are often claviform and swollen (Fig. 124). Branch growth tips are blunt and well-rounded (Fig. 125A). Branches bifurcate at irregular intervals and at angles up to 90°. The colony base is small, slightly expanded and has a high density of kenozooecia. More than one erect stem may arise from each colony base, and early bifurcations may be closely spaced. The proximal fractured ends of branches are







igs 125–127 *Clausa zonifera* Canu & Bassler. Fig. 125, BM(NH) D57719; 125A, growth tip, × 52; 125B, autozooecia and open kenozooecia, × 100. Fig. 126, BM(NH) D57720, autozooecia and occluded kenozooecia, × 138. Fig. 127, BM(NH) D57735, concave proximal fracture surface of a branch, × 35.

ometimes concave (Fig. 127), breakage apparently occurring t a position of weakness, possibly a growth check. Ill-defined naculae are usually developed and consist of bands, aligned ransverse to growth direction, which are rich in kenozooecia.

Autozooecia have open, circular apertures, lack frontal alls, and are surrounded by kenozooecia (Figs 125B, 126).

Kenozooecia have smaller, more variably-sized apertures han autozooecia. Occlusion of kenozooecial apertures is ommon (Fig. 126); occluded apertures appear polygonal hereas open apertures appear rounded. Terminal diaphragms re apparently pseudoporous and are situated slightly below e level of the aperture so that the interzooecial walls stand ut as low ridges.

Brood chambers are unknown.

In section, zooecial walls are indistinctly laminated and elatively thick in the endozone. Diaphragms other than erminal diaphragms have not been observed. Kenozooecia re seen to bud in the exozone which is poorly differentiated om the endozone.

EASUREMENTS. TAM, 0·10–0·14 mm; KAM, 0·02–0·09 mm.

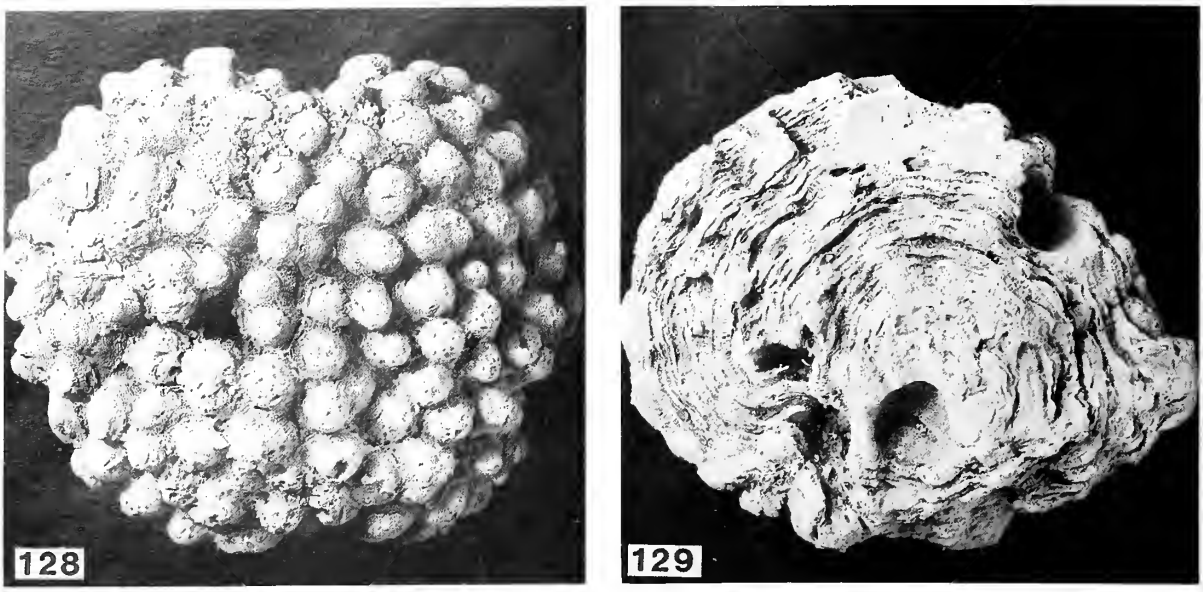
EMARKS. This species is very common at Faringdon but has ot been recorded elsewhere. It is most likely to be confused with *Tetrocycloecia multiporosa* which shares with *Clausa zonifera* a similar arrangement of autozooecia and kenozooecia in the dendroid colony branches. However, there are several points of distinction including: the larger size of colony branches and autozooecial apertures in *C. zonifera*; the slight autozooecial peristomes and typically funnel-shaped kenozooecia in *T. multiporosa*; and the occurrence of maculae, swollen branches, and kenozooecia occluded by terminal diaphragms in *C. zonifera*.

Family **incertae sedis**

Genus ***SEMIMULTICAVEA*** d'Orbigny, 1854

TYPE SPECIES. *Ceriopora landrioti* Michelin, 1841, by subsequent designation of Gregory, 1909*a*; Albian of Grandpré, France.

REMARKS. Walter (1975) redescribed the type material of the type species of *Semimulticavea*. The multilamellar colony is constructed of stacked polygonal subcolonies with radially-arranged autozooecia separated by polymorphs (termed cancelli by Walter). Unfortunately, brood chambers are not



Figs 128–129 *Semimulticavea marginata* (Canu & Bassler), optical photographs. Fig. 128, BM(NH) D55117, mammilate colony surface with numerous subcolonies, × 2·1. Fig. 129, BM(NH) D55114, fractured colony with bivalve boring (*Gastrochaenolites*), × 1·8.

described and therefore the subordinal status of the genus is unclear. Brood chambers in *S. marginata* are, however, described below and imply that *Semimulticavea*, in spite of the presence of possible pseudolunaria (see Brood 1972: 71 for a definition of these structures), may be a cerioporine and not a rectangulate as previously considered (e.g. Bassler 1953).

RANGE. Aptian to ?Campanian.

Semimulticavea marginata (Canu & Bassler, 1926)

Figs 128–136

1909*a* *Radiopora neocomiensis* (d'Orbigny); Gregory: 284; text-figs 74–75.
1926 *Radiopora tuberculata* (d'Orbigny); Canu & Bassler: 63; pl. 20, figs 2–5.
1926 *Multigalea canui* (Gregory); Canu & Bassler: 61; pl. 19, figs 1–6 [non *Reptomulticava canui* Gregory 1909*b*].
1926 *Multigalea marginata* Canu & Bassler: 62; pl. 19, figs 7–10.

HOLOTYPE. USNM 69911, figd Canu & Bassler, 1926: pl. 19, figs 7–10.

OTHER MATERIAL. BM(NH) 10178, 10189, 10300, Mantell Colln; D3143 (with 3 remnants and 3 thin sections), figd as *Radiopora neocomiensis* (d'Orbigny) by Gregory (1909*a*); D4985, Brown Colln; D52203, D55365, D55367–8, Little Coxwell Pit, Pitt Colln; D55114, D55364, D55372, Bowler's Pit, Pitt Colln; D55113, Little Coxwell Pit, A.G. Davis Colln; D55117, D57722 (3 thin sections), Bowler's Pit, Gaster Colln; D55366, Little Coxwell Pit, Cleevely Colln; D55369, Little Coxwell Pit, Thomas Colln; D57723 (3 thin sections), Little Coxwell Pit, A. G. Davis Colln.

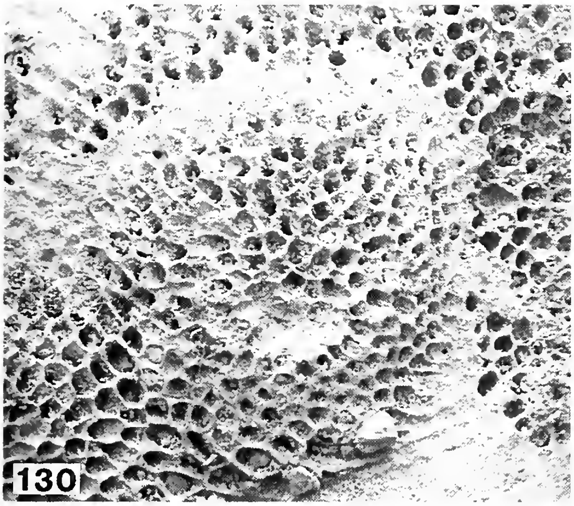
DESCRIPTION. Zoarium massive and multilamellar (Figs 128–129, 135), typically large (up to 70 mm across), usually irregularly hemisperical, but occasionally shaped like a carrot and up to 95 mm high with an axial hole (due to growth around an unpreserved substrate). In some places the successive layers are tightly packed, but elsewhere there may be significant amounts of void space between the layers (Fig. 132). Each layer consists of numerous low and broad, inverted cup-shaped subcolonies which are fused with adjacent subcolonies along part or all of their edges, and are subcircular to polygonal in plan view (Fig. 131B). The surface of the colony is monticulate, the monticule summits being the centres of the subcolonies. Each subcolony has an axial area of kenozooecia surrounded by radiating, uniserial rows, sometimes ill-defined, of autozooecia which are separated by kenozooecia (Fig. 131B); in worn specimens the distinction between autozooecia and kenozooecia is not appartent (Fig. 130). Subcolonies of successive layers are aligned directly above one another (Figs 132, 136A), reflecting the origin of new subcolonies from the centres of established subcolonies.

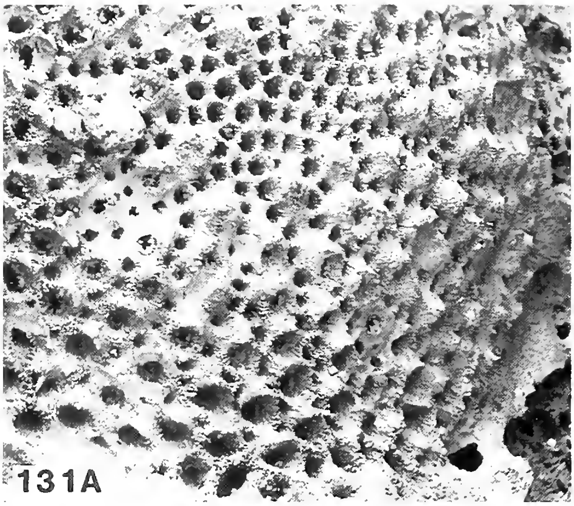
Autozooecial apertures are polygonal to subcircular and vary greatly in size, decreasing towards the centre of the subcolonies. In well-preserved specimens (e.g. in sheltered recesses) crescent-shaped ?pseudolunaria (Figs 131A, 134), up to 0·1 mm high, may occur on the sides of the apertures closest to the centres of the subcolonies.

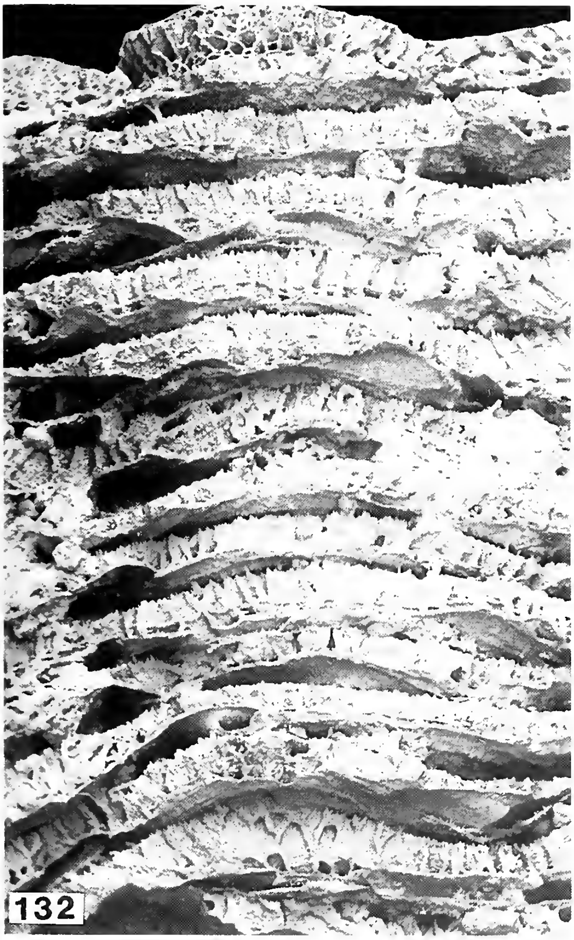
Kenozooecia are located at the centres of subcolonies and between the rows of autozooecia, and have small subcircular apertures lacking ?pseudolunaria.

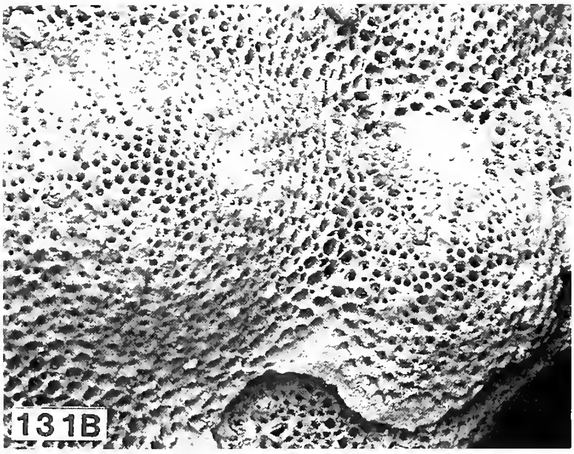
Gynozooecia (Fig. 133) are uncommon and in surface outline appear to be ring-shaped and centred on a subcolony, or possibly crescent-shaped. The frontal wall is a smooth-textured, probable exterior wall (though pseudopores have not been observed) and is pierced by autozooecia arranged in typical uniserial rows. All observed gynozooecia are broken and no unequivocal ooeciostomes have been identified.

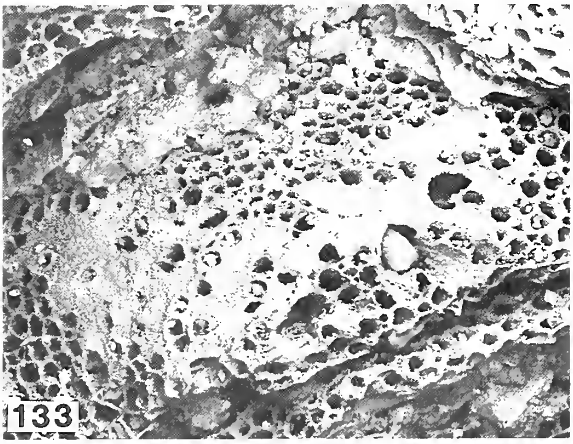
In thin section the zooecial walls have a granular, cloudy microstructure without clearly visible laminations. Interzooecial walls are thin in the endozone and thick and moniliform (with interzooidal pores) in the exozone (Fig. 136B). A few zooecia have single, thin diaphragms of the











Figs 130–133 *Semimulticavea marginata* (Canu & Bassler). Fig. 130, USNM 69911, holotype, abraded subcolony, × 15. Fig. 131, BM(NH) D55113; 131A, autozooecia with ?pseudolunaria flanking a monticular subcolony, × 31; 131B, two subcolonies, × 10. Fig. 132, BM(NH) D55371, part of a fractured colony showing multilayered structure, × 15; see also Fig. 134. Fig. 133, BM(NH) D55368, gynozooecium, × 21.

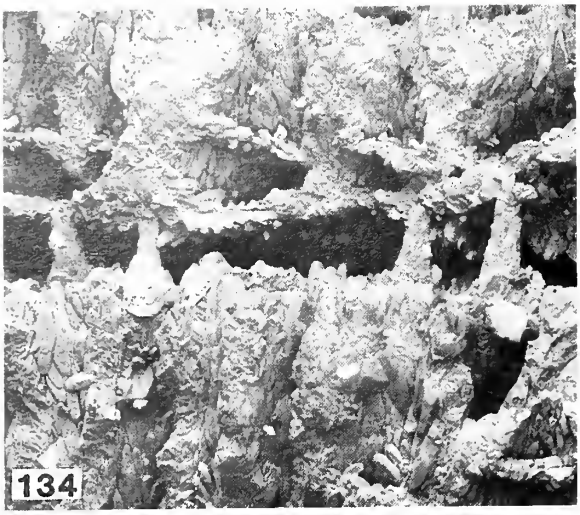


Fig. 134 *Semimulticavea marginata* (Canu & Bassler), BM(NH) D55371, part of a fractured colony showing four spine-like ?pseudolunaria covered by the next layer of colony growth, × 103; see also Fig. 132.

intermediate type which are flexed aborally at their contacts with the zooecial walls. Zooecial chambers near the centres of the subcolonies may be seen to continue into overlying subcolonies (Fig. 136B). The distinction between autozooecia and kenozooecia is not readily made in thin section.

MEASUREMENTS. TAM, 0·10–0·15 mm; KAM, 0·04–0·05 mm.

REMARKS. Specimens of this species from Faringdon have usually been referred to as *Radiopora neocomiensis* d'Orbigny. However, there are complex systematic problems resulting from the use of this name.

Firstly, *Radiopora* d'Orbigny, 1849 is an inappropriate genus for the Faringdon species. The type species, by original designation, is *Ceriopora formosa* Michelin from the Cenomanian of Le Mans, which has a ramose colony-form with stellate subcolonies. D'Orbigny (1854: 992–998) attributed 10 species to *Radiopora*, including *Radiopora formosa* (Michelin) from the type locality of Le Mans. D'Orbigny's illustrations of *R. formosa* are reproduced or redrawn from Michelin's original figures; the dendroid branches are almost certainly not multilayered and therefore unlike so-called *Radiopora* from the Faringdon Sponge Gravel.

The species *neocomiensis* was originally described in the binomen *Monticulipora neocomiensis* d'Orbigny (1850: 95) and characterized thus: 'Éspece tubereuse, à monticules très reguliers. Fontenoy, Chenay'. D'Orbigny later (1854: 993–994), placed his species in synonymy with *Alveolites heteropora* Roemer, 1836 [*sic*], as *Radiopora heteropora* d'Orb. 1852 [*sic*], and figured (1854: pl. 781, figs 13–16) a massive multilayered colony with monticules and radiating rows of autozooecial apertures. The species *heteropora* had been first described by Roemer (1839, not 1836) from the Neocomian of Germany in the binomen *Alveolites heteropora* (1839: 14; pl. 17, figs 7–8). Roemer's poor illustrations depict a small encrusting species with thick walls surrounding tiny apertures. This is clearly not the same as the species which was called *Radiopora heteropora* by d'Orbigny (1854).

A second genus to which the Faringdon species has been referred is *Multigalea*. This genus was proposed by Canu & Bassler (1926: 61), who designated *Reptomulticava canui* Gregory, 1909*b* as the type species. Unfortunately, the identity of *R. canui* is in doubt. *R. canui* was erected by Gregory as a 'nov. nom.' for *Reptomulticava tuberosa* (Roemer), *sensu* d'Orbigny (1854), which Gregory believed to differ from *Alveolites tuberosa* Roemer. In fact the species *R. canui* is not a new name but a new species. Gregory (1909*b*) did not figure *R. canui* in his original paper, and failed to do so also in his subsequent catalogue (1909*a*). Ascertaining the identity of *R. canui* is further complicated by Gregory's (1909*a*: 130) statement: 'The specimen figured by d'Orbigny [as *Reptomulticava tuberosa*], according to M. Pergens, is lost; accordingly the Museum specimen, D.7077, had better be regarded as type [of *R. canui*]'. This statement can be interpreted as an effective neotype designation; however, the specimen cited cannot serve as a neotype because it is from Goslar rather than one of the two type localities (St Dizier and Vassy, France) given by Gregory (1909*b*). Therefore, there is no valid type specimen for *R. canui* and, as Gregory's two descriptions (1909*b*,*a*) are inadequate to characterize the species, the identity of the genus *Multigalea* of which it is the type species cannot be ascertained at present.

After dismissing *Radiopora* and *Multigalea* as appropriate genera to accommodate the Faringdon species, *Semimulticavea* d'Orbigny remains as the most suitable generic assignment. The type species of *Semimulticavea* is *Ceriopora landrioti* Michelin, redescribed by Walter (1975), from the Albian of the Ardennes. Colonies of this species are multilamellar and are constructed of numerous subcolonies each with radial rows of autozooids separated by kenozooids.

In describing their new species *Multigalea marginata*, Canu & Bassler (1926) provided the correct specific name for the

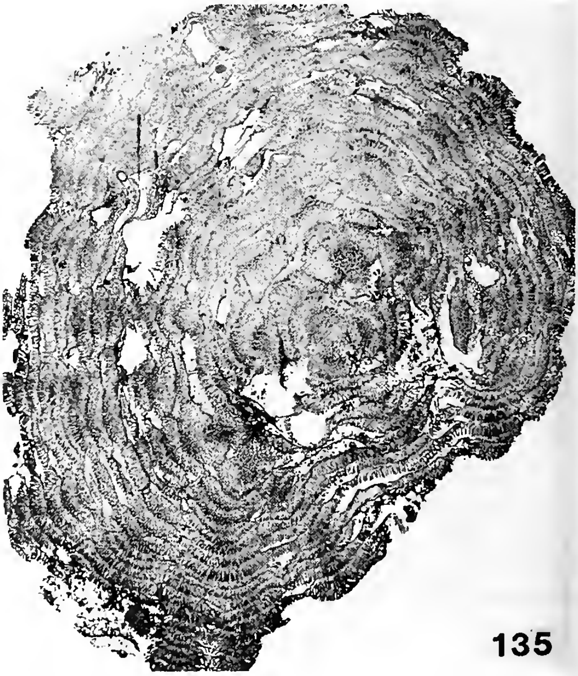


Fig. 135 *Semimulticavea marginata* (Canu & Bassler), BM(NH) D57722, thin section showing multilayered structure of colony, × 2·6; see also Fig. 136.

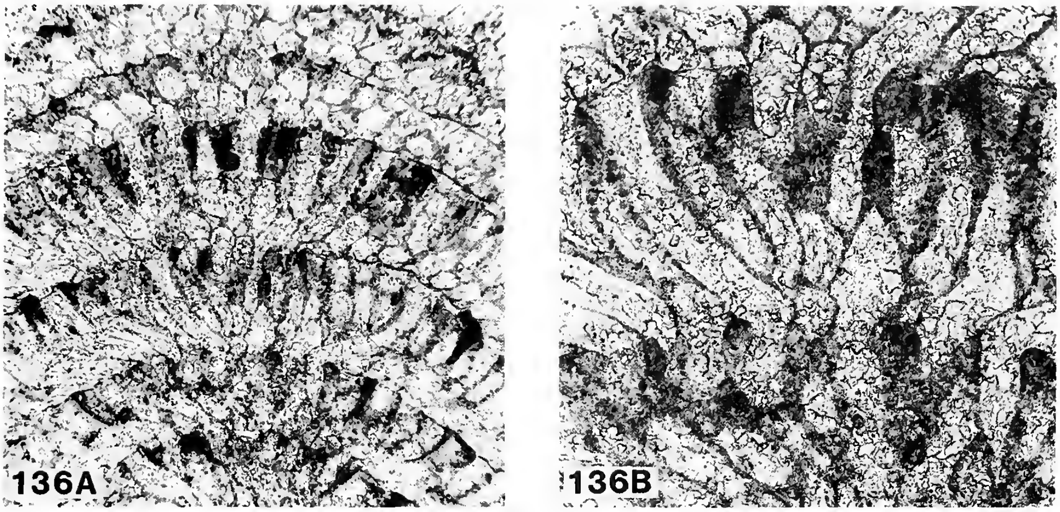


Fig. 136 *Semimulticavea marginata* (Canu & Bassler), BM(NH) D57722, thin section; 136A, vertical section through the origins of a stack of subcolonies, × 22; 136B, detail showing some zooecia continuing from parent to daughter subcolony, × 55; see also Fig. 135.

common Faringdon species. Unfortunately, the holotype of *S. marginata* (Canu & Bassler) is heavily worn (Fig. 130) and does not show the ?pseudolunaria of the autozooecia.

S. marginata bears a close resemblance to *Ceriopora (Reptonodicava) nodosa* Keeping, 1883, the syntypes (SM B26133–9) of which have been studied. Keeping's specimens of this species from the Aptian of Upware share with *S. marginata* large multilamellar colonies composed of numerous subcolonies. However, the subcolonies are larger and the monticules typically higher than in *S. marginata*. Furthermore, dimorphism of the zooecia is not clearly developed and pseudolunaria cannot be observed, though this may be because of the abraded state of the material.

Colonies of *S. marginata* are distinctive on account of their multilayered structure and typically large size. Probably the carrot-shaped colonies of *S. marginata* came from a pit closed long ago; none have been found in the last fifty years (carrot-shaped colonies also occur in *C. nodosa* Keeping, e.g. SM specimens B26137 and B29139). Hemispherical colonies are also much less commonly found nowadays than they were in the past.

Serpulid tubes are encountered embedded within colonies between successive layers. These worms evidently fouled the surfaces of living colonies and were subsequently trapped by the growth of new overarching subcolonies. Also commonly associated with *S. marginata* are boring bivalves whose crypts (ichnogenus *Gastrochaenolites*) are found penetrating many colonies (Fig. 129).

Genus ***SEMINODICRESCIS*** d'Orbigny, 1854

TYPE SPECIES. *Seminodicrescis nodosa* d'Orbigny, 1854, by monotypy; Aptian of Saint-Dizier (Haute-Marne) and Croutes (Aube), France.

REMARKS. *Seminodicrescis* was founded by d'Orbigny (1854) for a heteroporid-like Aptian species, *S. nodosa*, with a hollow tubular colony-form. Unfortunately. the type material of *S. nodosa* has yet to be revised, and the detailed morphology of the genus is not apparent from d'Orbigny's description and figures. However, the Faringdon species *Semimulticavea variolata* of Gregory (1909*a*), which may occur as hollow tubular colonies or as conventional encrusting colonies on shells, etc., sufficiently resembles the type species of *Seminodicrescis* for provisional assignment to this genus.

RANGE. Aptian.

Seminodicrescis variolata (Gregory, 1909*a*)

Figs 110, 137–139

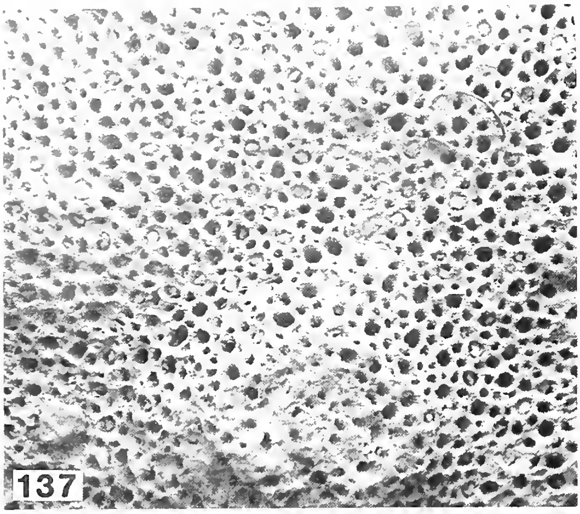
1909*a* *Semimulticavea variolata* Gregory: 241; pl. 5, figs 5a, c.
1926 *Multicrescis mammillosa* Canu & Bassler: 16; pl. 21, figs 5–6 [pl. 21 includes two figures labelled 6; that in the centre of the plate may not be this species].
1926 *Seminodicrescis nodosa* d'Orbigny; Canu & Bassler: 19; pl. 22, fig. 1.
1986 *Multicrescis mammillosa* Canu & Bassler; Wilson: 694.

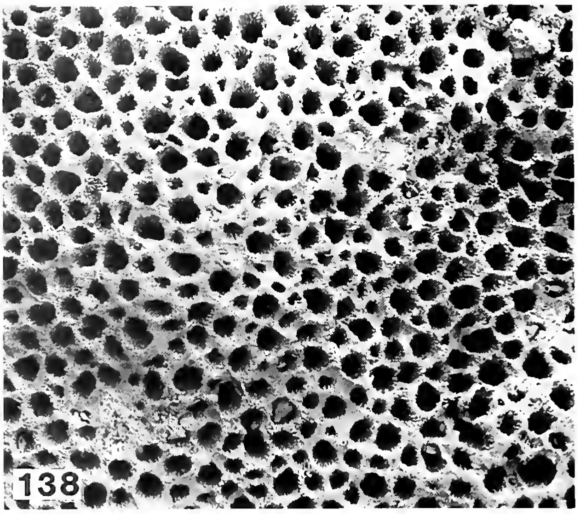
HOLOTYPE. BM(NH) D3027.

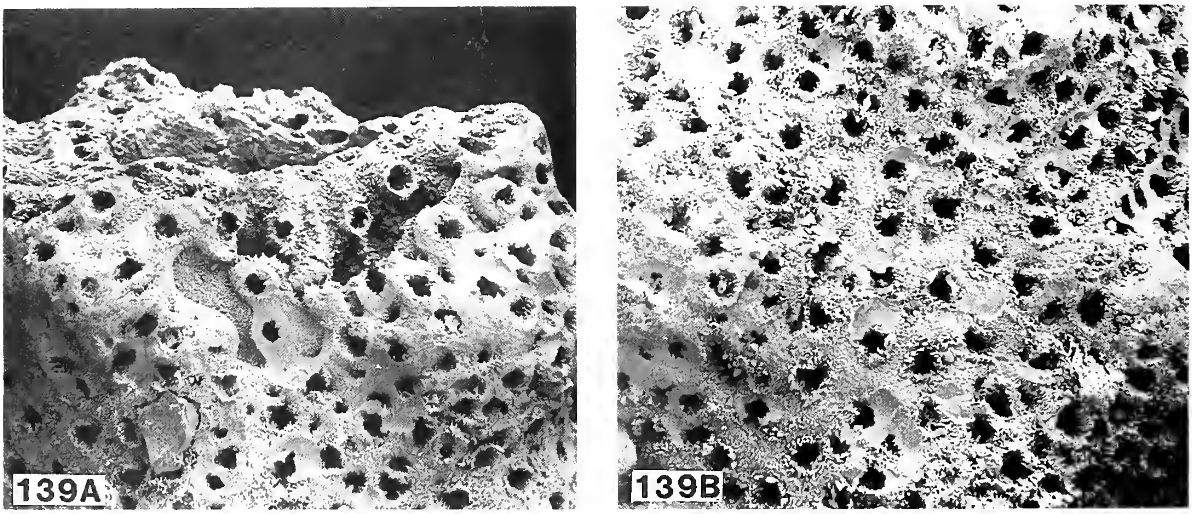
OTHER MATERIAL. BM(NH) D52169 (sample), Little Coxwell Pit, Pitt Colln; D52296 (sample), D55300, D57721 (sample), Little Coxwell Pit, Thomas Colln; D55295, Hinde Colln; D55297 (3), locality presumed to be Faringdon, *ex* Durham University Colln; D55298–9, D55203–5, Little Coxwell Pit, Gaster Colln; D55427, Wicklesham Pit, Wilson Colln. USNM 69860, type specimen of *Multicrescis mammillosa* Canu & Bassler, 1926.

DESCRIPTION. Zoarium encrusting (Fig. 110, p. 115), sometimes tubular, usually unilamellar but occasionally multilamellar, with moderately to well developed monticules (Fig. 138) which may possess smaller kenozooecia than the intermonticular areas. The observation of zooecia apparently giving rise to new buds by intrazooecial fission suggests that this process may have been responsible for multilamellar overgrowth.

Autozooecial apertures are small, polygonal to subcircular,


137


138


139A
139B

Figs 137–139 *Seminodicrescis variolata* (Gregory). Fig. 137, USNM 69860, type specimen of *Multicrescis mammilosa* Canu & Bassler, × 15. Fig. 138, BM(NH) D55297a, monticule, × 36. Fig. 139, BM(NH) D52169a; 139A, broken gynozooecium, × 48; 139B, gynozooecium with poorly-preserved but intact frontal wall, × 52.

and may have slight peristomes which help distinguish them from kenozooecia.

Kenozooecial apertures are smaller and more angular than the autozooecia which they surround.

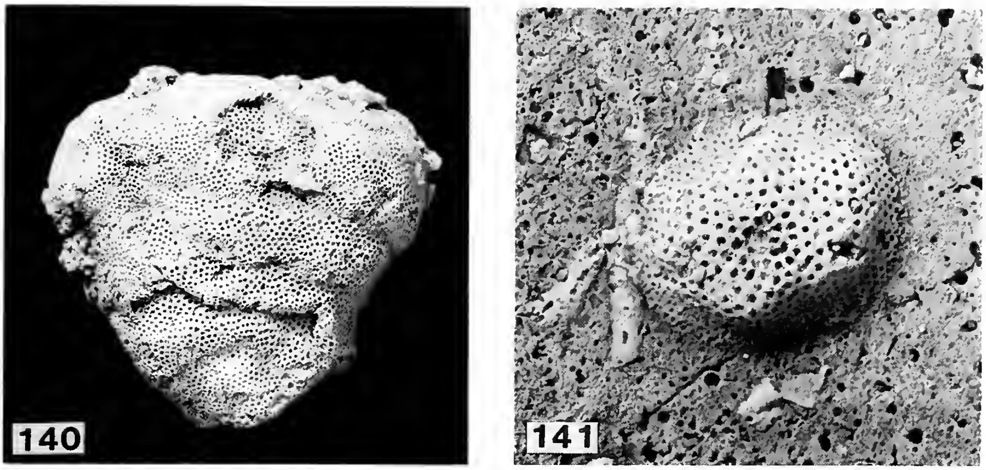
Brood chambers (?gynozooecia) are rare (Fig. 139). They are more-or-less circular in outline, about 1·2 mm in diameter, and are roofed by a probable exterior wall which is penetrated by numerous autozooecia. In addition to these penetrating autozooecia, the roof is supported by septa-like internal walls. The ooeciopore has not been observed.

MEASUREMENTS. TAM, 0·07–0·10 mm, mean 0·08 mm; KAM, 0·03–0·06 mm, mean 0·05 mm.

REMARKS. This species is distinguished from *S. nodosa* d'Orbigny by the considerably smaller size of the autozooecia; Walter *et al.* (1975) give the diameter of the autozooecial apertures in *S. nodosa* as 0·15–0·16 mm, whereas those of *S. variolata* are 0·07–0·10 mm.

The oldest available name for this species derives from Gregory (1909*a*) who provided a short description based on a single specimen. In their description of the Faringdon bryozoan fauna, Canu & Bassler (1926) appear to have overlooked Gregory's species and proposed *Multicrescis mammillosa* for their material. They also used the name *Seminodicrescis nodosa* d'Orbigny for hollow tube colonies of *S. variolata* which apparently encrusted perishable cylindrical substrates.

S. variolata is especially common encrusting small terebratulid brachiopods, usually on the pedicle valve (Fig. 110). On articulated specimens the bryozoan colony often extends to the edge of the pedicle valve but does not cross the commissure. One such colony (BM(NH) D55297) is penetrated by a paraboloid boring which passes through both bryozoan and brachiopod shell and may be the hole made by a predator of the brachiopod. If so, some colonies of *S. variolata* may have been symbionts of living brachiopods (i.e. true epizoans). However, other colonies of *S. variolata* are tubular and encrust vinculariiform bryozoans, erect serpulid worm tubes,



Figs 140–141 *Reptomulticava brydonei* (Gregory), optical photographs. Fig. 140, BM(NH) D77753, × 4·2. Fig. 141, BM(NH) D55325, young colony encrusting a bivalve shell, × 11·5.

echinoid spines or soft-bodied substrates. Small shell fragments were also occasionally used but the species has not been found among the diverse encrusting bryozoan fauna developed on sponges or pebbles.

Genus *REPTOMULTICAVA* d'Orbigny, 1854

TYPE SPECIES. *Reptomulticava pyriformis* d'Orbigny, 1854, designated herein; Valanginian, Ste Croix, Switzerland.

REMARKS. *Reptomulticava* was founded by d'Orbigny (1854) who assigned 12 described species (4 of them new) and a further 16 listed species to the genus. The type species of this genus is usually given as *Alveolites heteropora* Roemer, 1839 (e.g. Bassler 1953; Hillmer 1971), which appears to have been selected as the type by Gregory (1909*a*). However, as *Alveolites heteropora* is not among the 28 species assigned by d'Orbigny (1854) to *Reptomulticava* in his original description of this genus, it has no validity as the type species. Therefore, *Reptomulticava pyriformis* d'Orbigny, 1854 is here designated as the type species of *Reptomulticava. R. pyriformis*, redescribed by Walter (1972), was not only included in the original description of *Reptomulticava*, but it also seems to correspond with the general useage of the name *Reptomulticava* (e.g. Hillmer 1971; Hillmer, Gautier & McKinney 1975; Nye & Lemone 1978).

RANGE. Valanginian to ?Maastrichtian.

Reptomulticava brydonei (Gregory, 1909*b*)

Figs 140–143

?1854 *Reptomulticava collis* d'Orbigny: 1036; pl. 792, figs 1–3.
1909*b* *Zonatula brydonei* Gregory: 64.
1909*a* *Zonatula brydonei* Gregory; Gregory: 215; pl. 4, fig. 10.
909*a* *Ceriopora collis* (d'Orbigny); Gregory: 163; pl. 5, figs 5a–b.
926 *Reptomulticava fungiformis* Gregory; Canu & Bassler: 29; pl. 24, figs 14–17 (?11–13).

HOLOTYPE. BM(NH) 10297, Mantell Colln, the single specimen described and figured by Gregory (1909*a*, *b*) as *Zonatula brydonei*.

OTHER MATERIAL. BM(NH) D52113–8, D52181 (sample), D52204–6, D52207 (sample), D52212 (sample), D55546–7, D57744, D57745 (thin section), D57746 (sample), D57747, D57753, Little Coxwell Pit, Pitt Colln; D52208 (sample), D57748–50, Faringdon Pit, Pitt Colln; D52209 (sample), Wicklesham Pit, Pitt Colln; D55325–7, Little Coxwell Pit, Gaster Colln; D55328 (sample), Little Coxwell Pit, Cleevely Colln; D55331, D57752 (sample), Little Coxwell Pit, Thomas Colln; D57751, Bowler's Pit, Pitt Colln.

DESCRIPTION. Zoarium (Fig. 140) of short, thick stems which are occasionally bifurcate, more rarely clavate, composed of tightly packed layers of stacked, basally growing subcolonies. Young zoaria (Fig. 141) are bun-shaped and unilamellar (described as *Ceriopora collis* by Gregory, 1909*a*).

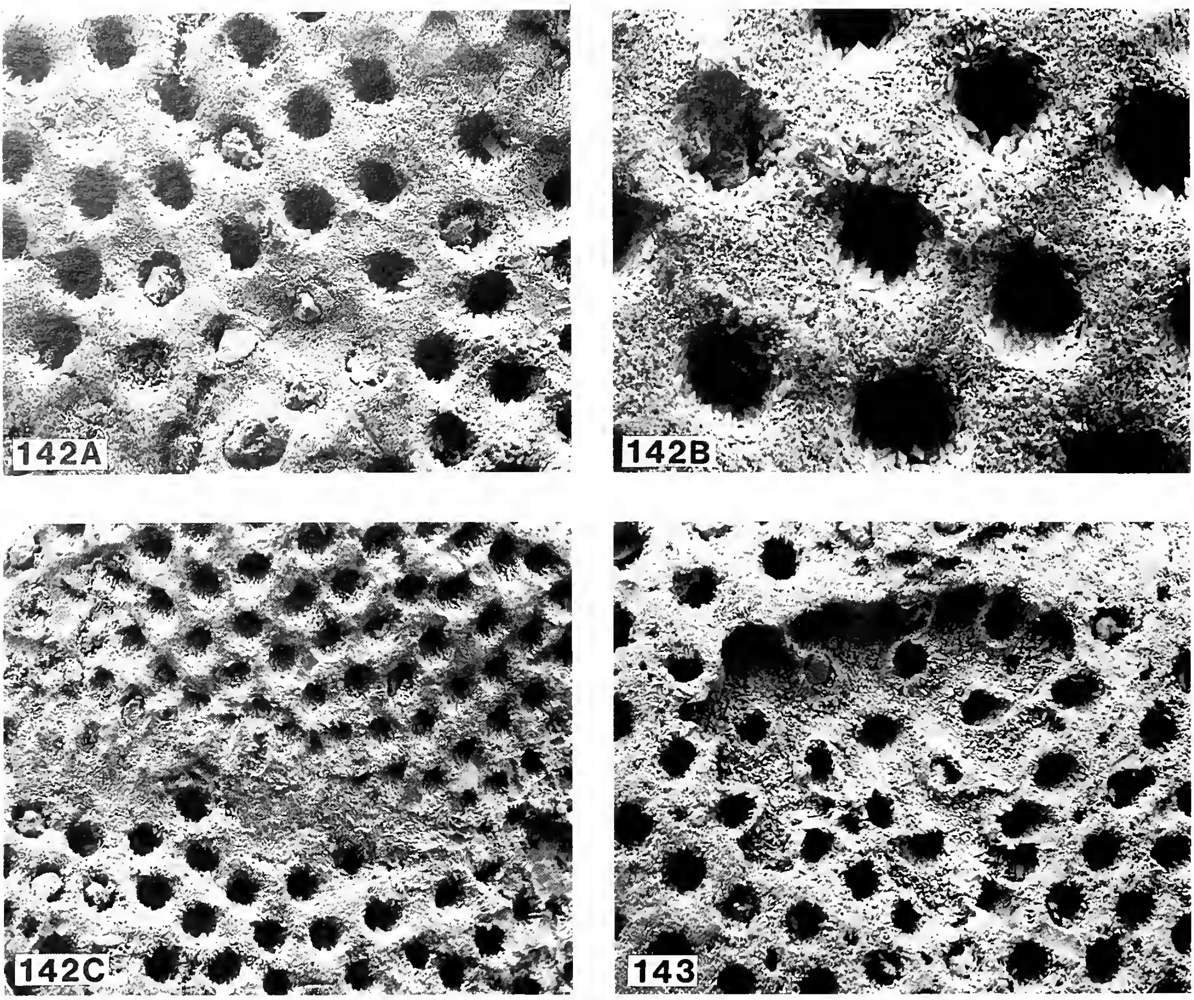
Autozooecia have circular apertures (Fig. 142), arranged in near quincunx, and are very thick-walled (wall thickness is commonly about the same as apertural diameter). Well-preserved autozooecia possess short, blunt mural spines within the apertures.

Kenozooecia are lacking.

Brood chambers (Fig. 143) are uncommon, approximately circular in outline and about 1 mm in diameter, pierced by autozooecia which apparently support the roof of the chamber together with radial septa. The ooeciopore has not been observed.

In thin section, the multilamellar form of the zoaria is clearly evident; each layer is about 0·9–1·3 mm in height, tapering towards the edges of the colony, and is generally formed by the coalesence of several subcolonies of independent origin. The 'pseudoancestrulae' at the focus of subcolonies continue upwards into the new daughter subcolony. Zooecial walls are thin proximally (close to the base of the subcolonies) but rapidly thicken distally where they may attain a thickness of 0·09 mm. Walls are indistinctly laminated and have a cloudy microstructure. Diaphragms are apparently absent or rare.

MEASUREMENTS. TAM, 0·08–0·10 mm.



Figs 142–143 *Reptomulticava brydonei* (Gregory). Fig. 142, BM(NH) 10297, holotype; 142A, × 65; 142B, thick-walled zooecia, × 152; 142C, edge of overgrowing subcolony, × 42. Fig. 143, BM(NH) D57744, worn gynozooecium, × 53.

REMARKS. *R. brydonei* is often mis-identified (e.g. Canu & Bassler 1926) as *Reptomulticava fungiformis* Gregory, 1909*b*, a species which is here regarded as a 'sclerosponge'. Although assigned to *Zonatula* Hamm, 1881 by Gregory (1909*b*), a more appropriate genus to accommodate this common Faringdon bryozoan is *Reptomulticava* d'Orbigny, 1854, a genus whose identity is discussed above. The type species of *Zonatula, Plethopora pseudotorquata* Hagenow, 1851 from the Maastrichtian, does not have zoaria constructed of a series of multilamellar subcolonies. Many species of *Reptomulticava* develop larger colonies than *R. brydonei* with a growth-form resembling that of *Semimulticavea marginata*.

Small colonies of *R. brydonei* may be found encrusting bivalve shells or sponges, but larger colonies are generally recovered detached from their substrata as short stems which are commonly worn. Zoarial morphology resembles that of *Tholopora* spp. from which *R. brydonei* can be distinguished by the absence of kenozooecia and the presence of extremely thick-walled autozooecia.

Genus *THOLOPORA* Gregory, 1909*a*

TYPE SPECIES. *Ceriopora clavata* Goldfuss, 1827, by original designation; Cenomanian, Essen, W. Germany.

REMARKS. Gregory (1909*a*) founded this genus to embrace compound 'Radioporidae' composed of superimposed subcolonies forming short, thick, blunt cylindrical stems. In it he placed seven species: *Ceriopora clavata* Goldfuss, 1827, the type species; *Ceriopora muletiana* d'Orbigny, 1850; *Domopora colligata* Gregory, 1909*b*; *Domopora polytaxis* (Hagenow, 1851)?, *sensu* Vine, 1885 (= *Domopora vinei* Gregory, 1909*b*); *Ceriopora stellata* (pars) Goldfuss, 1829 (= *Tholopora virgulosa* Gregory, 1909*b*); *Heteropora variabilis* (d'Orbigny 1852), *sensu* Novak, 1877 (= *Domopora novaki* Gregory, 1909*b*); and *Multicrescis variabilis* (d'Orbigny, 1854), *sensu* Gamble, 1896 (= *Domopora cantiana* Gregory, 1909*b*).

T. colligata (Gregory 1909*b*) was founded on one specimen (BM(NH) D7288), stated to be from Faringdon; but in the register it is listed as '?Faringdon, ?Baker Collection'. Unlike typical Faringdon Sponge Gravel, the matrix is greeny-grey and hard, and this suggests that the locality information is in error. There are no other Baker Colln Faringdon specimens in the BM(NH) but we know that Baker collected material from the Upper Greensand of Warminster which is of a similar lithology to Gregory's type specimen of *T. colligata*. There is no evidence that *T. colligata* actually occurs at Faringdon.

Canu & Bassler (1926) and Pitt (1949) misidentified Faringdon material as *T. virgulosa* (Gregory 1909*b*), another species originally described from the Upper Greensand of Warminster. *T. virgulosa*, redescribed by Voigt (1975), is here regarded as synonymous with *T. colligata*.

The present study has revealed the existence of three species of *Tholopora* at Faringdon: *T. dightoni* sp. nov., *T. hastingsae* sp. nov. and *T. thomasi* Pitt, 1949. The appearance of all three species in thin section is very similar, but external morphology reveals clear differences in the size and arrangement of the zooecial apertures.

RANGE. ?Hauterivian to ?Santonian.

Fig. 144 *Tholopora dightoni* sp. nov., BM(NH) D57672, **holotype**, × 15; see also Fig. 145.

Tholopora dightoni sp. nov. Figs 144–145

1926 *Tholopora virgulosa* Gregory [*sic*]; Canu & Bassler: 63; pl. 20, fig. 1 [non *Tholopora virgulosa* (Gregory)].

HOLOTYPE. BM(NH) D57672, Little Coxwell Pit, Pitt Colln.

PARATYPES. BM(NH) D52161, D57664 (remnant & thin section), D57665 (remnant & thin section), D57666 (sample), D57667 (5), Little Coxwell Pit, Pitt Colln; D57673, Bowler's Pit, Pitt Colln; D57656 (sample), D57657 (3), D57660–1, Little Coxwell Pit, Thomas Colln; D57662, Faringdon Pit, Thomas Colln; D57663 (8), Little Coxwell Pit, Elliott Colln; D57664, Cleevely Colln.

NAME. For the late Dr H. Dighton Thomas, who originally suspected this to be a new species.

DESCRIPTION. Zoarium (Fig. 144) of short thick stems, up to 12 mm high, irregular in diameter (up to 6 mm) and composed of stacked, bun-shaped subcolonies, averaging 0·9 mm in height. Branching occurs but is rare.

Autozooecia are arranged regularly in uniserial connate rows, separated by kenozooecia, which radiate from subcolony centres (Fig. 145B). Autozooecial apertures are of moderate size, consecutive apertures within each row increasing in size centrifugally (i.e. towards the periphery of the subcolony). At high magnifications short mural spines (*c*. 0·006 mm long) can be seen inside the autozooecial apertures (Fig. 145C).

Kenozooecial apertures are small and have mural spines like those of the autozooecia but present in a slightly higher density.

The only brood chambers (Fig. 145D) observed are very small, broken, and roughly elliptical in outline. Occluded kenozooecia form the floor of the brood chamber, and some autozooecia pass through the chamber, presumably supporting the roof.

In thin section the wall microstructure is not distinctly laminated but is granular with dark patches which may be arranged in transverse bands resembling monilae. Interzooecial walls thicken gradually from the basal lamina of the subcolony upwards, attaining a maximum thickness of about 0·03 mm. A few probable basal diaphragms occur. The mode of origin of new subcolonies is not evident from the sections available, but the chambers of some centrally-located zooecia are seen to be continous from one subcolony to the next.

MEASUREMENTS (TAM and KAM measured from zooecia midway out from subcolony centres). TAM, 0·08–0·10 mm; KAM, 0·02–0·03 mm; GDL, 0·66 mm; GW, 1·2 mm.

REMARKS. This species is very similar to *T. thomasi* but differs in the significantly smaller dimensions of the zooecia and branch diameter. It is distinguished from *T. hastingsae* by the regular arrangement of autozooecia in rows and the larger size of the zooecia.

Tholopora hastingsae sp. nov. Figs 146–148

HOLOTYPE. BM(NH) D55336, Little Coxwell Pit, Pitt Colln.

PARATYPES. BM(NH) D52227, Faringdon Pit, Pitt Colln; D55120, D55335 (4), D57677–82, D55337–8 (4 thin sections), D57683 (thin section & remnant), D57684 (thin section & remnant), Little Coxwell Pit, Pitt Colln; D55344 (2 thin sections), D55346, Little Coxwell Pit, Thomas Colln; D55345 (2 thin sections), D57675–6, Little Coxwell Pit, Gaster Colln.

NAME. For the late Dr A. B. Hastings, bryozoologist wife of Dr H. D. Thomas for whom *T. thomasi* Pitt and *T. dightoni* sp. nov. are named.

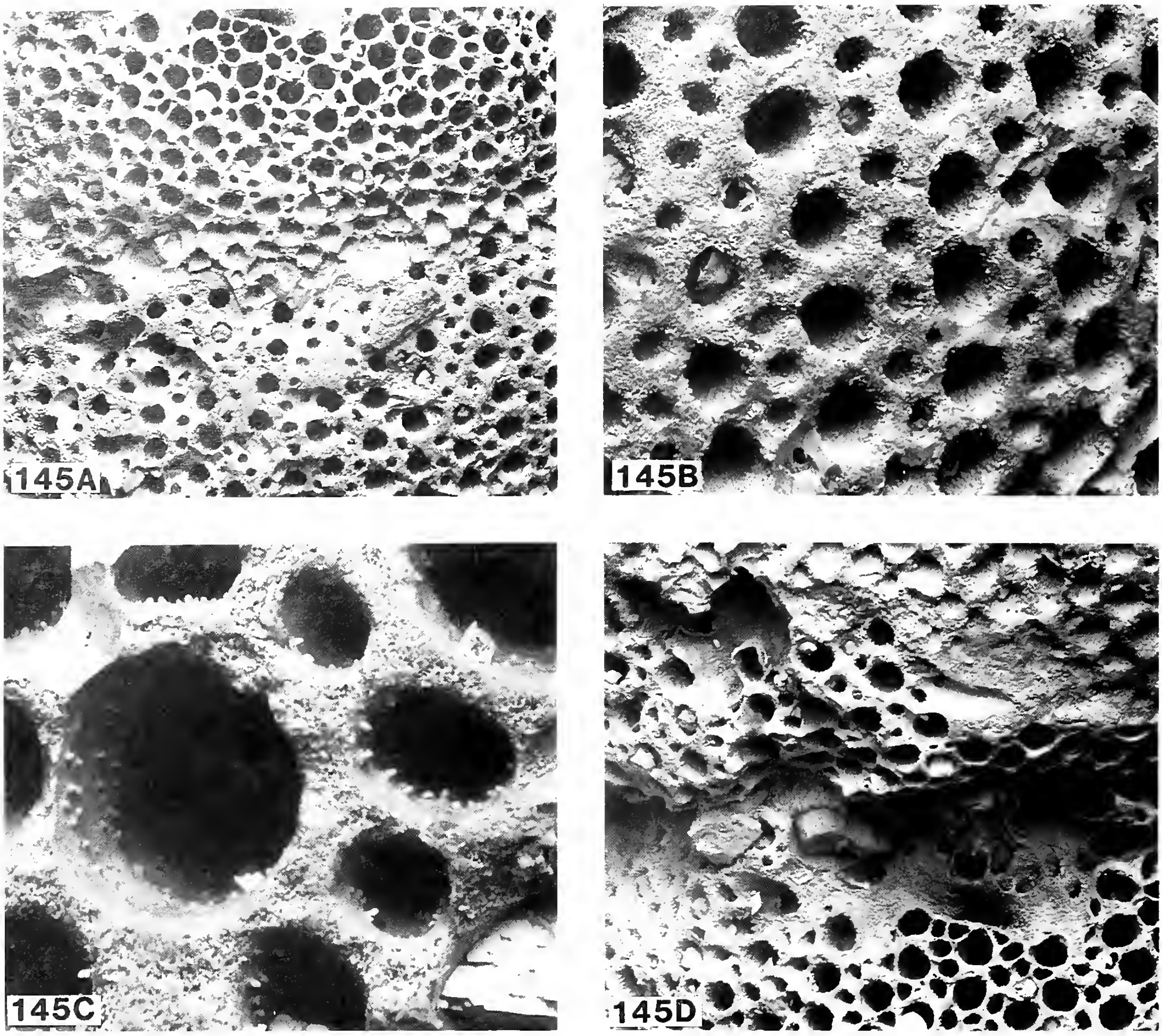


Fig. 145 *Tholopora dightoni* sp. nov., BM(NH) D57672, **holotype**; 145A, colony surface showing parts of two subcolonies, × 30; 145B, rows of autozooecia separated by kenozooecia, × 85; 145C, mural spines in autozooecia and kenozooecia, × 300; 145D, partly overgrown and broken gynozooecium, × 38; see also Fig. 144.

Description. Zoaria are short (Figs 146, 147A), generally less than 1 cm in height, and consist of a series of stacked bun-shaped subcolonies, sometimes bifurcating. Branches are typically 3–4 mm in diameter with annular constrictions between the subcolonies, each of which is about 0·9 mm in height. New subcolonies originate close to the centres of existing subcolonies and zooecial chambers may be continuous between parent and daughter subcolonies when seen in thin section.

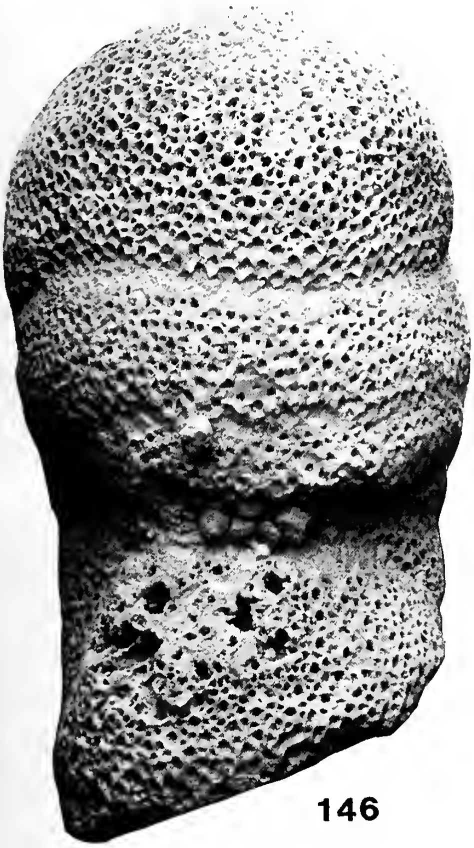
Autozooecia are variable in size and arranged in irregular ill-defined radiating uniserial rows (Fig. 147B) separated by smaller kenozooecia, also irregularly arranged and variable in size. Within each row successive autozooecia are not always contiguous but may be separated by kenozooecia (cf. *T. thomasi* and *T. dightoni*). No mural spines have been observed, but details of fine preservation are obscured by secondary crystals of calcite in available material.

The single brood chamber observed (Fig. 148B) is roughly circular in outline, about 1·6–2·0 mm in diameter, with autozooecia passing through the chamber to support the roof together with internal vertical septa. The ooeciostome is not recognizable.

In thin section zooecial walls have a cloudy, granular appearance without obvious laminations. Dark transverse bands may occur which resemble monilae but the walls are parallel-sided. Exozonal wall thickness attains 0·03 mm. Of common occurrence are thin, aborally-flexed diaphragms (probable subterminal diaphragms) located 0·2–0·3 mm proximal of the zooecial aperture. Distinction between autozooecia and kenozooecia is not obvious in thin section.

Measurements (measured from zooecia midway out from subcolony centres). TAM, 0·06–0·08 mm; KAM, 0·02–0·03 mm.

Remarks. *T. hastingsae* is distinguished from *T. thomasi* and *T. dightoni* by the smaller size of the zooecial apertures and the less regular arrangement of the autozooecia which do not form such distinct rows and are not connate.



146

Fig. 146 *Tholopora hastingsae* sp. nov., BM(NH) D55336, **holotype**, × 22; see also Fig. 148.

'holopora thomasi Pitt, 1949 Fig. 149

949 *Tholopora thomasi* Pitt: 154; pl. 5, figs 1a, b; pl. 6.

IOLOTYPE. BM(NH) D37291, Little Coxwell Pit, Pitt Colln.

'ARATYPES. BM(NH) D37292–3, Little Coxwell Pit, Pitt 'olln. A third paratype is in the Treacher Colln, University f Reading.

)THER MATERIAL. BM(NH) D47402, D55339, D55340, Little 'oxwell Pit, Cleevely Colln; D52160 (sample), D55121,)57699 (sample), D57700 (thin section & remnant), D57701 thin section), Little Coxwell Pit, Pitt Colln; D55341,)57697–8, Bowler's Pit, Thomas Colln; D55559, D57693–6, ittle Coxwell Pit, Thomas Colln; D55342, Little Coxwell Pit, Vise Colln; D55343, D57685–90, Little Coxwell Pit, Gaster 'olln.

)ESCRIPTION. Zoaria are typically short (up to 12 mm), with iick branches which divide occasionally. The holotype olony is unusual in having a greatly expanded distal part rmed by numerous closely-spaced branch divisions (Fig. 49A). Branches consist of a stack of bun-shaped subcolonies, ach about 1·5 mm in height. The axial zone of the sub-olonies comprises undifferentiated zooecia and is surrounded y a zone with well-defined, radiating uniserial rows of utozooecia separated by generally uniserial rows of kenozooecia. There can be as many as 50 radial rows of autozooecia in each subcolony.

Autozooecia have large rounded-polygonal apertures, those within a row being connate (Fig. 149B). Short mural spines can be seen within the apertures of well-preserved specimens (Fig. 149C).

Kenozooecial apertures are less than half the diameter of autozooecial apertures and are less rounded and more irregular in size. Short mural spines may be visible within kenozooecial apertures in slightly higher densities than in the autozooecia.

Brood chambers (Fig. 149D) have only been observed broken, lacking roof and ooeciopore. They are digitate in outline shape, with lobes parallel to the rows of kenozooecia, indented marginally by autozooecia.

In thin section the zooecial walls have a cloudy, granular appearance without distinct laminations. Transverse bands of darker material resemble monilae, but zooecial walls are apparently parallel-sided. Wall thickness increases markedly in the exozones of subcolonies where it may attain 0·06 mm. Basal, older subcolonies have thicker walls than younger subcolonies. Thin, aborally-flexed diaphragms are sporadically developed. Many zooecial chambers in the axial parts of subcolonies are continuous between succesive subcolonies, and budding by intrazooecial fission apparently contributed to the formation of new subcolonies.

MEASUREMENTS (measured from zooecia midway out from subcolony centres). TAM, 0·16–0·20 mm; KAM, 0·05–0·08 mm.

REMARKS. This is the commonest of the three species of *Tholopora* at Faringdon and is distinguished from the other two by the larger size of the autozooecia.

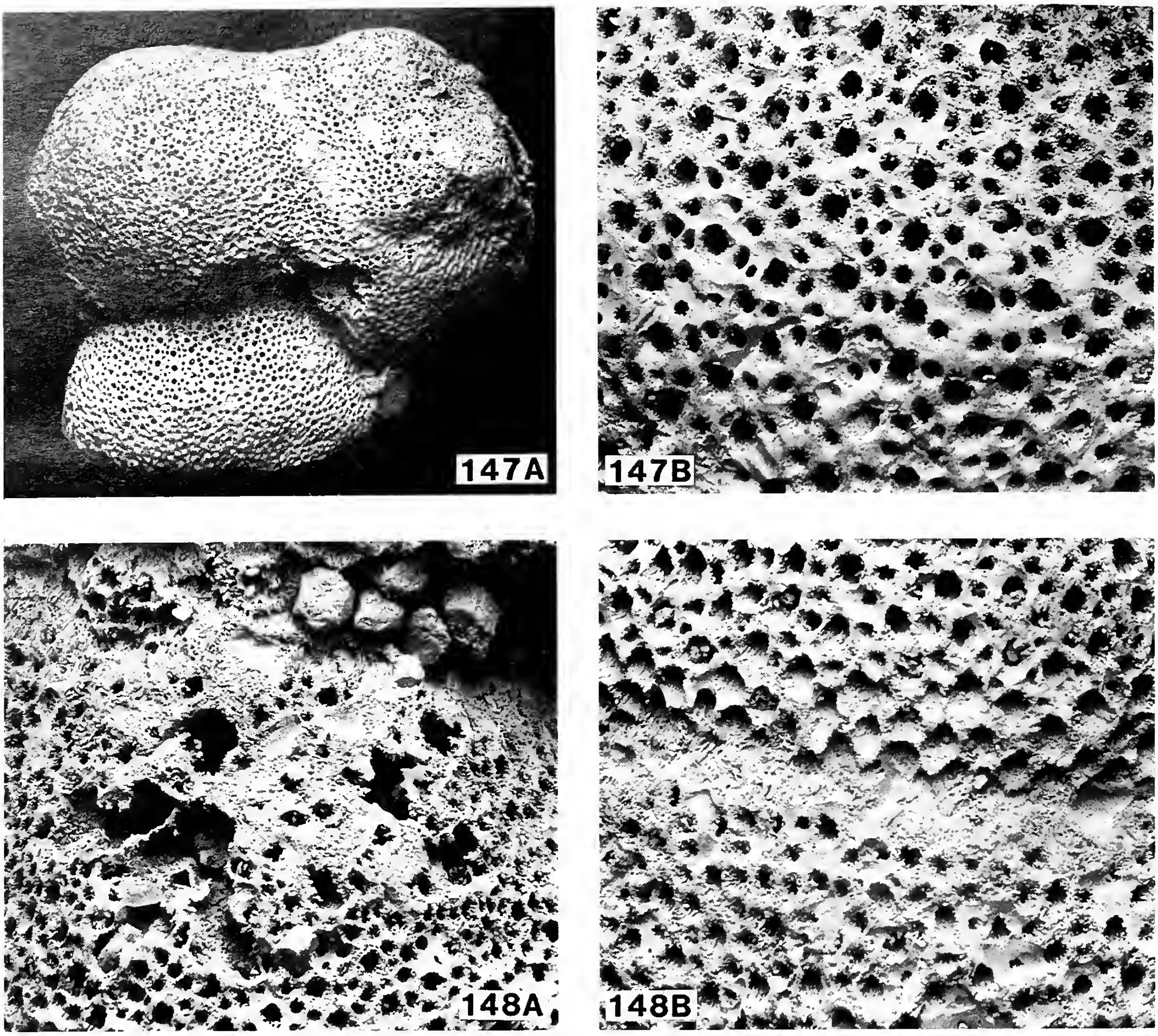
Suborder **CANCELLATA** Gregory, 1896
Family **HORNERIDAE** Gregory, 1899

Genus ***SIPHODICTYUM*** Lonsdale, 1849

TYPE SPECIES. *Siphodictyum gracile* Lonsdale, 1849, by monotypy; Atherfield Clay (Aptian), Isle of Wight.

REMARKS. The distinction between *Siphodictyum* and the well-known Tertiary to Recent genus *Hornera* Lamouroux, 1821 (see Mongereau, 1972), is not firmly established. The two genera share a vinculariiform colony morphotype with autozooecia opening on one side only of the branches, cancelli between the autozooecial apertures, and gynozooecia on branch reverse sides with roofs of calcified interior wall. Canu & Bassler (1926) removed *Siphodicytum* from the Family Horneridae, to which it had been assigned by Gregory (1899), and transferred it to the Family Ascosoeciidae because they wrongly thought that the gynozooecium was perforated by zooecial tubes. However, some other differences do exist between *Hornera* and *Siphodictyum*: in the type species of *Hornera*, *Hornera frondiculata* Lamouroux, the zooecia are arranged in distinct longitudinal rows; the presence of the subapertural pore described below for *Siphodictyum* has yet to be demonstrated in *Hornera*; and whereas *Siphodictyum* has a bushy colony-form, the branches of *Hornera* are generally arranged in planar fans.

As the type species of *Semicellaria* d'Orbigny, 1853 (= *Hemicellaria* d'Orbigny, 1850), *S. ramosa* d'Orbigny, is a subjective junior synonym of the type species of *Siphodictyum*, d'Orbigny's genus is placed in synonymy with Lonsdale's.



Figs 147–148 *Tholopora hastingsae* sp. nov. Fig. 147, BM(NH) D55120; 147A, bifurcating stem, × 10; 147B, autozooecia arranged crudely i rows, × 50. Fig. 148, BM(NH) D55336, **holotype**; 148A, poorly-preserved gynozooecium; 148B, edge of overgrowing subcolony, × 54; see als Fig. 146.

RANGE. Lower Cretaceous (Barremian to Aptian).

Siphodictyum gracile **Lonsdale, 1849** Figs 150–153

1847 *Cricopora gracile* Fitton: 302 (name only).
1849 *Siphodictyum gracile* Lonsdale: 94; pl. 5, figs 16–23.
1850 *Hemicellaria ramosa* d'Orbigny: 86.
1853 *Semicellaria ramosa* (d'Orbigny) d'Orbigny: 935; pl. 772, figs 11–14.
1899 *Siphodictyum gracile* Lonsdale; Gregory: 363; pl. 12, figs 14–15.
1926 *Siphodictyum gracile* Lonsdale; Canu & Bassler: 87; pl. 14, figs 14–21.
1926 *Siphodictyum irregulare* Canu & Bassler: 89; pl. 14, figs 1–11.
1971 *Siphodictyum gracile* Lonsdale; Walter & Busnardo: 96; pl. 7, figs 1–10.
1974 *Siphodictyum gracile* Lonsdale; Masse & Walter: 191; pl. 36, figs 2–3.
1975 *Siphodictyum gracile* Lonsdale; Walter *et al.*: 111; pl. 9, figs 10–11.
1975 *Siphodictyum irregulare* Canu & Bassler; McKinney: 72; pl. 3, fig. 1.
1977 *Siphodictyum gracile* Lonsdale; Walter: 328; pl. 1, fig. 2.
1979 *Siphodictyum gracile* Lonsdale; Walter & Clavel: 822; pl. 2, figs 5–7.
1981 *Siphodictyum gracile* Lonsdale; Voigt: 441; figs 1A–B.
1984 *Siphodictyum gracile* Lonsdale; Delamette & Walter: 34; pl. 11, figs 7, 9.

HOLOTYPE. BM(NH) 46804, Atherfield Clay (Aptian) Atherfield, Isle of Wight, Morris Colln.

OTHER MATERIAL. BM(NH) D55107, D55108, D55334 D57946–7, Little Coxwell Pit, Gaster Colln; D55109, D5533 (sample), D55255 (5), Little Coxwell Pit, Thomas Colln D37322–3, D52215 (sample), D55333 (sample), D5763

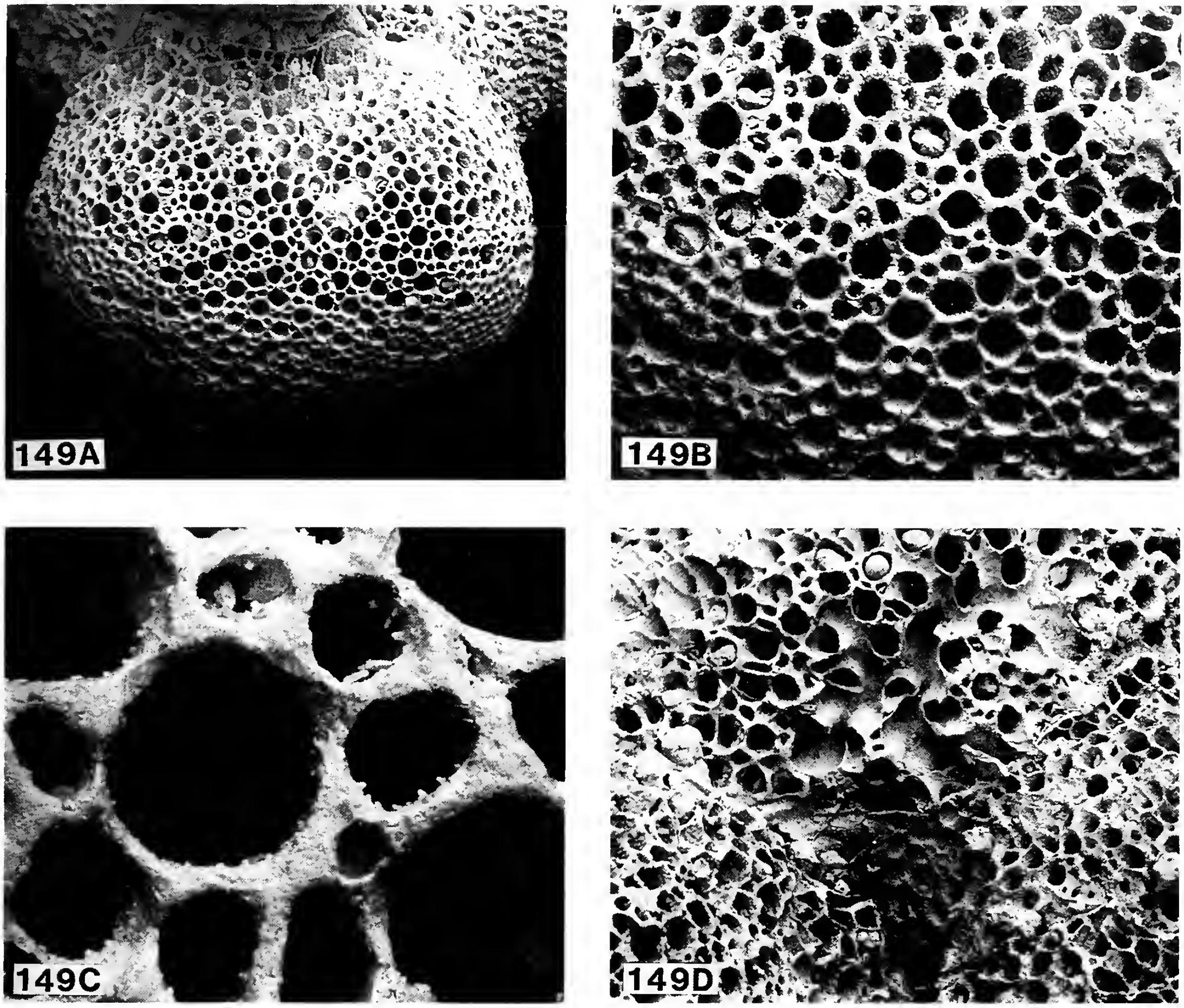


Fig. 149 *Tholopora thomasi* Pitt, BM(NH) D37291, holotype; 149A, × 16; 149B, autozooecia and kenozooecia, × 30; 149C, short mural spines visible within zooecial apertures, × 160; 149D, worn gynozooecium, × 22.

Little Coxwell Pit, Pitt Colln; D57639–41, Little Coxwell Pit, Elliott Colln; D57642, Davis Colln. USNM 69944 (including 3 thin sections also registered as 248243), syntypes of *S. irregulare* Canu & Bassler, 1926.

Description. Zoarium arborescent, of narrow (mean diameter *c.* 0·6 mm) cylindrical branches (vinculariiform), which bifurcate dichotomously; successive bifurcations usually occur in slightly different planes with the result that the colony is a 3-dimensional bush rather than a planar fan. Branch anastomoses are rare. The colony base is a slightly expanded cone.

Autozooecial apertures open on one side only of the branch (the obverse) and are arranged sometimes in transverse rows, sometimes in approximate quincunx (Fig. 150A). They are small, circular to slightly longitudinally elongate, and may have a gently raised rim (Fig. 150B). In exceptionally well preserved specimens, blunt mural spines may be visible within the apertures, and a minute 'subapertural pore' (*c.* 0·01–0·02 mm) can be observed just proximally of the aperture (Fig. 150C).

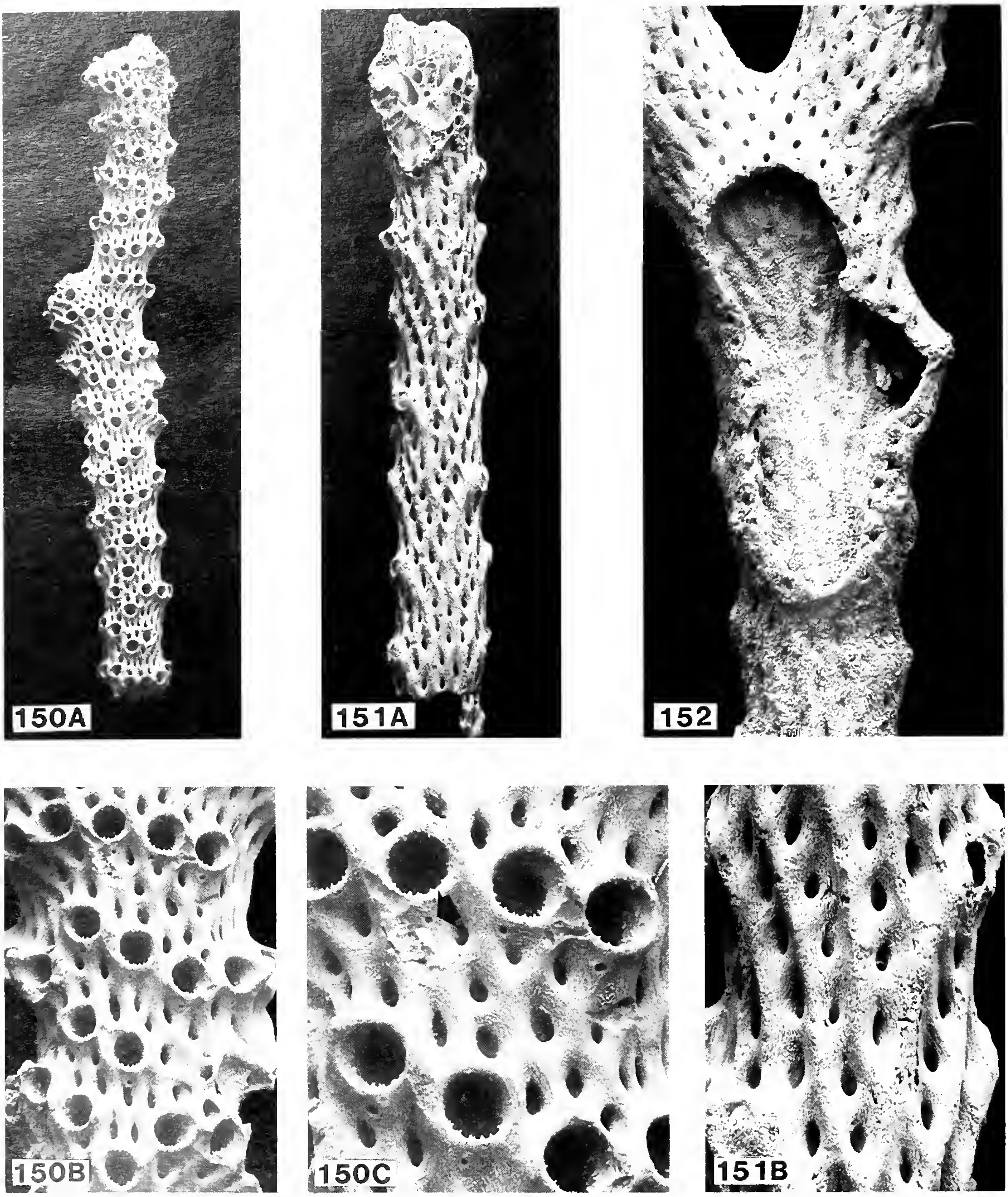
Cancelli occupy the reverse sides of branches (Fig. 151) and the areas between autozooecial apertures on the obverse sides of branches (Fig. 150C). They have small, thick-walled apertures, often rather longitudinally elongated and often funnel-shaped. The arrangement of cancelli on the branch obverse may be in longitudinal lines.

The gynozooecium (Fig. 152) is a longitudinally elliptical, bulbous swelling situated on the branch obverse which may bifurcate if positioned over a branch division. The roof of the gynozooecium is formed of porous apparent interior wall calcification resembling cancelli, and a calcified lamina forms the floor. The ooeciopore is distal, large and transversely elliptical.

In thin section (Fig. 153) branches are seen to have thin-walled endozones surrounded by exozones with thick, laminated walls.

Measurements. TAM, mean 0·06 mm; GDL, up to 0·40 mm; GW, up to 0·25 mm; LOSM, 0·04 mm; TOSM, 0·14 mm.

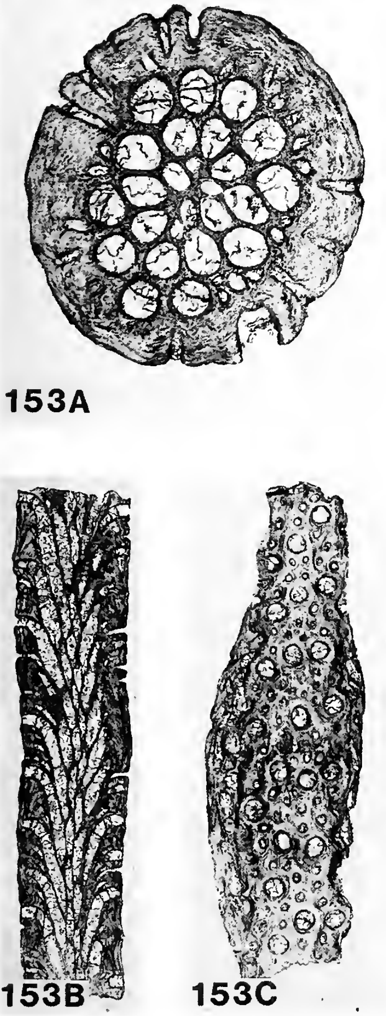
Remarks. Fitton's (1847) specific name for this species was later adopted by Lonsdale (1849) when validly describing the



Figs 150–152 *Siphodictyum gracile* Lonsdale. Fig. 150, BM(NH) D55107; 150A, obverse side of branch, × 23; 150B, × 64; 150C, detail showing subapertural pores (one is arrowed), × 130. Fig. 151, BM(NH) D57946; 151A, reverse side of branch, × 33; 151B, detail showing cancelli, × 90. Fig. 152, BM(NH) D57947, gynozooecium located on branch reverse and lacking a frontal wall, × 47.

species for the first time as *Siphodictyum gracile*. As Fitton merely mentioned the species without description, definition or indication, his citation does not constitute a valid publication of *gracile* because it fails to satisfy Article 12 of the Code of Zoological Nomenclature.

Lonsdale's type specimen (BMNH 46804) from the Atherfield Clay of the Isle of Wight is a large arborescent colony o closely-packed branches embedded in matrix. Branc diameter is a little greater than in most Faringdon specimen but zooecial characteristics appear identical. *S. irregular* Canu & Bassler does not differ significantly from *S. gracile* slight variations in the arrangement of apertures of the type



'ig. 153 *Siphodictyum gracile* Lonsdale, USNM 248243, syntype thin sections of *S. irregulare* Canu & Bassler; 153A, transverse section, × 70; 153B, longitudinal section, × 21; 153C, shallow tangential section, × 34.

ısed to distinguish *S. irregulare* are unsuitable for species liscrimination in *Siphodictyum*.

The slender branches of this species are common at Faringlon, and the species is widely distributed in the Barremian ınd Aptian of Europe. It is distinguished from the similar *aterocavea? intermedia* Canu & Bassler by the confinement f the autozooecial apertures to one side of the branches vhereas they occur on two sides in *L.? intermedia*.

Family PETALOPORIDAE Gregory, 1899

Genus *LATEROCAVEA* d'Orbigny, 1853

YPE SPECIES. *Laterocavea dutempleana* d'Orbigny, 1853, by ubsequent designation of Canu & Bassler, 1926; Albian of randpré.

EMARKS. *Laterocavea* is a cancellate genus characterized by slight flattening of the branches with autozooecia opening on both sides (cf. *Siphodictyum*, p. 133). Gregory (1899) regarded *Laterocavea* as a synonym of *Hemicellaria* d'Orbigny, 1850 (=*Semicellaria* d'Orbigny, 1853). However, the type species of *Hemicellaria, H. ramosa* d'Orbigny, has an 'eccentric bifoliate' colony-form (*sensu* McKinney 1986) with branches which possess a distinct upper surface, as in genera such as *Reticulipora* and the cystoporates *Goniocladia* and *Ramipora* (see Utgaard *in* Boardman *et al.* 1983).

RANGE. Aptian to Albian, ?Campanian; it is unclear whether a second, U. Cretaceous species, *L. punctata* (d'Orbigny) which was attributed by d'Orbigny (1850) to his genus, is really congeneric with *L. dutempleana*.

Laterocavea dutempleana d'Orbigny, 1853

Figs 154–156

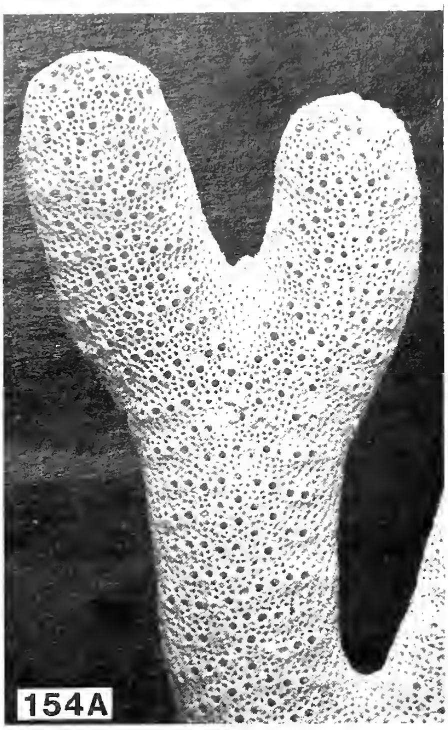
1853	*Laterocavea dutempleana* d'Orbigny: 933; pl. 772, figs 7–10.
1889	*Idmonea dutempleana* (d'Orbigny) Pergens: 350.
1899	*Hemicellaria dutemplei* (d'Orbigny); Gregory: 370.
1899	*Petalopora cunningtoni* Gregory: 376; pl. 12, figs 11–13.
1926	*Laterocavea dutempleana* d'Orbigny; Canu & Bassler: 85; pl. 15, figs 1–6.
1977	*Laterocavea dutempleana* d'Orbigny; Walter: 329; pl. 1, figs 3, 6.
1979	*Laterocavea dutempleana* d'Orbigny; Walter & Clavel: 821; pl. 2, figs 1, 3, 4, 10.
1981	*Laterocavea dutempleana* d'Orbigny; Voigt: 441; fig. 1c–d.

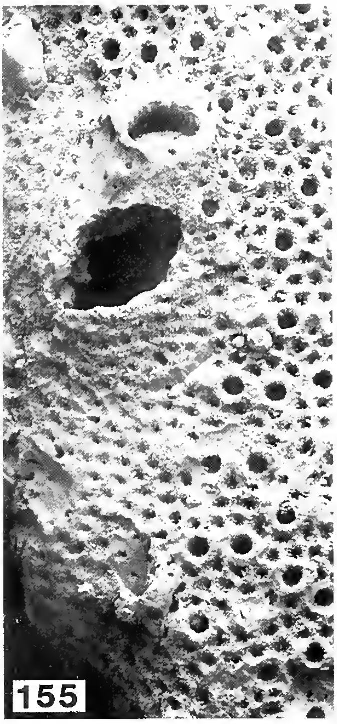
MATERIAL. BM(NH) D5130 (specimen and thin section), D7104, Cunnington Colln, figd syntypes of *Petalopora cunningtoni* Gregory (1899: pl. 12, figs 12 & 13 respectively); D55100, D55248, D55251 (3), D55252 (peel), D57644 (sample), D57709–10, D57948, Little Coxwell Pit, Pitt Colln; D55246 (sample), D55247 (sample), D57708 (6), Little Coxwell Pit, Thomas Colln; D55249 (sample), D55250, Little Coxwell Pit, Gaster Colln; D55253, Little Coxwell Pit, Cleevely Colln; D55254, collection and locality unknown.

DESCRIPTION. Zoarium erect, arborescent, with slightly compressed branches (Fig. 154A) which are ovate in transverse section, 1·5 to 1·8 mm wide. The colony base is a low cone of circular cross section. The surface of the base and proximal parts of the first branch are covered entirely with cancelli which are slit-like and aligned in vertical rows parallel to growth direction. Successive branch dichotomies are usually in the same plane as branch compression, and the two daughter branches of a dichotomy may bend towards one another until subparallel.

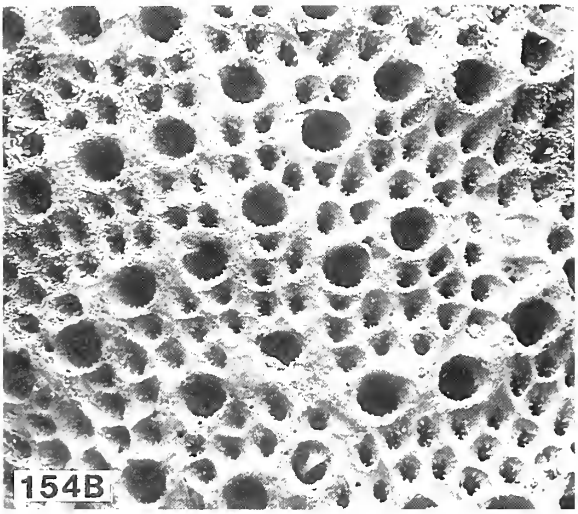
Autozooecia open on the two wide faces of the branches, their apertures arranged more-or-less in transverse rows (Fig. 154B), often with an offset along the midline of each face. Autozooecial apertures are small, circular or transversely elliptical, have a slightly raised rim and may be contiguous with laterally adjacent apertures in the same transverse row. Blunt mural spines are visible within the autozooecial apertures of well-preserved specimens (Fig. 154C).

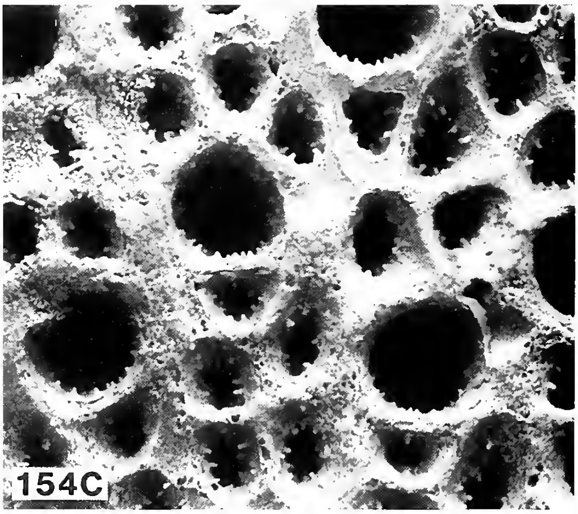
Cancelli occupy the areas between autozooecial apertures, the entire surface of the narrow edges of the branches, and the basal parts of colonies. They are small (*c.* 0·03 mm in diameter), rounded polygonal in outline shape, sometimes longitudinally elongate and funnel-like, tapering inwards


154A


155


156


154B


154C

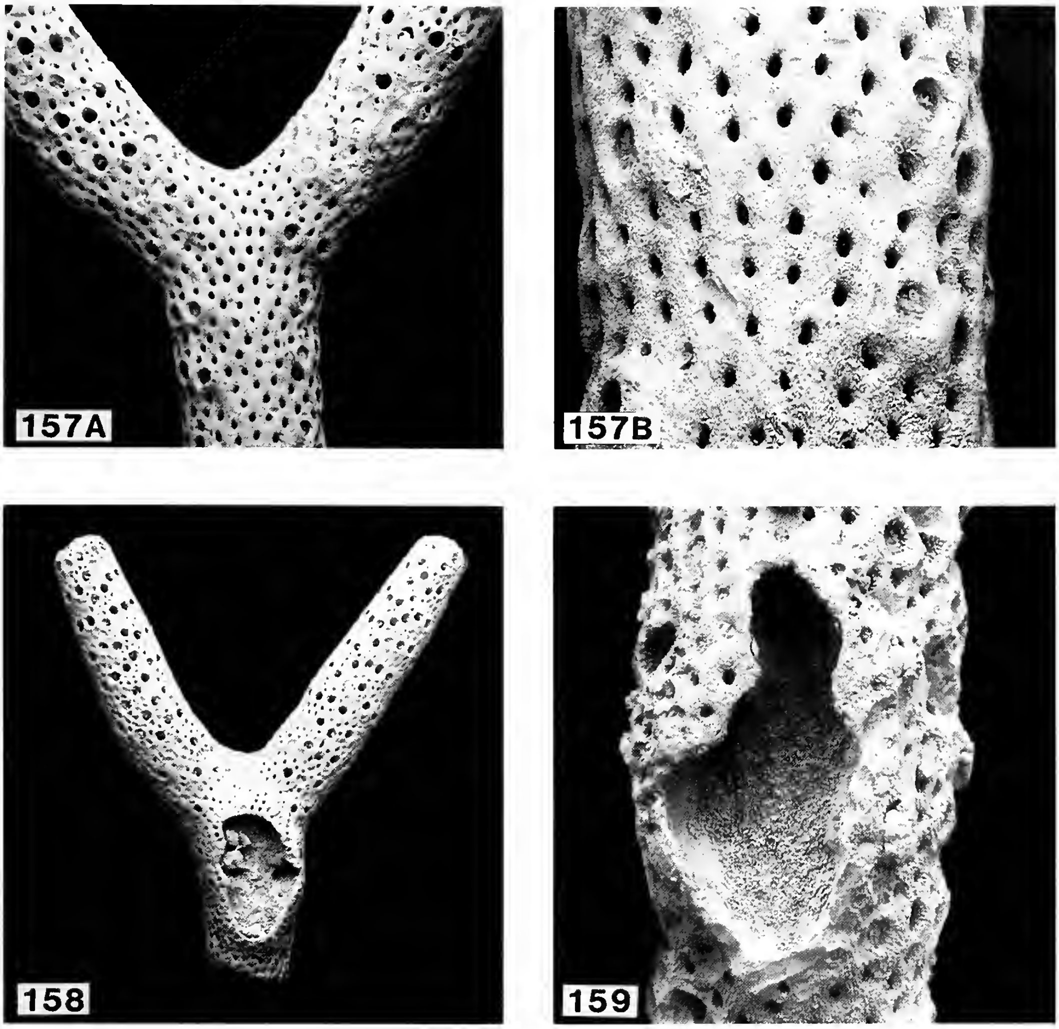
Figs 154–156 *Laterocavea dutempleana* d'Orbigny. Fig. 154, BM(NH) D57948; 154A, bifurcating branch with growth tips, × 15; 154B, autozooecia and cancelli, × 71; 154C, short mural spines visible within apertures of autozooecia and cancelli, × 210. Fig. 155, BM(NH) D55709 gynozooecium with well-preserved frontal wall and ooeciopore, × 39. Fig. 156, BM(NH) D55250, gynozooecium with abraded frontal wall, × 47.

from the colony surface. Blunt mural spines occur within the cancelli and are somewhat larger than those in the autozooecia (Fig. 154C).

Gynozooecia (Figs 155–156) are situated on the narrow faces of the branches or close to the edges of the broad faces. They are large and longitudinally elongate, form a slight swelling of the branch, and have a frontal wall composed apparently of cancelli which are smaller in size than normal cancelli. The floor of the gynozooecium (Fig. 156) appears to be formed of a calcified interior wall which is penetrated in one example (BM(NH) D55250) by a pore the size of an autozooecial aperture situated near the chamber edge abou mid-length; this may represent the proximal part of the fertil zooecium. The ooeciopore is located distally and is large transversely elongate and crescent-shaped owing to the occur rence of a curved internal platform which indents its proxima edge (Fig. 155).

Measurements. TAM, 0·05–0·06 mm; TPM, 0·08–0·10 mm GDL, up to 2·0 mm; GW, up to 1·0 mm; TOPM, 0·25 mm TOSM, 0·40 mm.

Remarks. *Laterocavea dutempleana* was first described fron



Figs 157–159 *Laterocavea? intermedia* Canu & Bassler. Fig. 157, BM(NH) D55102; 157A, bifurcating branch, × 26; 157B, alveoli, × 77. Fig. 158, USNM 69942a, **lectotype** (herein selected), bifurcating branch with worn gynozooecium, × 14. Fig. 159, BM(NH) D57937, worn gynozooecium, × 63.

the Albian of Grandpré. D'Orbigny's type specimen could not be located at the MNHN during May 1985, although a tablet (numbered 6027) bearing the appropriate label but with no specimen attached was found.

Gregory (1899) did not record *Laterocavea dutempleana* from Faringdon but described a new species, *Petalopora cunningtoni*, which is undoubtedly a junior synonym of *L. dutempleana*. There are 3 syntypes of *P. cunningtoni*, two from Faringdon (BM(NH) D5130, D7104) and one (BM(NH) D2301) in an argillaceous matrix from an unknown locality. BM(NH) D7104 is herein chosen as the lectotype of *P. cunningtoni*.

Laterocavea? intermedia Canu & Bassler, 1926

Figs 157–159

1926 *Laterocavea intermedia* Canu & Bassler: 86; pl. 13, figs 9–17.

1926 *Clausa cranei* Canu & Bassler: 79; pl. 17, figs 6–7.

LECTOTYPE. USNM 69942a, selected herein, the specimen figured by Canu & Bassler 1926: pl. 13, figs 16–17.

PARALECTOTYPES. USNM 69942b–k, the remaining syntypes, some of which were figured by Canu & Bassler (1926).

MATERIAL. BM(NH) D55249 (2), D55101 (3), D55102, Little Coxwell Pit, Gaster Colln; D55255, D55485, Little Coxwell Pit, Thomas Colln; D55256 (5), D55257, D55636, Little Coxwell Pit, Pitt Colln; D57643 (2), D57937, Little Coxwell Pit, Davis Colln; D55638, Little Coxwell Pit, Elliott Colln.

DESCRIPTION. Zoarium erect, vinculariiform (Figs 157A, 158), with narrow cylindrical branches, 0·6–0·9 mm in diameter. Autozooecia open on two opposite faces of the branch with longitudinal cancelli occupying the strips between. Branches bifurcate in the plane formed by joining the two autozooecial faces (i.e. at right angles to the plane formed by joining the two cancellate faces). Successive bifurcations are often in a plane at right angles to one another, the distribution of autozooecia and cancelli reversing after the division. The colony base is a slightly expanded cone with the surface and lower part of the stem composed of cancelli.

Autozooecial apertures are small, circular or slightly longitudinally elongated, and often arranged in transverse rows, adjacent apertures being connate. Apertural rims are slightly raised, and terminal diaphragms may occur. Well-preserved autozooecia reveal the presence of a minute subapertural pore just proximal of the aperture.

Cancelli occupy the branch surface between transverse rows of autozooecial apertures, and form the edge strips (Fig. 157B) and colony base. They are small (about 0·03 mm in diameter) and circular or a little longitudinally elongated.

The gynozooecium (Figs 158–159) is a bulbous, longitudinally elongate swelling developed on a cancellate branch face, bifurcating if coincident with a branch division, and with the edges occasionally digitate. Broken roofs, apparently formed of cancelli, reveal a calcified floor which in some cases contains an opening, midlength and close to the edge of the chamber, possibly representing the proximal part of the fertile zooecium. The ooeciopore is situated distally, and is large and transversely elongate.

MEASUREMENTS. TAM, 0·07–0·09 mm; GDL, 1·20–1·60 mm; GW, 0·40–0·45 mm; LOSM, 0·06 mm; TOSM, 0·18 mm.

REMARKS. Walter & Clavel (1979) regarded *L. intermedia* as a junior synonym of *Siphodicytum gracile* Lonsdale (see p. 134). The two species undoubtedly have many features in common, notably the subapertural pore and the overall form of the gynozooecium, but there appear to be consistent differences in the distribution of the cancelli (on the branch obverse in *S. gracile*, and on the two opposite lateral branch faces in *L.? intermedia*) and branching pattern (successive branch bifurcations being in subparallel planes in *S. gracile* but commonly in perpendicular planes in *L.? intermedia*). No colonies have been found of intermediate type or having a mixture of the characters of the two species.

Whereas the distribution of the cancelli favours assignment of the species to *Laterocavea* in the Family Petaloporidae, the presence of the subapertural pore suggests a closer relationship with *Siphodictyum* which is placed in the Family Horneridae. Pending a better understanding of familial concepts in cancellates, a conservative policy is adopted here and the species is questionably retained within *Laterocavea*.

This is a rare species at Faringdon and is apparently unknown elsewhere. It is distinguished from *L. dutempleana* by the distribution of the autozooecia and cancelli, the circular section of the branches and the right-angle branching pattern.

Family **CYTIDIDAE** d'Orbigny, 1854

Genus ***ECHINOCAVA*** d'Orbigny, 1854

TYPE SPECIES. *Ceriopora raulinii* Michelin, 1841, by monotypy; Albian of Grandpré, Belgium.

REMARKS. *Echinocava* is distinguished by the dendroid colony branches on which are situated raised autozooecial fascicles, approximately subcircular in outline, separated by areas of apparent cancelli.

D'Orbigny (1850) first described this genus as *Echinopora*, assigning to it only Michelin's (1841) species *Ceriopora raulinii* (as *Echinopora raulini*; deletion of the second 'i' in *raulinii* is an unjustified amendment of Michelin's original specific name). *Echinopora* d'Orbigny, 1850 is a junior homonym of *Echinopora* Lamarck, 1816; this homonymy was later (1854) recognized by d'Orbigny himself who proposed the replacement name *Echinocava* and redescribed for a second time Michelin's species from the Albian of Grandpré.

160

Fig. 160 *Echinocava raulinii* (Michelin), BM(NH) D55103, optical photograph of a colony branch, × 5·3.

Voigticytis Walter, 1986, type species *Cyrtopora campicheana* d'Orbigny, 1853 from the Valanginian of Ste Croix, Switzerland, is here regarded as a subjective junior synonym of *Echinocava*. The only important difference between the type species of the two genera appears to be the longitudinal ridges formed by the walls of the cancelli in *V. campicheana*.

The presence of cancelli together with brood chambers roofed by interior wall (Walter 1986: pl. 9, fig. 6) implies that *Echinocava* belongs to the Suborder Cancellata.

RANGE. Valanginian to Albian.

Echinocava raulinii (Michelin, 1841) Figs 160–163

1841	*Ceriopora raulinii* Michelin: 2; pl. 1, figs 7a, b.
1850	*Echinopora raulini* (Michelin) d'Orbigny: 141.
1854	*Echinocava raulini* (Michelin) d'Orbigny: 1013; pl. 788, figs 7–8.
1883	*Ceriopora (Echinocava) raulini* Michelin; Keeping: 139.
1926	*Plethopora aptensis* Canu & Bassler: 53; pl. 7, figs 3–4.
1974	*Echinocava raulini* (Michelin); Masse & Walter: 194; pl. 788, figs 7–8.
1981	*Plethopora aptensis* Canu & Bassler; Voigt: 441, fig. 1g.

1984 *Echinocava raulini* (Michelin); Delamette & Walter: 35; pl. 5, fig. 5.

1984 *Plethopora* cf. *aptensis* Canu & Bassler; Delamette & Walter: 35; pl. 5, fig. 7.

MATERIAL. BM(NH) D52195 (3), D55306, Little Coxwell Pit, Pitt Colln; D55103, D57727 (3 thin sections), D57949–50, Little Coxwell Pit, Thomas Colln; D55301, Little Coxwell Pit, Elliott Colln; D57652–5, Davis Colln. USNM 69903, 5 syntypes of *Plethopora aptensis* Canu & Bassler, 1926. OUM K.82, K.83, Davey Colln.

DESCRIPTION. Zoarium of thick dendroid branches (Figs 160–161), occasionally bifurcating, astogenetically variable in diameter (1·5–6 mm), with blunt rounded growth tips. The autozooecia are in fascicles (Fig. 163A), about 1 mm in diameter, subcircular in outline and projecting above the general level of the colony surface as rounded mamelons; the remainder of the colony surface is covered with cancelli (Fig. 162).

Autozooecial apertures are polygonal and increase in size towards the centre of the fascicle. Outer parts of autozooecia are directed distally up the branch.

Cancelli have small funnel-shaped, subcircular apertures and thick walls (Fig. 163B).

Thin sections show that the autozooecia are long, slender tubes budded within branch endozones, whereas cancelli are very short tubes budded close to the branch surface within the exozone. No diaphragms have been observed. The microstructure of the zooecial wall is amorphous and cloudy in appearance without distinct lamination, but the thick walls of the kenozooecia have laminations subparallel to the colony surface.

An apparent brood chamber is present on the proximolateral side of a fascicle in BM(NH) D57949 (Fig. 163C). It is a convex swelling roofed by cancellate interior wall. A hole within the structure may be a broken and enlarged ooeciopore.

MEASUREMENTS. TAM (at centre of fascicle), *c.* 0·12 mm; cancelli diameter, 0·02–0·06 mm.

REMARKS. This is a comparatively rare species at Faringdon which was described as *Plethopora aptensis* by Canu & Bassler (1926). However, to judge by the figures of Michelin (1841), *P. aptensis* is a junior synonym of Michelin's species *Ceriopora raulinii* from the Albian of Grandpré. Unfortunately, Michelin's types appear to be lost; they were not mentioned by Walter (1975) in his revision of Albian and Cenomanian bryozoans from the Michelin Collection in the MNHN. *E. raulini* is recorded also from the Barremian and Aptian of SE France (Masse & Walter 1974; Delamette & Walter 1984), and Aptian of Upware, Cambridgeshire (Keeping 1883).

Available material from Faringdon is often worn. In extreme cases of wear, the autozooecial fascicles may be hollowed out and left as depressions on the colony surface (cf. Delamette & Walter 1984: pl. 5, fig. 5). This pattern of wear, which results in colonies with a coral-like appearance, presumably reflects the thicker calcification of the surrounding cancelli.

161

ig. 161 *Echinocava raulinii* (Michelin), USNM 69903a, syntype of *Plethopora aptensis* Canu & Bassler, × 22; see also Fig. 162.

?Suborder **RECTANGULATA** Waters, 1887
?Family **LICHENOPORIDAE** Smitt, 1866

Genus ***PARACRESCIS*** nov.

TYPE SPECIES. *Paracrescis boardmani* sp. nov., Faringdon Sponge Gravel, Faringdon, Oxfordshire. See p. 142.

DIAGNOSIS. Colony encrusting, unilamellar or multilamellar, maculate; apertures of autozooecia and apparent alveoli widely spaced, separated by areas of pustulose calcification; maculae lack autozooecial apertures; pseudolunaria may sharply indent outline shape of autozooecial apertures, especially close to maculae; brood chamber cavernous.

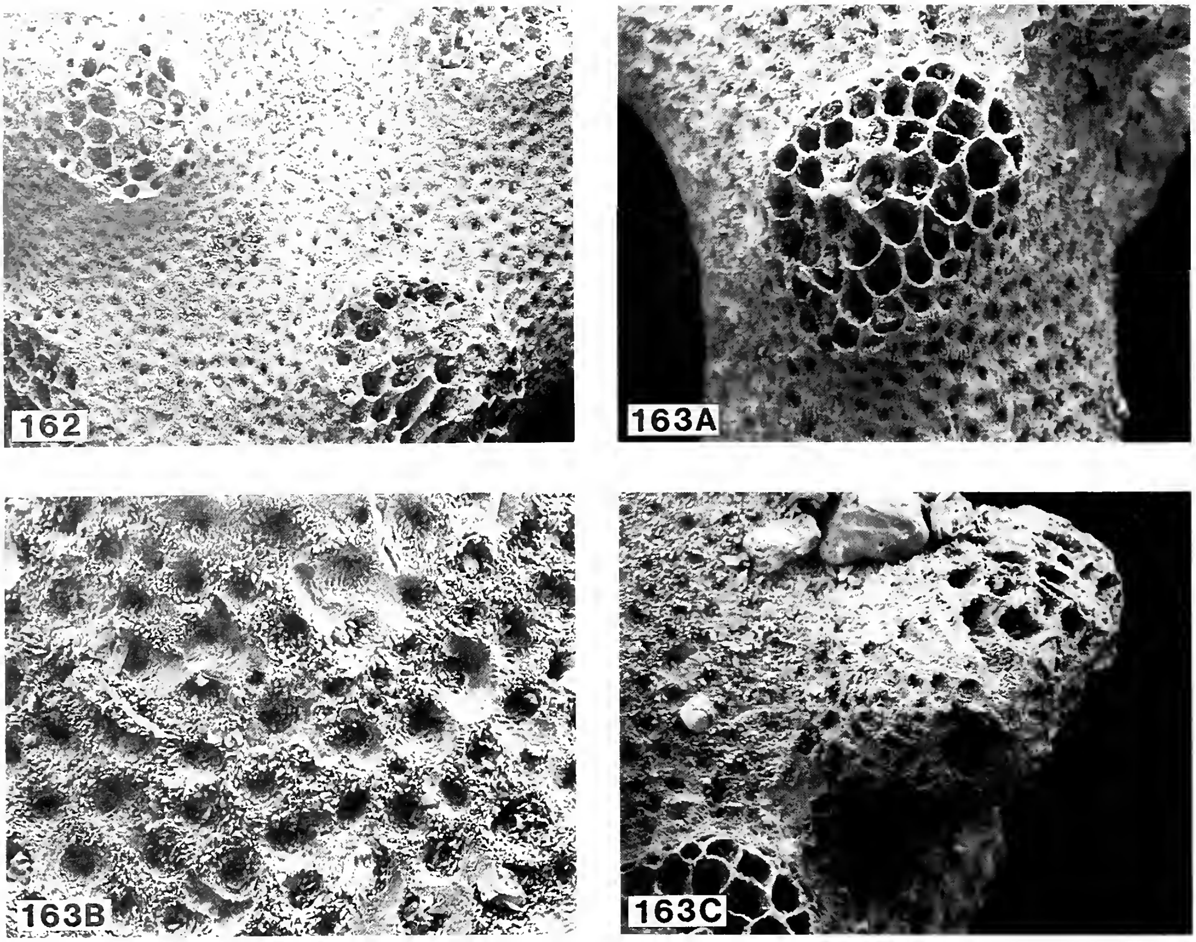
NAME. Somewhat like *Crescis*.

REMARKS. This new monospecific genus is characterized particularly by the wide areas of pustulose calcification which separate the apertures on the colony surface.

In the presence of pseudolunaria, *Paracrescis* resembles *Semicrescis* d'Orbigny whose type species is *Semicrescis tubulosa* d'Orbigny, 1854 from the Upper Cretaceous of France. External morphology in *S. tubulosa* has not been properly illustrated, but Boardman (1984: fig. 9C–D) has figured thin sections prepared from the type specimen. Boardman's tangential section depicts autozooecia with well-defined pseudolunaria. However, the large apertures are more closely spaced than in *P. boardmani*, and there is no indication of a wide expanse of pustulose calcification between apertures.

Crescis d'Orbigny is represented by one species, *C. dumetosa* (Lamouroux, 1821) from the M. Jurassic (see Walter 1970). This also has autozooecia with pseudolunaria but lacks the extensive development of pustulose calcification found in *Paracrescis*.

The pustulose calcification and pseudolunaria present in



Figs 162–163 *Echinocava raulinii* (Michelin). Fig. 162, USNM 69903a, × 40; see also Fig. 161. Fig. 163, BM(NH) D57949; 163A, autozooecial fascicle, × 39; 163B, alveoli between fascicles, × 102; 163C, possible broken brood chamber attached to a fascicle, × 48.

Paracrescis are features typifying lichenoporid rectangulates among living cyclostomes. However, the affinity of *Paracrescis* with the Lichenoporidae is difficult to demonstrate in the absence of well-preserved brood chambers. The brood chambers of lichenoporids are roofed by highly perforate interior walls (see Hayward & Ryland 1985). A second possibility is that *Paracrescis* is more closely related to the cerioporine cyclostomes; brood chambers in the similar genus *Crescis* appear to be roofed by pseudoporous exterior wall. Finally, on the basis of the lunaria/pseudolunaria and extrazooidal vesicles, Boardman (1984) believed *Semicrescis*, in which brood chambers are also unknown (E. Voigt, personal communication 1987), to be closely related to the Cystoporata, a stenolaemate order more usually regarded as exclusively Palaeozoic in its distribution.

Paracrescis is here questionably assigned to the Family Lichenoporidae of the Suborder Rectangulata. Accordingly, the small apertures between the autozooecia are labelled as ?alveoli rather than kenozooecia as they would be if *Paracrescis* were assigned to the Cerioporina.

RANGE. Aptian.

Paracrescis boardmani sp. nov. Figs 164–165

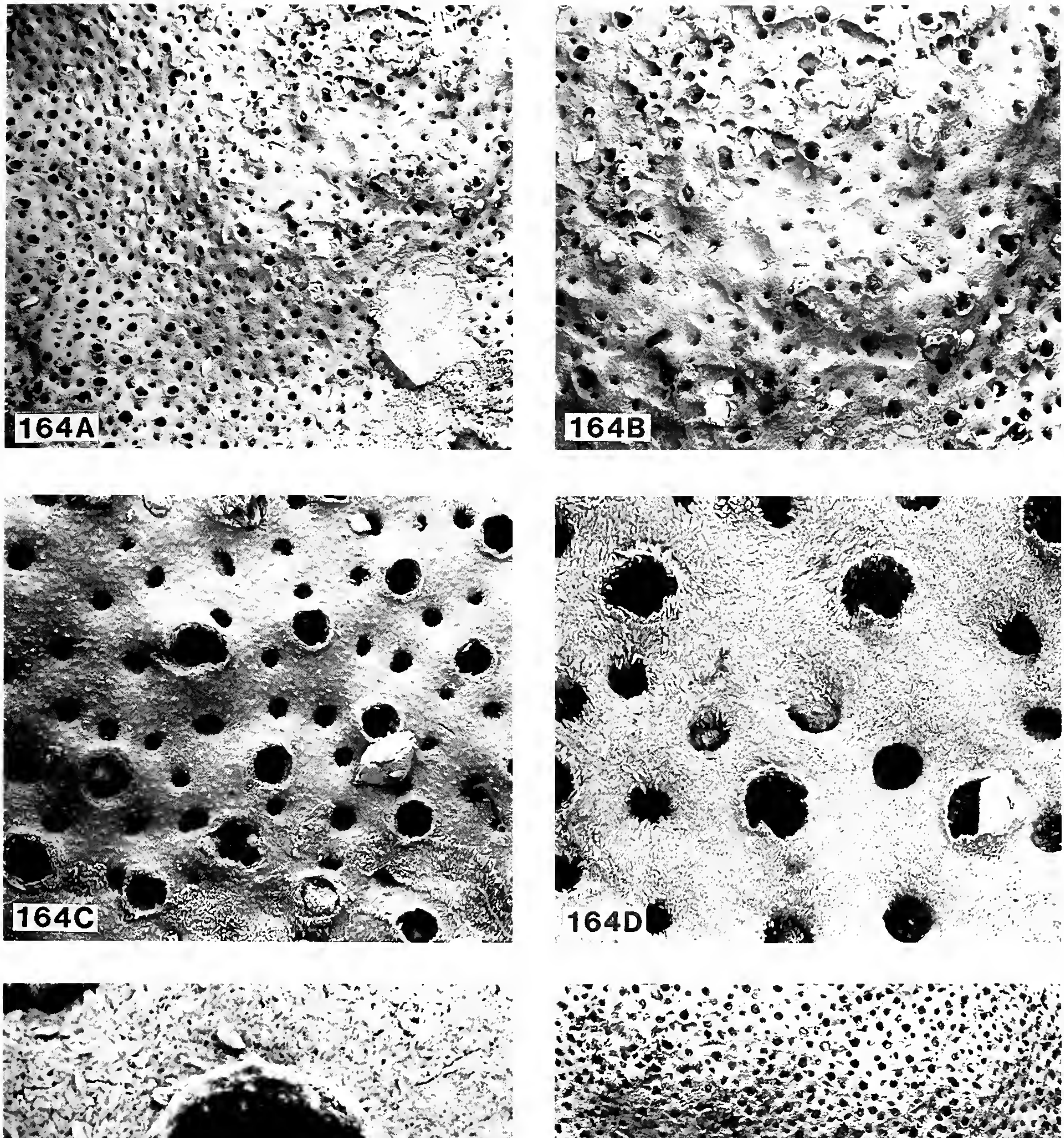
HOLOTYPE. BM(NH) D57711 (specimen and thin section), Little Coxwell Pit, Pitt Colln.

PARATYPES. BM(NH) D57712–3, Little Coxwell Pit, Davis Colln; D58207, west face of Badbury Hill, Faringdon, Pitt Colln.

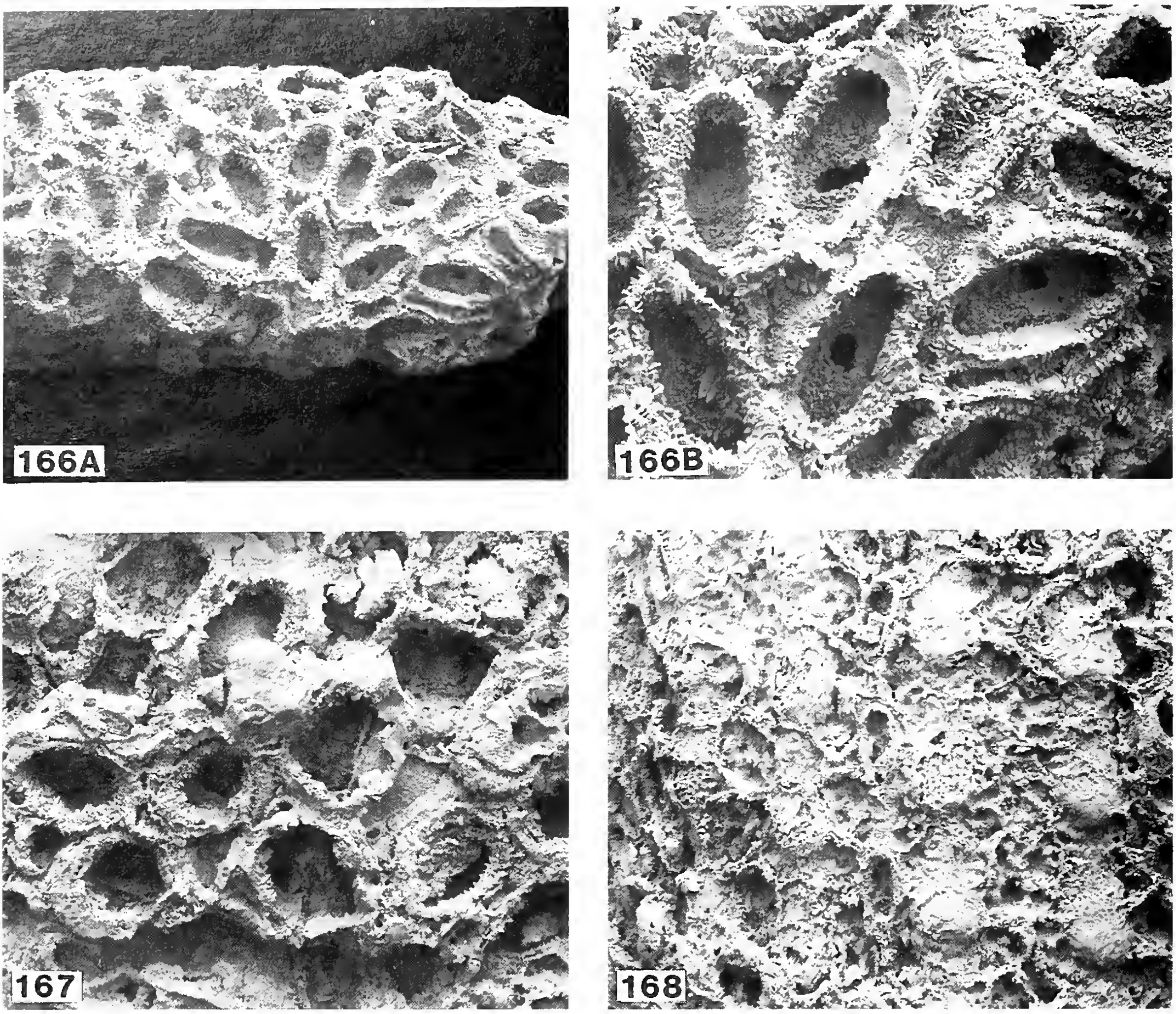
NAME. For R. S. Boardman, in recognition of his major contributions to the study of stenolaemate bryozoans.

DESCRIPTION. Zoarium encrusting, multilamellar with wide spaces often present between successive zoarial layers. The colony surface bears distinct maculae raised as monticules (Figs 164A, 165) and recognizable by their lack of autozooecial apertures and widely spaced ?alveoli. New layers seemingly originate as overgrowths on the flanks of maculae (Fig. 164B). Wide expanses of calcified interior wall, ornamented by small tubercles, occupy the colony surface between autozooecial apertures and ?alveoli (Fig. 164C).

Autozooecial apertures are very small, tending to be larger adjacent to the maculae (Fig. 164C), subcircular to elliptical in shape, with a narrow raised rim which is occasionally



gs 164–165 *Paracrescis boardmani* sp. nov. Fig. 164, BM(NH) D57711, **holotype**; 164A, maculum (top right) and surrounding intermacular area, × 22; 164B, maculum with developing overgrowth (top), × 39; 164C, zooecia and ?alveoli at edge of maculum (note tubercles ornamenting walls), × 86; 164D, zooecial apertures and ?alveoli, × 170; 164E, autozooecial aperture with well-developed pseudolunarium, × 550. Fig. 165, BM(NH) D57712, worn, mammilate colony surface, × 18.



Figs 166–168 *Charixa lhuydi* (Pitt). Fig. 166, BM(NH) D55068; 166A, × 39; 166B, detail of cement encrusted zooecia, × 104. Fig. 167, BM(NH) D54167, typical irregular arrangement of zooecia, × 50. Fig. 168, BM(NH) D54191, part of a worn colony encrusting an echinoid spine, showing a row of three caudate zooecia following a vertical groove in the spine (centre), × 34.

developed into a pseudolunarium (Fig. 164D, E) sharply indenting the proximal edge of the aperture, particularly in zooecia close to maculae. The widely spaced apertures are arranged more-or-less in quincunx in intermacular areas.

Apparent alveoli (Fig. 164D) have small, sunken apertures with inwardly-sloping sides, and are about 0·02–0·03 mm in diameter.

Brood chamber, only observed fractured in one poorly-preserved specimen (D58207), is cavernous and is pierced by autozooecia which apparently support the roof.

In tangential section the zooecial walls are thick, and indistinctly laminated or granular in appearance, with clearer linings visible in some of the autozooecia.

MEASUREMENTS. LAM, mean 0·06 mm; TAM, mean 0·05 mm.

REMARKS. *P. boardmani* is clearly distinguished from other early Cretaceous cyclostomes by the pustulose frontal calcification and pseudolunaria. There is a slight resemblance to the Valanginian species *Reptocavea rugosa* d'Orbigny, 1853, revised by Cotillon & Walter (1965; see also Walter 1972, Walter *et al.* 1975) as *Petalopora rugosa* (d'Orbigny), but this lacks these two characteristic features, and has autozooecial apertures about twice the size of those in *P. boardmani*.

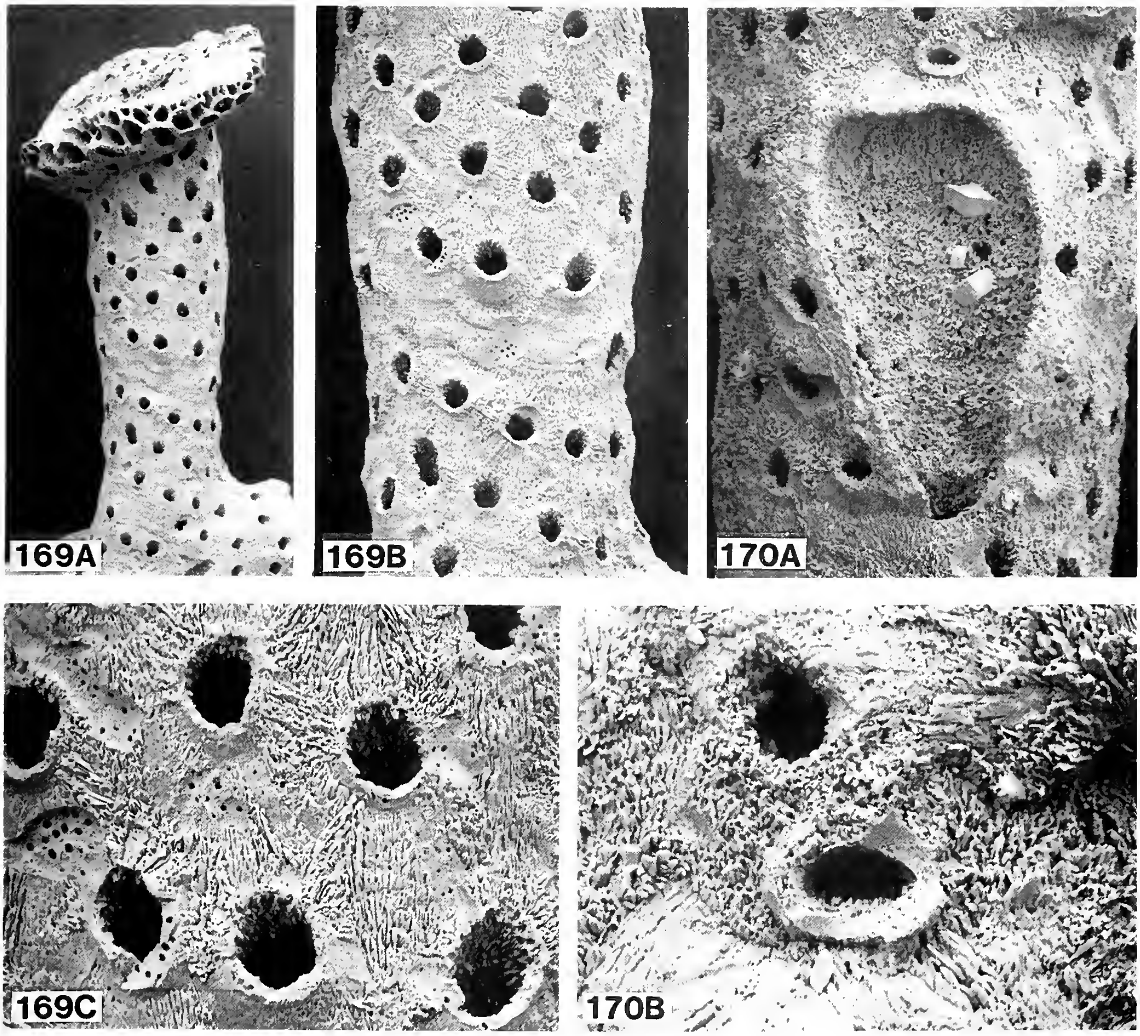
Only four specimens are known of *P. boardmani*. The holotype is a small colony encrusting a branch of an erect cyclostome, while one of the paratypes (BM(NH) D57712) is a large, hollow, flabellate colony which apparently encrusted an erect soft-bodied organism.

Class **GYMNOLAEMATA** Allman, 1856
Order **CHEILOSTOMATA** Busk, 1852
Suborder **ANASCA** Levinsen, 1909

Genus ***CHARIXA*** Lang, 1915

TYPE SPECIES. *Charixa vennensis* Lang, 1915, by original designation; Albian, Dorset.

REMARKS. The genus *Charixa* is used in accordance with



Figs 169–170 *Collapora hillmeri* sp. nov. (p. 87). Fig. 169, BM(NH) D58209; 169A, branch with flattened attachment structure at the distal end, × 20; 169B, band of long autozooecia, × 42; 169C, autozooecia, × 140. Fig. 170, BM(NH) D58208, **holotype**; 170A, gynozooecium with abraded frontal wall, × 55; 170B, ooeciopore with autozooecial aperture above, × 225.

Taylor (1986*b*) for primitive anascans with irregularly pluriserial colonies and zooecia which have a simple morphology and either lack or have sporadically-developed spine bases.

RANGE. Aptian (?Barremian) to Albian (? Campanian).

Charixa lhuydi (Pitt, 1976) Figs 166–168

1976 *'Membranipora' lhuydi* Pitt: 65; pl. 1, figs A–D.
1986*b* *Charixa lhuydi* (Pitt) Taylor: 203; figs 4, 5.

HOLOTYPE. BM(NH) D52494, Little Coxwell Pit, Pitt Colln.

PARATYPE. BM(NH) D52495, Little Coxwell Pit, Pitt Colln.

OTHER MATERIAL. BM(NH) D54190–200, Hinde Colln; D55067, Little Coxwell Pit, Davis Colln; D55068, Little Coxwell Pit, Elliott Colln.

DESCRIPTION. Colonies are encrusting and comprise irregular pluriserial patches of zooecia (Fig. 166A) which sometimes show multilamellar overgrowth. Zooecial orientations and budding positions are difficult to ascertain in the poorly-preserved material which is available. However, in one specimen a line of caudate autozooecia (Fig. 168) appears to bud distolateral non-caudate autozooecia of the type more typical of the species.

Autozooecia are usually elliptical in outline (Fig. 168B) and have a slight proximal gymnocyst. Rarely, autozooecia are pyriform and have a caudate proximal gymnocyst about half the length of the zooecium. In the holotype, autozooecial length averages 0·44 mm and width 0·33 mm. Opesiae are elongate elliptical and occupy most of the frontal surface of the majority of autozooecia. Cryptocysts are usually obscured by calcite cement but appear to be steeply sloping and seem to be pustulose. Unequivocal closures and regenerations have not been observed.

Communication pores are present as windows in vertical walls (see Pitt 1976: pl. 1, fig. D), but the expected presence of pore chambers has not been confirmed in this poorly-preserved material.

Some of the irregular spaces between autozooecia appear to be occupied by kenozooecia with extensive opesiae. These were perhaps misidentified by Pitt (1976) as broken ovicells. Avicularia and unequivocal ovicells are absent. The ancestrula is unknown.

MEASUREMENTS. Zooecial length 0·36–0·45 mm, mean 0·41 mm; zooecial width 0·20–0·35 mm, mean 0·25 mm.

REMARKS. This is the only cheilostome species known from Faringdon, and one of relatively few early Cretaceous cheilostomes described from anywhere in the world (Taylor 1986*b*). Since Pitt's (1976) original description of this species several additional specimens have become available, but unfortunately these share the poor preservation of the holotype and paratype. A considerable growth of calcite cement obscures surface details, and several colonies are abraded (e.g. Fig. 167). However, the finding of a colony with a line of caudate autozooecia (Fig. 168) prompts assignment of the species to *Charixa* Lang, 1915 (type species *C. vennenensis* from the Albian of Dorset). These caudate autozooecia follow a furrow in the echinoid spine encrusted by the colony. Their distolateral buds appear to be non-caudate autozooecia of the kind which predominate in *C. lhuydi* colonies. By comparison with *Spinicharixa dimorpha* (see Taylor 1986*b*), it is thought that the caudate autozooecia represent an initial runner-like growth across the substrate.

With one exception, all known specimens encrust regular echinoid spines. Colonies often occupy the entire circumference of the spine and are usually absent from the collar region. Spines of Recent echinoids are frequently fouled by epizoans (including bryozoans) while the echinoid is still alive (Mortensen 1928: 27), but remain free of encrusters on the collars of the spines where muscles attaching the spine to its base are situated. Therefore, it appears possible that *C. lhuydi* was a life associate of echinoids, though the single colony (D55068) encrusting an erect branch of the cyclostome *Meliceritites* shows that the association was not entirely obligatory for *C. lhuydi*.

ACKNOWLEDGEMENTS. We are grateful to the late Drs H. D. Thomas and A. B. Hastings who originally encouraged one of us (L. J. P.) to study the bryozoan fauna of the Faringdon Sponge Gravel. Curators in the following museums kindly permitted us to examine and borrow material: Drs A. H. Cheetham and R. S. Boardman (Smithsonian Institution), Dr E. Buge (Muséum National d'Histoire Naturelle, Paris), Dr D. Decrouez (Muséum d'Histoire Naturelle, Geneva), the late Mr J. M. Edmonds (Oxford University Museum), Mr A. Morter (British Geological Survey), the late Mr A. Brighton and Dr D. Price (Sedgwick Museum, Cambridge), and the late Prof. H. L. Hawkins and Dr R. Goldring (University of Reading). Professor E. Voigt (Universität Hamburg) was generous in his advice on Cretaceous bryozoans. We are grateful to Andrew Butterworth who worked as a vacation student at the BM(NH), completing a short project on the ecology of erect bryozoans from Faringdon, and curating part of the collections. Assistance with SEM work was kindly provided by Ms A. J. Faulkner, Ms S. Barnes, Mr D. Claugher and Mr J. Spratt. The work of the staff of the Photographic Unit at the BM(NH), especially Mr N. Fletcher, is greatly appreciated.

REFERENCES

Arkell, W. J. 1947. *Geology of Oxford*. 267 pp. Oxford.

Audoin, V. 1826. Explication sommaire des planches de Polypes de l'Égypte et de la Syrie, publiées par Jules-César Savigny. *In: Description de l'Égypte, Histoire naturelle*, **1** (4): 225–244. Paris.

Balavoine, P. 1958. Nouvelle contribution a l'étude des Bryozoaires de la région de Dinard et de Saint-Malo. *Bull. Lab. marit. Dinard*, **43**: 52–68.

Balson, P. S. & Taylor, P. D. 1982. Palaeobiology and systematics of large cyclostome bryozoans from the Pliocene Coralline Crag of Suffolk. *Palaeontology*, London, **25**: 529–554.

Bassler, R. S. 1935. Bryozoa. *In* Quenstedt, W. (ed.), *Fossilium Catalogue I: Animalia*, 's-Gravenhage, **67**. 229 pp.

—— 1953. Bryozoa. *In* Moore, R.C. (ed.), *Treatise on Invertebrate Paleontology* G. 253 pp. Lawrence, Kansas.

Blainville, H. M. D. de 1830. Zoophytes. *In: Dictionnaire des Sciences naturelles*. 631 pp. Paris.

Boardman, R. S. 1984. Origin of the post-Triassic Stenolaemata (Bryozoa): a taxonomic oversight. *J. Paleont.*, Lawrence, **58**: 19–39.

—— *et al.* 1983. Bryozoa. *In* Robison, R. A. (ed.), *Treatise on Invertebrate Paleontology* G (revised) (1). 625 pp. Lawrence, Kansas.

Borg, F. 1933. A revision of the Recent Heteroporidae (Bryozoa). *Zool. Bidr. Uppsala*, **14**: 253–394.

—— 1944. The stenolaematous Bryozoa. *In* Bock, S. (ed.), *Further Zoological Results of the Swedish Antarctic Expedition 1901–1903*, **3** (5): 1–276. Stockholm.

Bridges, P. H. 1982. Ancient offshore tidal deposits. *In* Stride, A. H. (ed.), *Offshore tidal sands*: 172–192. London.

Bronn, H. G. 1825. *System der urweltlichten Pflanzenthiere durch Diagnose, Analyse und Abbildung der Geschlechter erlautert* .... [&c.]. 47 pp., 7 pls. Heidelberg.

Brood, K. 1972. Cyclostomatous Bryozoa from the Upper Cretaceous and Danian in Scandanavia. *Stockh. Contr. Geol.*, Stockholm, **26**: 1–464.

—— 1975. Cyclostomatous Bryozoa from the Silurian of Gotland. *Stockh. Contr. Geol.*, Stockholm, **28**: 45–196.

Buge, E. & Voigt, E. 1972. Les *Cellulipora* (Bryozoa, Cyclostomata) du Cenomanien français et le famille des Celluliporidae. *Geobios*, Lyon, **5**: 121–150.

Canu, F. 1897. Bryozoaires du Cénomanien de Saint-Calais (Sarthe). *Bull. Soc. géol. Fr.*, Paris, (3) **25**: 737–754.

—— 1917. Études sur les ovicelles des Bryozoaires cyclostomes. *Bull. Soc. géol. Fr.*, Paris, (4) **17**: 345–347.

—— 1918. Les ovicelles des Bryozoaires cyclostomes. Études sur quelques familles nouvelles et anciennes. *Bull. Soc. géol. Fr.*, Paris, (4) **16** [for 1916]: 324–335.

—— **& Bassler, R. S.** 1920. North American early Tertiary Bryozoa. *Bull. U.S. natn. Mus.*, Washington, **106**: 1–879 + atlas.

—— —— 1922–26. Studies on the cyclostomatous Bryozoa. *Proc. U.S. natn. Mus.*, Washington, **61** (22): 1–154 (1922); **67** (21): 1–124 (1926).

—— —— 1929. Études sur les ovicelles des bryozoaires jurassiques. *Bull. Soc. linn. Normandie*, Caen, (8) **2**: 113–131.

Casey, R. 1961. The stratigraphical palaeontology of the Lower Greensand. *Palaeontology*, London, **3**: 487–621.

Cheetham, A. H., Hayek, L.-A. C. & Thomsen, E. 1981. Growth models in fossil arborescent cheilostome bryozoans. *Paleobiol.*, Lancaster, Pa, **7**: 68–86.

Cotillon, P. & Walter, B. 1965. Essai pétrogénétique et paléoécologique sur un niveau de calcaires bioclastiques dans le Crétacé Inférieur des Basses-Alpes et du Var. Étude systématique de ses bryozoaires. *Bull. Soc. géol. Fr.*, Paris, (7) **7**: 929–936.

Couch, R. Q. 1844. *A Cornish Fauna. Part 3. The Zoophytes and Calcareous Corallines*. xvii + 164 pp. Truro.

Davey, E. C. 1877. *Catalogue of Fossils from the Cretaceous Beds of Berkshire*. 16 pp. Wantage.

—— n.d. [c.1905]. *The Neocomian sponges, Bryozoa, Foraminifera and other fossils of the Sponge-Gravel Beds at Little Coxwell, near Faringdon*. 42 pp. Bath.

Delamette, M. & Walter, B. 1984. Les faunes de bryozoaires de l'Aptien Superieur et de l'Albien en Haute-Savoie et dans l'Ain. *Revue Paleobiol.*, Geneva, **3**: 27–51.

Dixon, F. 1850. *The geology and fossils of the Tertiary and Cretaceous Formations of Sussex*. xvi + 423 pp. London.

Edmonds, J. M. 1973. Lhwyd, Edward. *In* Gillespie, C. C. (ed.), *Dictionary of Scientific Biography*, New York, **8**: 307–308.

Eggleston, D. 1972. Factors influencing the distribution of sublittoral ectoprocts off the south of the Isle of Man. *J. nat. Hist.*, London, **6**: 247–260.

Fitton, W. H. 1847. A Stratigraphical Account of the Section from Atherfield to Rocken End, on the South-West Coast of the Isle of Wight. *Q. Jl geol. Soc. Lond.*, **3**: 289–328.

Flor, F. D. 1972. Biometrische Untersuchungen zur Autökologie oberkretazischer Bryozoen. *Mitt. geol.-paläont. Inst. Univ. Hamburg*, **41**: 15–128.

—— **& Hillmer, G.** 1970. Rhythmische Wachstumvorgänge bei *Multicrescis tuberosa* (ROEMER) [Bryoz. Cycl.]. *Paläont. Z.*, Stuttgart, **44**: 171–181.

Gamble, W. 1896. *Supplementary list of the Bryozoa of the Chatham Chalk.* 7 pp. London.

Goldfuss, G. A. 1826–33. *Petrefacta Germaniae.* Teil **1**. 76 pp. Dusseldorf.

Gregory, J. W. 1896. The Jurassic Bryozoa. *Catalogue of the Fossil Bryozoa in the Department of Geology, British Museum (Natural History).* 239 pp. London.

—— 1899–1909. The Cretaceous Bryozoa, **1**. *Catalogue of the Fossil Bryozoa in the Department of Geology, British Museum (Natural History).* viii + 457 pp. (1899). **2**. *loc. cit.* xlviii + 346 pp. (1909*a*). London.

—— 1909*b*. New Cretaceous Bryozoa. *Geol. Mag.*, London, (n.s., 5) **6**: 61–66. (Publ. before 1909*a*, above).

Hagenow, F. von 1851. *Die Bryozoen der Maastrichter Kreidebildung.* xv + 111 pp. Cassel.

Hamm, H. 1881. *Die Bryozoen des Maastricher Ober-Senon. I. Die Cyclostomen Bryozoen.* 47 pp. Berlin.

Harmelin, J.-G. 1974*a*. À propos d'une forme stomatoporienne typique, *Stomatopora gingrina* Jullien, 1882 (Bryozoaires Cyclostomes), et de son gonozöide. *J. nat. Hist.*, London, **8**: 1–9.

—— 1974*b*. *Les Bryozoaires Cyclostomes de Méditerranée. Écologie et systématique.* 356 pp. Thèse présentée à l'Université d'Aix-Marseille.

—— 1976. Le sous-ordre des Tubuliporina (Bryozoaires Cyclostomes) en Méditerranée. *Mém. Inst. océanogr. Monaco*, **10**: 1–326.

Hastings, A. B. 1963. Notes on Polyzoa (Bryozoa), V. Some Cyclostomata considered by R. C. Osburn in 1933 and 1953. *Ann. Mag. nat. Hist.*, London, (13) **6**: 113–127.

Hayward, P. J. & Ryland, J. S. 1985. Cyclostome Bryozoans. *Synopses of the British Fauna*, London, (n.s.) **34**: 1–147.

Hillmer, G. 1971. Bryozoen (Cyclostomata) aus dem Unter-Hauterive von Nordwestdeutschland. *Mitt. geol.-pälaont. Inst. Univ. Hamburg*, **40**: 5–106.

——**, Gautier, T. G. & McKinney, F. K.** 1975. Budding by intrazooecial fission in the stenolaemate bryozoans *Stenoporella, Reptomulticava*, and *Canalipora. Mitt. geol.-pälaont. Inst. Univ. Hamburg*, **44**: 123–132.

Hincks, T. 1860. Zoophytology. Descriptions of new Polyzoa from Ireland. *Q. Jl microsc. Sci.*, London, **8**: 275–285.

—— 1880. *A History of the British Marine Polyzoa.* 601 pp. London.

Hinds, R. 1975. Growth mode and homeomorphism in cyclostome Bryozoa. *J. Paleont.*, Lawrence, Kans., **49**: 875–910.

Illies, G. 1968. On the gonozooecium of *Collapora straminea* (Phillips) (Bryozoa Cyclostomata). *Atti Soc. ital. Sci. nat.*, Milan, **108**: 71–74.

—— 1973. Different budding patterns in the genus *Stomatopora* (Bryozoa, Cyclostomata). *In* Larwood, G. P. (ed.), *Living and fossil Bryozoa*: 307–315. London.

—— 1974. 'Uniseriale' cyclostome Bryozoen mit vielknospigem Protoecium. *Oberrhein. geol. Abh.*, Karlsruhe, **23**: 127–136.

—— 1975. On the genus *Stomatoporina* Balavoine, 1958 (Bryozoa Cyclostomata). *Docums Lab. Géol. Fac. Sci. Lyon* (H. S.) **3** (1): 51–57.

—— 1976. Budding and Branching Patterns in the Genera *Stomatopora* BRONN, 1825 and *Voigtopora* BASSLER, 1952. *Oberrhein. geol. Abh.*, Karlsruhe, **25**: 97–110.

—— 1981. Evolutionary trends in budding patterns of stomatoporid cyclostomatous Bryozoa and *Stomatoporopsis* n. gen. *Oberrhein. geol. Abh.*, Karlsruhe, **30**: 27–42.

Johnston, G. 1847. *A history of British zoophytes*, 2nd edn. 488 pp. London.

Kade, G. 1852. *Die losen Versteinerungen des Schanzenberges bei Meseritz.* 35 pp. Meseritz.

Kaźmierczak, J. & Hillmer, G. 1974. Sclerosponge nature of the Lower Hauterivian 'bryozoan' *Neuropora pustulosa* (Roemer, 1839) from western Germany. *Acta palaeont. pol.*, Warsaw, **29**: 443–453.

Keeping, W. 1883. *The fossils and palaeontological affinities of the Neocomian deposits of Upware and Brickhill (Cambridgeshire and Bedfordshire).* xi + 167 pp. Cambridge.

Krantz, R. 1972. Die Sponge-Gravels von Faringdon (England). *N. Jb. Geol. Paläont. Abh.*, Stuttgart, **140**: 207–231.

Lagaaij, R. & Gautier, Y. V. 1965. Bryozoan assemblages from marine sediments of the Rhône delta, France. *Micropaleont.*, New York, **11**: 39–58.

Lamarck, J. B. de 1816. *Histoire naturelle des animaux sans vertèbres,* **2**. 568 pp. Paris.

Lamouroux, J. 1821. *Exposition méthodique des genres de l'ordre des polypiers.* viii + 115 pp. Paris.

Lang, W. D. 1915. On some new uniserial Cretaceous cheilostome Polyzoa. *Geol. Mag.*, London, (6) **2**: 496–504.

Levinsen, G. M. R. 1912. Studies on Cyclostomata Operculata. *K. dansk. Vidensk. Selsk. Skr.*, Copenhagen, (Mat.-nat., 7) **10**: 1–52.

Lonsdale, W. 1849. Notes on Fossil Zoophytes found in the deposits described by Dr Fitton in his Memoir entitled 'A Stratigraphical Account of the Section from Atherfield to Rocken End'. *Q. Jl geol. Soc. Lond.*, **5**: 55–103.

—— 1850. See Dixon.

Loriol, P. de 1863. *Description des animaux invertébrés fossiles contenus dans l'étage Néocomien Moyen du Mont Salève.* 214 pp. Geneva.

—— 1868. Monographie des couches de l'étage valangien des carrières d'Arzier (Vaud). *Mat. paléont. Suisse*, Geneva, (4) **2**: 1–110.

McKinney, F. K. 1975. Autozooecial budding patterns in dendroid stenolaemate bryozoans. *Docums Lab. Géol. Fac. Sci. Lyon* (H.S.) **3** (1): 65–76.

—— 1986. Historical record of erect bryozoan growth forms. *Proc. R. Soc. Lond.*, London, (B) **228**: 133–149.

Mantell, G. 1844–54. *The Medals of Creation.* 1st Edn. xxviii + viii + 1016 pp. (1844). 2nd Edn. xxxii + xii + 930 pp. (1854). London.

Marsson, T. F. 1887. Die Bryozoen der weissen Schreibkreide der Insel Rügen. *Paläont. Abh.*, Berlin, **4**: 1–112.

Masse, J.-P. & Walter, B. 1974. Les bryozoaires du Crétáce Inférieur Provençal. Biostratigraphique et Paléoécologie. *Géobios*, Lyon, **7**: 183–210.

Meyer, C. J. A. 1864. Three days at Farringdon. Position of the Sponge Gravels. *Geologist*, London, **7**: 5–11.

Michelin, H. 1841–48. *Iconographie Zoophytologique.* xii + 348 pp. Paris.

Middlemiss, F. A. 1959. English Aptian Terebratulidae. *Palaeontology*, London, **2**: 94–142.

Milne Edwards, H. 1838. Mémoire sur les Crisies, les Hornères et plusieurs autres Polypes. *Ann. Sci. nat.*, Paris, **9**: 193–238.

Mongereau, N. 1972. Le genera *Hornera* Lamouroux, 1821 en Europe. *Annln naturh. Mus. Wien*, **76**: 311–373.

—— **& Walter, B.** 1965. Description d'un néotype d'*Idmonea triquetra* Lamouroux, 1821 (Bryozoa Cyclostomata). *Trav. Lab. Géol. Fac. Sci. Lyon*, (n.s.) **12**: 19–21.

Mortensen, T. 1928. *A monograph of the Echinoidea*, **1**. Cidaroidea. 551 pp. Copenhagen.

Novak, O. 1877. Die Bryozoen der böhemischen Kreideformation. *Denkschr. Akad. Wiss. Wien*, **37**: 79–118.

Nye, O. B. 1976. Generic revision and skeletal morphology of cerioporid cyclostomes (Bryozoa). *Bull. Am. Paleont.*, Ithaca, N.Y., **69**: 1–222.

—— **& Lemone, D. V.** 1978. Multilaminar growth in *Reptomulticava texana*, a new species of cyclostome Bryozoa. *J. Paleont.*, Lawrence, Kans., **52**: 830–845.

Orbigny, A. d' 1849. Description de quelques genres nouveaux de Mollusques bryozoaires. *Rev. Mag. Zool.*, Paris, (2) **1**: 499–504.

—— 1850–52. *Prodrome de Paléontologie* ... **1** (1850), lx + 394 pp. **2** (1850), 427 pp. **3** (1852), 196 pp. Paris.

—— 1851–54. *Paléontologie française. Terrains Crétacés. V. Bryozoaires.* 1191 pp. Paris.

Pergens, E. 1889. Revision des Bryozoaires du Crétacé figurés par d'Orbigny. 1. Cyclostomata. *Bull. Soc. belge Géol. Paléont. Hydrol.*, Brussels, **3**: 305–400.

Phillips, J. 1829. *Illustrations of the geology of Yorkshire. Part I. The Yorkshire Coast.* 192 pp. York.

Pitt, L. J. 1949. A new species of polyzoan from the English Lower Cretaceous. *Proc. Geol. Ass.*, London, **60**: 154–156.

—— 1976. A new cheilostome bryozoan from the British Aptian. *Proc. Geol. Ass.*, London, **87**: 65–68.

Pohowsky, R. A. 1978. The boring ctenostomate Bryozoa: taxonomy and paleobiology based on cavities in calcareous substrata. *Bull. Am. Paleont.*, Ithaca, N.Y., **73**: 1–192.

Probert, P. K., Batham, E. J. & Wilson, J. B. 1979. Epibenthic macrofauna off southeastern New Zealand and mid-shelf bryozoan dominance. *N.Z. Jl mar. freshw. Res.*, Wellington, **13**: 379–392.

Quenstedt, F. A. 1881. *Petrefactenkunde Deutschlands. VI. Korallen.* 1093 pp. Leipzig.

Reuss, A. E. 1848. Die fossilen Polyparien des Wiener Tertiärbeckens. *Naturw. Abh. Wien*, **2**: 1–109.

—— 1867. Die Bryozoen, Anthozoen, und Spongiaren des braunen Jura von Balin bei Krakau. *Denkschr. Akad. Wiss. Wien*, **30**: 215–298.

Roemer, F. A. 1839. *Die Versteinerungen des norddeutschen Oolithen-Gebirges. Ein Nachtrag.* 59 pp. Hannover.

—— 1840–41. *Die Versteinerungen des norddeutschen Kreidegebirges.* 145 pp. Hannover.

Ryland, J. S. 1970. *Bryozoans.* 175 pp. London.

Sharpe, D. 1854. On the age of the fossiliferous Sands and Gravels of Faringdon and its Neighbourhood. *Q. Jl geol. Soc. Lond.*, **10**: 176–198.

Simonowitsch, S. 1871. Beiträge zur Kenntnis der Bryozoen des Essener Grünsandes. *Verh. naturh. Ver. preuss. Rheinl.*, Bonn, **28**: 1–70.

Stach, L. W. 1936. Correlation of zoarial form with habitat. *J. Geol.*, Chicago, **44**: 60–65.

Strand, F. 1928. Miscellanea nomenclatorica zoologica et palaeontologica. I-II. *Arch. Naturgesch.*, Berlin, **92** (A, 8): 30–75.

Taylor, P. D. 1976. Multilamellar growth in two Jurassic cyclostomatous Bryozoa. *Palaeontology*, London, **19**: 293–306.

—— 1980. Two new Jurassic Bryozoa from southern England. *Palaeontology*, London, **23**: 699–706.

—— 1984. Adaptations for spatial competition and utilization in Silurian encrusting bryozoans. *Spec. Pap. Palaeont.*, London, **32**: 197–210.

—— 1985. Polymorphism in melicerititid cyclostomes. *In* Nielsen, C. & Larwood, G. P. (eds), *Bryozoa: Ordovician to Recent*: 311–318. Fredensborg.

—— 1986*a*. Scanning electron microscopy of uncoated fossils. *Palaeontology*, London, **29**: 685–690.

—— 1986*b*. *Charixa* Lang and *Spinicharixa* gen. nov., cheilostome bryozoans from the Lower Cretaceous. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **40**: 197–222.

—— 1986*c*. The ancestrula and early growth pattern in two primitive cheilostome bryozoans: *Pyripora catenularia* (Fleming) and *Pyriporopsis portlandensis* Pohowsky. *J. nat. Hist.*, London, **20**: 101–110.

—— **& Sequeiros, L.** 1982. Toarcian bryozoans from Belchite in north-east Spain. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **36**: 117–129.

Tillier, S. [1975.] *Recherches sur le structure et revision systematique des Heteroporides (Bryozoa, Cyclostomata) des Faluns de Touraine.* 102 pp. Unpubl. thesis, Univ. Paris, Orsay.

Vine, G. R. 1885. Notes on the Cambridge Greensand. *Proc. Yorks Geol. Polytech. Soc.*, Leeds, (n.s.) **9**: 10–29.

—— 1889. Further notes on the Polyzoa of the Lower Greensand and the Upper Greensand of Cambridge. *Proc. Yorks Geol. Polytech. Soc.*, Leeds, (n.s.) **11**: 250–275.

—— 1891. Report of the committee, consisting of Dr. H. Woodward, Mr. G. R. Vine (Secretary), Drs. P. M. Duncan, H. C. Sorby, and Mr. C. E. DeRance, appointed to prepare a report on the Cretaceous Polyzoa. *Rep. Br. Ass. Advmt Sci.*, London, **1890**: 378–396.

—— 1893. Notes on the Polyzoa, *Stomatopora* and *Proboscina* groups, from the Cornbrash of Thrapston, Northamptonshire. *Proc. Yorks Geol. Polytech. Soc.*, Halifax, (n.s.) **12**: 247–258.

Voigt, E. 1973. Environmental conditions of bryozoan ecology of the hardground biotope of the Maastrichtian Tuff-Chalk, near Maastricht (Netherlands). *In* Larwood, G. P. (ed.), *Living and fossil Bryozoa:* 185–197. London.

—— 1975. Ist *Domopora stellata* (Goldfuss, 1826) (Bryoz. Cyclost.) = *Coronopora truncata* (Fleming, 1828) ein lebendes fossil aus der Oberkreide? *Zool. Anz.*, Jena, **195**: 186–200.

—— 1981. Répartition et Utilisation Stratigraphique des Bryozoaires du Crétacé Moyen (Aptien–Coniacien). *Cretaceous Res.*, London, **2**: 439–462.

—— **& Soule, J. D.** 1973. Cretaceous burrowing bryozoans. *J. Paleont.*, Lawrence, Kans., **47**: 21–33.

—— **& Viaud, J.-M.** 1983. Bryozoaires du Sénonien de Vendée (Bassin de Challans-Commequiers). *Géol. méditerr.*, Aix-en-Provence, **10**: 219–228.

Walter, B. 1966. Les Bryozoaires du Néocomien de Mièges (Jura). *Bull. Soc. géol. Fr.*, Paris, (7) **8**: 896–900.

—— 1967. Les Bryozoaires Hauteriviens de la partie occidentale du Département de l'Ain. *Trav. Lab. Géol. Fac. Sci. Lyon*, (N.S.) **14**: 53–62.

—— 1970. Les Bryozoaires Jurassiques en France. *Docums Lab. Géol. Fac. Sci. Lyon*, **35** (for 1969): 1–328.

—— 1972. Les Bryozoaires Neocomiens du Jura Suisse et Français. *Géobios*, Lyon, **5**: 277–354.

—— 1975. Révision des types de bryozoaires Albiens et Cénomaniens de la Collection Michelin. *Géobios*, Lyon, **8**: 307–316.

—— 1977. Un Gisement de Bryozoaires Aptiens dans le Gard. *Géobios*, Lyon, **10**: 325–336.

—— 1983. *Poriceata ardescensis* nouveau genre et novelle espèce de Bryozoaire Cyclostome du Crétacé Inférieur d'Europe occidentale. *Géobios*, Lyon, **16**: 251–255.

—— 1985. Les 'Mésentéripores' (Bryozoaires Cyclostomes) du Néocomien du Jura Suisse et Français. *Géobios*, Lyon, **18**: 5–27.

—— 1986. Les Bryozoaires Fasciculés Néocomiens. *Palaeontographica*, Stuttgart, (A) **195**: 75–99.

—— 1987*a*. Les bryozoaires cyclostomes Neocomiens de forme '*Entalophora*' et '*Spiropora*'. *Rev. Paléobiol.*, Geneva, **6**: 29–53.

—— 1987*b*. Le genre *Unitubigera* d'Orbigny (Bryozoaire cyclostome), Theonoidae primitif ou '*Plagioecia*' évolué? *Bull. Mus. natn. Hist. nat. Paris*, (4) **9**: 405–413.

—— 1989. Les Diastoporidae bereniciformes Neocomiens du Jura Franco-Suisse. Étude systematique et parallelisme entre leurs genres et ceux des 'Diastopores' et 'Mesenteripores'. *Palaeontographica*, Stuttgart, (A) **207**: 107–145.

——**, Arnauld-Vanneau, A., Arnauld, H., Busnardo, R. & Ferry, S.** 1975. Les Bryozoaires Barrémo-Aptiens du sud-est de la France. Gisements et paléoécologie, biostratigraphie. *Géobios*, Lyon, **8**: 83–117.

—— **& Busnardo, R.** 1971. Un Gisement Aptien de Bryozoaires dans les Alpes Françaises (Vercors, Isère). *Géobios*, Lyon, **4**: 87–99.

—— **& Clavel, B.** 1979. Nouveux apports à la connaissance de la faune Aptienne de Bryozoaires du Sud-est de la France. *Géobios*, Lyon, **12**: 819–837.

Ware, S. 1975. British Lower Greensand Serpulidae. *Palaeontology*, London, **18**: 93–116.

Wass, R. E., Conolly, J. R. & Macintyre, R. J. 1970. Bryozoan carbonate sand continuous along southern Australia. *Marine Geol.*, Amsterdam, **9**: 63–73.

Waters, A. 1904. Bryozoa. *Résult. Voyage S.Y. Belgica*, Antwerp, (Zool.). 114 pp.

Wilson, M. 1986. Coelobites and spatial refuges in a Lower Cretaceous cobble-dwelling hardground fauna. *Palaeontology*, London, **29**: 691–703.

GLOSSARY

This terminological glossary is included for two reasons: firstly, many terms in bryozoology are unfamiliar to the non-specialist; and secondly, there is no consensus of opinion among bryozoologists about the definition of many terms (see Boardman *et al.* 1983: 304).

Adnate: Encrusting, closely cemented to a substrate.

Ancestrula: The founding zooid of the colony formed by settlement and metamorphosis of the larva.

Alveoli: Apparent interzooidal spaces between the autozooecia in rectangulate cyclostomes which are enclosed by interior wall calcification.

Aperture: The opening at the distal end of the zooecium through which the tentacle crown is protruded (in cheilostomes, 'aperture' is sometimes used in place of 'opesia').

Astogeny: The development of the colony.

Astogenetic zones: Developmental zones of the colony which are distinguished by the morphology of their constituent zooids: progressive elaboration of zooid morphology and, usually, increase in zooid size occurs distally through zones of astogenetic change, including a zone of primary astogenetic change around the colony origin; zones of astogenetic repetition contain zooids of similar morphology (excepting polymorphic, ontogenetic and ecophenotypic differences).

Atrial ring: A ring-like ridge located inwards of the ooeciopore in melicerititid gynozooecia.

Autozooecium: The skeleton of an inferred feeding zooid.

Avicularium: Cheilostome polymorph with a modified operculum and orifice.

Basal lamina: The basal calcified layer of a cyclostome colony usually closely adnate to the substrate but occasionally becoming free.

Bereniciform: An adnate, single-layered, multiserial fan-like to discoidal colony-form in cyclostomes (see Taylor 1976: text-fig. 2).

Bifoliate: Erect colony construction with two layers of zooids back-to-back.

Brood chamber: Any chamber for the brooding of larvae; includes cyclostome gynozooecia and so-called zoarial brood chambers, and cheilostome ovicells.

Cancelli: Small pits on the surface of cancellate cyclostome colonies which may be kenozooids or interzooidal spaces.

Colony: The aggregate of zooids (and any extrazooidal parts) derived from a single larva.

Cryptocyst: Interior body wall calcification (grown beneath a covering of soft tissue), often pustulose, which may contribute to the frontal wall of the cheilostome zooid surrounding the opesia and surrounded by the gymnocyst.

Dendroid: An erect, tree-like branching pattern.

Diaphragm: A horizontal plate partitioning or sealing the zooecium in cyclostomes. Basal diaphragms are secreted from the oral side and form a floor to the living chamber of the zooid. Terminal diaphragms are secreted from the aboral side and occlude the zooecium close to the level of the aperture.

Dichotomous branching: Symmetrical branch bifurcation.

Eleozooecium: Polymorph of melicerititid cyclostomes in which the aperture and operculum is modified.

Endozone: The inner zone of a massive or erect colony composed of the thin-walled proximal parts of the zooecia typically orientated subparallel to branch growth direction.

Exozone: The outer zone of a massive or erect colony composed of the thick-walled distal parts of the zooecia typically orientated subperpendicular to branch growth direction.

Fascicle: A bundle of autozooecial apertures.

Frontal wall: A wall on the frontal surface of the zooid which is parallel or subparallel to the colony growth direction.

Gymnocyst: Exterior body wall calcification (cuticle-covered during life) in cheilostome zooids which commonly forms the zooidal vertical walls and may contribute to the frontal wall.

Gynozooecium: A polymorph formed by a single fertile zooid used to brood larvae in many cyclostomes; gynozooecia generally have bulbous distal parts in which the frontal wall bears a higher density of pseudopores than in the autozooecia, and apertures (ooeciopores) smaller than autozooecial apertures. Synonymous with gonozooecium as commonly used.

Kenozooecium: The skeleton of an inferred kenozooid, a polymorph lacking functional gut and tentacles, and usually smaller than an autozooid; in tubuloporine cyclostomes kenozooecia usually have frontal walls without apertures.

Lateral branching (or ramification): When daughter branches arise from the sides of existing branches, typically at about 90° to the parent branch and sometimes proximally of the branch growth tip.

Maculum: A distinct patch on the colony surface, usually marking the site of an excurrent chimney, often formed by a cluster of polymorphs or new zooecial buds.

Moniliform: Term used to describe zooecial walls (in thin section) with periodic thickenings.

Monticule: A hummock on the colony surface which probably formed an excurrent chimney.

Multilamellar: Multilayered colony construction achieved by self-overgrowth.

Mural spines (= intrazooecial spines): Small spines projecting inwards from the walls of the zooecia in cyclostomes; often visible inside zooecial apertures.

Ontogeny: The development of a zooid (cf. astogeny).

Operculum: A hinged plate which closes the cyclostome aperture or cheilostome orifice when the tentacles are retracted; opercula are rarely calcified in cheilostomes; among cyclostomes, opercula are present only in the Family Eleidae (melicerititids) in which they are calcified.

Orifice: The opening, closed by the operculum, in cheilostomes which allows the tentacle crown access to the exterior.

Opesia: The uncalcified 'window' on the frontal surface of a cheilostome zooid; during life, it is occupied by the frontal membrane and the operculum.

Ovicell: Small calcified larval brood chamber immediately distal of the orifice of the maternal zooid in cheilostomes.

Peristome: A tubular prolongation around the zooecial aperture.

Proboscinifirm: An adnate, oligoserial, ribbon-like growth-form in cyclostomes (see Taylor 1976: text-fig. 2).

Protoecium: The bulb-like proximal part of a cyclostome ancestrula.

Pseudolunarium: A hood-like spine or shield projecting above the surface of the aperture or indenting the outline of the aperture on its proximal side in some rectangulate cyclostomes.

Pseudopores: Minute pores present in the frontal, calcified exterior walls of cyclostomes which are cuticle-covered during life.

Vinculariiform: Colony growth-form, originally applied to cheilostomes, in which the rigidly erect and bush-like colony consists of narrow, bifurcating branches.

Zoarium: The skeletal remains of a colony.

Zooecium: The skeletal remains of a zooid.

Zooid: The modular unit of a bryozoan colony, homologous with the individual in a unitary animal.

IDENTIFICATION KEY

Identification of many of the Faringdon bryozoan species is difficult. This is particularly true of the bereniciform tubuloporines (species of *Plagioecia, Hyporosopora, Mesonopora* and '*Berenicea*') in which the slight differences between some species can only be appreciated by direct comparison of specimens. The common absence of gynozooecia also provides a problem when trying to identify species; therefore, gynozooecial characters have been omitted from this key, but they can be found in the species descriptions. Furthermore, poorly preserved material which is abraded, or obscured by calcite cement may be impossible to determine. Identifications made using this key should be carefully checked against the full descriptions and illustrations of the species.

1\. Zoaria encrusting or massive 2
Zoaria erect 30

2\. Branching colony-form 3
Sheet-like colony-form 13

3\. Branches uniserial or partly biserial 4
Branches multiserial ('ribbon-like') 8

4\. Branches zig-zag with zooecia facing alternately to left and right .... ***Stomatoporina alternata***
Otherwise 5

5\. Zooecia narrow (width <0·2 mm) 6
Zooecia broad (width >0·2 mm) 7

6\. Branches bifurcating .... **Stomatoporid sp. 2**
Branches with lateral ramifications... **Stomatoporid sp. 1**

7\. Zooecia barrel-like, narrowing distally .... ***Voigtopora calypso***
Zooecia parallel-sided; branches sometimes biserial following bifurcation .... ***'Stomatopora' melvillei***

8\. Branches of low profile, flat-topped or gently convex 9
Branches of high profile, distinctly arched or ridged 12

9\. Zooecial apertures >0·10 mm 10
Zooecial apertures <0·10 mm 11

10\. Branches with border of kenozooecia; lateral ramifications sometimes present .... ***Proboscinopora marginata***
Branches lacking border of kenozooecia .... ***Oncousoecia depressa***

11\. Zooecia minute (<0·4 mm long); frontal walls convex; apertures often longitudinally elongate .... ***Oncousoecia parvula***
Zooecia larger (<0·8 mm long); frontal walls flat; apertures often transversely elongate .... ***Oncousoecia coarctata***

12\. Zooecia broad (>0·15 mm wide); branches wide with rounded cross sections .... ***Idmonea radiolitorum***
Zooecia narrow (<0·15 mm wide); branches subtriangular in cross section; lateral ramifications may occur .... ***Idmonea denticulata***

13\. Zooecia ovoidal or caudate, irregularly and loosely arranged; apertures (opesiae) extensive .... ***Charixa lhuydi***
Otherwise 14

14\. Zooecia without frontal walls 15
Zooecia with frontal walls 18

15\. Large multilayered zoaria composed of numerous inverted cup-shaped subcolonies .... ***Semimulticavea marginata***

Otherwise 16

16. Zooecia monomorphic; zoaria thick, often with knobbly branches; maculae absent .. ***Ceriopora farringdonensis***

Zooecia dimorphic 17

17. Apertures separated by wide areas of calcification; pseudolunaria present in some autozooecial apertures. ***Paracrescis boardmani***

Apertures closely spaced; centres of maculae devoid of autozooecia .... ***Seminodicrescis variolata***

18. Apertures opening on frontal surface of zoaria 19

Apertures opening only at distal growing edge; typically small, thick zoaria .... ***Hyporosopora larwoodi***

19. Apertures opening on prominent ridges which are separated by low-lying areas of kenozooecia lacking apertures .... ***Reptoclausa hagenowi***

Otherwise 20

20. Apertures connate, aligned in radial rows .... ***Unitubigera* sp.**

Otherwise 21

21. Apertures 8-shaped; constricted medially by a group of mural spines .... ***Hyporosopora constricta***

Otherwise 22

22. Apertures absent from centre of zoaria, crowded at the distal edge .... ***Hyporosopora larwoodi***

Otherwise 23

23. Apertures very closely spaced; zooecia short; maculae may occur in which zooecia are longer than average ... ***Plagioecia spissa***

Apertures spaced well apart 24

24. Apertures >0·15 mm in diameter 25

Apertures <0·15 mm in diameter 26

25. Zooecia flask-shaped, their frontal walls convex; zoaria lobate .... ***'Berenicea' grandipora***

Zooecia immersed .... ***'Berenicea' faringdonensis***

26. Apertures distantly spaced, 0·12–0·13 mm in diameter; zoaria unilamellar .... ***'Berenicea' filifera***

Otherwise 27

27. Zoaria composed of discoidal subcolonies 28

Otherwise 29

28. Zoaria thin; zooecial frontal wall width >0·10 mm ...... ***'Berenicea'* cf. *sowerbyi***

Zoaria thick, several generations of buds visible at the growing edge; zooecial frontal wall width <0·10 mm... ***Mesonopora fecunda***

29. Apertures lacking peristomes or apertural rims; zoaria often with a lustrous surface ... ***Hyporosopora mantelli***

Apertures with well-defined rims .... ***Plagioecia orbifera***

30. Bilamellar fronds .... ***?Mesenteripora campicheana***

Otherwise 31

31. Zooecia with frontal walls 32

Zooecia lacking frontal walls 40

32. Zooecia opening all around branch circumference 33

Zooecia opening on one side only of branches which are short and have not been observed to bifurcate .... ***Filisparsa gasteri***

33. Apertures with a straight proximal edge; opercula may be present 34

Apertures circular or elliptical 37

34. Apertures small, <0·10 mm in transverse diameter; branches often <1 mm in diameter .... ***Meliceritites dendroidea***

Apertures >0·10 mm in transverse diameter 35

35. Apertures appreciably higher than wide, distinctly arch-shaped and flared with a deep distal ledge .... ***Meliceritites gracilis***

Otherwise 36

36. Apertures >0·15 mm in transverse width, closely spaced; branches thick, usually >1·5 mm in diameter .... ***Meliceritites cunningtoni***

Apertures <0·15 mm in transverse width; branches usually <1·5 mm in diameter .... ***Meliceritites transversa***

37. Branches narrow (generally <1 mm), subcircular in cross section, lacking a median budding lamina 38

Branches >1 mm in diameter, compressed, with a median budding lamina 39

38. Gynozooecia with lobes extending distally of a compressed ooeciopore; kenozooecia commonly interspersed among autozooecia .... ***Entalophoroecia quadripartita***

Otherwise .... ***Collapora hillmeri***

39. Apertures *c.* 0·08 mm in diameter; frontal walls delicate; branches usually <2 mm in diameter .. ***Ceata granulata***

Apertures 0·10–0·16 mm in diameter; frontal walls robust; branches generally 2–3 mm in diameter .... ***Cardioecia neocomiensis***

40. Zoaria seldom branching, composed of numerous stacked subcolonies 41

Otherwise 44

41. Zooecia dimorphic, thin-walled 42

Zooecia monomorphic, thick-walled .... ***Reptomulticava brydonei***

42. Autozooecia arranged in well-defined radial rows 43

Autozooecia not arranged in clearly-defined rows; apertures 0·06–0·08 mm in diameter . ***Tholopora hastingsae***

43. Autozooecial apertures >0·15 mm in diameter .... ***Tholopora thomasi***

Autozooecial apertures 0·08–0·10 mm in diameter ...... ***Tholopora dightoni***

44. Autozooecial apertures arranged in circular fascicles raised above the surrounding branch surface .... ***Echinocava raulinii***

Autozooecial apertures not in fascicles 45

45. Branches <4 mm in diameter 46

Branches >4 mm in diameter 51

46. Kenozooecia absent or very few; branches with median budding lamina ...... ***Ceata granulata*** (abraded state)

Kenozooecia abundant 47

47. Autozooecial apertures opening on one side only of branches; branches narrow, commonly *c.* 0·6 mm in diameter .... ***Siphodictyum gracile***

Autozooecial apertures not so restricted 48

48. Autozooecial apertures opening on 2 faces of the branches separated by strips of kenozooecia 49

Otherwise 50

49. Branches >1·4 mm in diameter, compressed in cross section .... ***Laterocavea dutempleana***

Branches <1 mm in diameter, subcircular in cross section ***Laterocavea? intermedia***

50. Autozooecial apertures <0·09 mm in diameter with

distinct rims; branches <1·5 mm in diameter; kenozooecial apertures funnel-shaped .... ***Tetrocycloecia multiporosa***

Autozooecial apertures >0·09 mm in diameter; branches >1·5 mm in diameter; kenozooecia sometimes occluded .... ***Clausa zonifera***

51\. Zooecia monomorphic; maculae absent; branches may be >20 mm in diameter .... ***Ceriopora farringdonensis***

Zooecia dimorphic or weakly so; branches usually <15 mm in diameter 52

52\. Well-developed maculae devoid of autozooecial apertures; bifurcating branches ...... ***Heteropora keepingi***

Maculae absent; branches clavate, commonly with overgrowths .... ***Heteropora clavata***

TAXONOMIC INDEX

Names of new taxa are given in **bold**, as are page numbers referring to species descriptions.

Bulletin of the British Museum (Natural History)

Geology Series

Most earlier Geology *Bulletins* are still in print. A full list of available titles can be obtained from Publication Sales (address inside front cover).

Vol. 36 No. 2 Miscellanea: Dinantian terebratulids—New microfossils—*Neseuretus*—*Archaeocidaris whatleyensis*—Carboniferous dasyclad—*Nanjinoporella*—Toarcian bryozoans—Drybrook Sandstone plants—British fossil bintoniellids—*Uraloporella*. 1982. Pp. 43–155. £19.80

Vol. 36 No. 3 The Ordovician Graptolites of Spitsbergen. R. A. Cooper & R. A. Fortey. 1982. Pp. 157–302, 6 plates, 83 figs, 2 tables. £20.50

Vol. 36 No. 4 Campanian and Maastrichtian sphenodiscid ammonites from southern Nigeria. P. M. P. Zaborski. 1982. Pp. 303–332, 36 figs. £4.00

Vol. 37 No. 1 Taxonomy of the arthrodire *Phlyctaenius* from the Lower or Middle Devonian of Campbellton, New Brunswick, Canada. V. T. Young. 1983. Pp. 1–35, 18 figs. £5.00

Vol. 37 No. 2 *Ailsacrinus* gen. nov., an aberrant millericrinid from the Middle Jurassic of Britain. P. D. Taylor. 1983. Pp. 37–77, 48 figs, 1 table. £5.90

Vol. 37 No. 3 Miscellanea: Permian *Glossopteris* in Turkey—Wealden *Theriosuchus*—Wealden conifer—Permian plants of Saudi Arabia—Carboniferous Edrioasteroidea—British cicadas—Dittonian cephalaspids. 1983. Pp. 79–171. £13.50

Vol. 37 No. 4 The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. B. G. Gardiner. 1984. Pp. 173–428, 145 figs, 4 plates. 0 565 00967 2. £39.00

Vol. 38 No. 1 New tertiary pycnodonts from the Tilemsi valley, Republic of Mali. A. E. Longbottom. 1984. Pp. 1–26, 29 figs, 3 tables. 0 565 07000 2. £3.90

Vol. 38 No. 2 Silicified brachiopods from the Viséan of County Fermanagh, Ireland. (III) Rhynchonellids, Spiriferids and Terebratulids. C. H. C. Brunton. 1984. Pp 27–130, 213 figs. 0 565 07001 0. £16.20

Vol. 38 No. 3 The Llandovery Series of the Type Area. L. R. M. Cocks, N. H. Woodcock, R. B. Rickards, J. T. Temple & P. D. Lane. 1984. Pp. 131–182, 70 figs. 0 565 07004 5. £7.80

Vol. 38 No. 4 Lower Ordovician Brachiopoda from the Tourmakeady Limestone, Co. Mayo, Ireland. A. Williams & G. B. Curry. 1985. Pp. 183–269, 214 figs. 0 565 07003 7. £14.50

Vol. 38 No. 5 Miscellanea: Productacean growth and shell shape—Jurassic alga *Palaeosiphonium*—Upper Ordovician brachiopods and trilobites—Lower Devonian Osteostraci from Podolia—*Hipparion* from Diavata—Preparation and study of Singa skull—Carboniferous and Permian bryozoa—Lower Eocene trionychid—Montsech fossil insects. 1985. Pp. 271–412. 0 565 07004 5. £24.00

Vol. 39 No. 1 Upper Cretaceous ammonites from the Calabar region, south-east Nigeria. P. M. P. Zaborski. 1985. Pp. 1–72, 66 figs. 0 565 07006 1. £11.00

Vol. 39 No. 2 Cenomanian and Turonian ammonites from the Novo Redondo area, Angola. M. K. Howarth. 1985. Pp. 73–105. 33 figs. 0 565 07006 1. £5.60

Vol. 39 No. 3 The systematics and palaeogeography of the Lower Jurassic insects of Dorset, England. P. E. S. Whalley. 1985. Pp. 107–189, 87 figs, 2 tables. 0 565 07008 8. £14.00

Vol. 39 No. 4 Mammals from the Bartonian (middle/late Eocene) of the Hampshire Basin, southern England. J. J. Hooker, 1986. Pp. 191–478, 71 figs, 39 tables. 0 565 07009 6. £49.50

Vol. 40 No. 1 The Ordovician graptolites of the Shelve District, Shropshire. I. Strachan. 1986. Pp. 1–58, 38 figs. 0 565 07010 X. £9.00

Vol. 40 No. 2 The Cretaceous echinoid *Boletechinus*, with notes on the phylogeny of the Glyphocyphidae and Temnopleuridae. D. N. Lewis. 1986. Pp. 59–90, 11 figs, 7 tables. 0 565 07011 8. £5.60

Vol. 40 No. 3 The trilobite fauna of the Raheen Formation (upper Caradoc), Co. Waterford, Ireland. A. W. Owen, R. P. Tripp & S. F. Morris. 1986. Pp. 91–122, 88 figs. 0 565 07012 6. £5.60

Vol. 40 No. 4 Miscellanea I: Lower Turonian cirripede—Indian coleoid *Naefia*—Cretaceous–Recent Craniidae—Lectotypes of Girvan trilobites—Brachiopods from Provence—Lower Cretaceous cheilostomes. 1986. Pp. 125–222. 0 565 07013 4. £19.00

Vol. 40 No. 5 Miscellanea II: New material of *Kimmerosaurus*—Edgehills Sandstone plants—Lithogeochemistry of Mendip rocks—Specimens previously recorded as teuthids—Carboniferous lycopsid *Anabathra*—*Meyenodendron*, new Alaskian lepidodendrid. 1986. Pp. 225–297. 0 565 07014 2. £13.00

Vol. 41 No. 1 The Downtonian ostracoderm *Sclerodus* Agassiz (Osteostraci: Tremataspididae), P. L. Forey. 1987. Pp. 1–30. 11 figs. 0 565 07015 0. £5.50

Vol. 41 No. 2 Lower Turonian (Cretaceous) ammonites from south-east Nigeria. P. M. P. Zaborski. 1987. Pp. 31–66. 46 figs. 0 565 07016 9. £6.50

Vol. 41 No. 3 The Arenig Series in South Wales: Stratigraphy and Palaeontology. I. The Arenig Series in South Wales. R. A. Fortey & R. M. Owens. II. Appendix. Acritarchs and Chitinozoa from the Arenig Series of South-west Wales. S. G. Molyneux. 1987. Pp. 67–364. 289 figs. 0 565 07017 7. £59.00

Vol. 41 No. 4 Miocene geology and palaeontology of Ad Dabtiyah, Saudi Arabia. Compiled by P. J. Whybrow. 1987. Pp. 365–457, 54 figs. 0 565 07019 3. £18.00

Vol. 42 Cenomanian and Lower Turonian Echinoderms from Wilmington, south-east Devon. A. B. Smith, C. R. C. Paul, A. S. Gale & S. K. Donovan. 1988. 244 pp., 80 figs, 50 pls. 0 565 07018 5. £46.50

Vol. 43 A Global Analysis of the Ordovician–Silurian boundary. Edited by L. R. M. Cocks & R. B. Rickards. 1988. 394 pp., figs. 0565 07020 7. £70.00

Vol. 44 No. 1 Miscellanea: Palaeocene wood from Mali—Chapelcorner fish bed—*Heterotheca* coprolites—Mesozoic Neuroptera and Raphidioptera. 1988. Pp. 1–63. 0 565 07021 5. £12.00

Vol. 44 No. 2 Cenomanian brachiopods from the Lower Chalk of Britain and northern Europe. E. F. Owen. 1988. Pp. 65–175. 0 565 07022 3. £21.00

Vol. 44 No. 3 The ammonite zonal sequence and ammonite taxonomy in the *Douvilleiceras mammillatum* Superzone (Lower Albian) in Europe. H. G. Owen. 1988. Pp. 177–231. 0 565 07023 1. £10.30

Vol. 44 No. 4 Cassiopidae (Cretaceous Mesogastropoda): taxonomy and ecology. R. J. Cleevely & N. J. Morris. 1988. Pp. 233–291. 0 565 07024 X. £11.00

Vol. 45 No. 1 Arenig trilobites—Devonian brachiopods—Triassic demosponges—Larval shells of Jurassic bivalves—Carboniferous marattialean fern—Classification of Plectambonitacea. 1989. Pp. 1–163. 0 565 07025 8. £40.00

Vol. 45 No. 2 A review of the Tertiary non-marine molluscan faunas of the Pebasian and other inland basins of north-western South America. C. P. Nuttall. 1990. Pp. 165–371. 456 figs. 0 565 07026 6. £52.00

CONTENTS

Bulletin British Museum (Natural History)
GEOLOGY SERIES
Vol. 46

Bulletin British Museum (Natural History)

Geology Series

Carboniferous pteridosperm frond *Neuropteris heterophylla*; Tertiary Ostracoda from Tanzania

VOLUME 46 NUMBER 2 31 JANUARY 1991

The *Bulletin of the British Museum (Natural History)*, instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

Papers in the *Bulletin* are primarily the results of research carried out on the unique and ever-growing collections of the Museum, both by the scientific staff and by specialists from elsewhere who make use of the Museum's resources. Many of the papers are works of reference that will remain indispensable for years to come.

A volume contains about 400 pages, made up by two numbers: published Spring and Autumn. Subscriptions may be placed for one or more of the series on an Annual basis. Individual numbers and back numbers can be purchased and a Bulletin catalogue, by series, is available. Orders and enquiries should be sent to:

Sales Department,
Natural History Museum Publications,
British Museum (Natural History),
Cromwell Road,
London SW7 5BD

Telephone: 071-938 9386
Fax: 071-938 8709

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Geol.)

ISBN 0 565 07028 2
ISSN 0007-1471

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Geology Series
Vol 46 No 2 pp 153–270

Issued 31 January 1991

Bull. Br. Mus. nat. Hist. (Geol.) **46** (2): 153–174 Issued 31 January 1991

The Carboniferous pteridosperm frond *Neuropteris heterophylla* (Brongniart) Sternberg

CHRISTOPHER J. CLEAL
Department of Botany, National Museum of Wales, Cardiff CF1 3NP

CEDRIC H. SHUTE
Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD

CONTENTS

SYNOPSIS. New evidence on the frond architecture of *Neuropteris heterophylla* (Brongniart) Sternberg is presented, based on well-preserved adpressions from Clay Cross, Derbyshire. Their cuticles provide the first reported evidence of epidermal structure for this species, including remains of trichomes apparently with *in situ* exudate. The new evidence indicates that this species is more closely related to *Neuropteris ovata* Hoffmann and *Neuropteris flexuosa* Sternberg, rather than to *Laveineopteris loshii* (Brongniart) Cleal *et al.* and *Laveineopteris tenuifolia* (Sternberg) Cleal *et al.*, as argued by some previous authors.

INTRODUCTION

Neuropteris (Brongniart) Sternberg is one of the most widely eported macrofossil form-genera from the Westphalian of Europe and North America. It represents foliage of an extinct group of gymnospermous plants known as the Trigonocarpales Meyen 1987 (Medullosales *auctt.*), which probably grew on evee banks and other raised areas within the equatorial delta plains of the time (Zodrow & Cleal 1988). Recently, our understanding of the form-genus has significantly improved, particularly as a result of frond architecture and cuticle tudies (Barthel 1961, 1962, 1976; Reichel & Barthel 1964; Laveine 1966*a*, 1966*b*, 1967, 1987; Laveine & Brousmiche 982; Zodrow & Cleal 1988; Cleal & Zodrow 1989), and it as become evident that the form-genus is far from homogeneous. As a result, some species have been transferred to other form-genera (e.g. *Paripteris* Gothan, *Neuralethopteris* Cremer *ex* Laveine – see Laveine, 1967) but, until recently, most have been retained in *Neuropteris*. This was partly because the frond of the type-species (*N. heterophylla* (Brongniart) Sternberg, 1825) had not been fully reconstructed, nor was anything known of its epidermal structure. Consequently, it was not possible to say which of the groups recognizable on, say, epidermal structure represented real *Neuropteris*, and which needed to be transferred to other form-genera.

The type species was first published as *Filicites (Nevropteris) heterophyllus* by Brongniart (1822), and was later changed to *Neuropteris heterophylla* (Brongniart) by Sternberg (1825). (Few subsequent authors have recognized the validity of Sternberg's initial publication of this combination, which is often attributed incorrectly to Brongniart (1828) – e.g. Crookall 1959, Laveine 1967). The small holotype was illustrated diagrammatically only (Brongniart 1822: pl. 2, figs 6a, b) and is now reported lost (Laveine 1967). Many authors have regarded it as conspecific with *Laveineopteris loshii* (Brongniart) Cleal *et al.* 1990 (e.g. Stockmans 1933, Havlena 1953, Crookall 1959), a common species distributed widely through the Westphalian A–C of Europe. Laveine (1967) has argued that this is unlikely, however, basing his contention mainly on a rather larger specimen of *N. heterophylla* figured by Brongniart (1831: pl. 71). This latter specimen is clearly quite different from *Laveineopteris loshii*, and hence many traditional conceptions about *N. heterophylla* (and consequently of the form-genus *Neuropteris* itself) would appear to be ill-founded. *N. heterophylla* as interpreted by Laveine (1967) is in fact an uncommon species; his synonymy refers to only ten undoubted specimens illustrated in the literature, and he figured another three.

The present paper documents some large and excellently preserved specimens in the palaeontological collections of the British Museum (Natural History), from which we have been able to provide a detailed reconstruction of the frond. Some of these specimens also yielded cuticles. The only previous record of *N. heterophylla* cuticles is by Wills (1914), based on specimens from North Wales. As we will argue later, however, Wills' material is almost certainly misidentified, and our specimens provide the first unequivocal evidence of the epidermal structure of this species. The results presented here have important consequences for the generic classification of neuropterid foliage, and have been the basis of the revised classification published by Cleal *et al.* (1990).

MATERIALS

This study is based largely on eight hand-specimens stored in the Department of Palaeontology, British Museum (Natural History) (Accession Numbers V.1797, V.1867, V.1868, V.1871, V.1872, V.2727, V.63152, V.63153). They are all labelled as originating from the 'Coal Measures, Clay Cross, Derbyshire'. No further stratigraphical details are given, but they probably came from the Westphalian B. Cuticles were prepared from four of these specimens: V.1867, V.1868, V.2727 and V.63152.

METHODS

The hand-specimens were photographed using crossed-polar filters. Because of limited page size, we cannot reproduce photographically all the specimens at the same scale; tracings from the photographs are therefore reproduced here at a uniform scale of × ⅓ (Figs 26–28).

Cuticles were prepared using the method outlined by Barthel (1962). Pieces of fossil were removed from the hand-specimens with a small chisel, and then placed in 40% hydrofluoric acid to remove the rock matrix (pre-treatment with hydrochloric acid was found to be unnecessary). The carbonaceous phytoleims (*sensu* Krystofovich 1944) were next oxidized in Schultze's Solution for 1–2 hours, and then treated with a 5% solution of ammonium hydroxide to remove the soluble oxidation products. The resulting cuticles were washed thoroughly in distilled water.

Most of the cuticles were mounted in glycerine jelly containing safranin dye. They were examined with a Leitz Ortholux II microscope, using differential interference phase contrast (Normarski contrast) at high magnifications. In addition, some cuticles were mounted on stubs, thinly coated with gold, and examined at 15 kV with an Hitachi S-800 field emission scanning electron microscope.

DESCRIPTIONS

Frond architecture

In their gross morphology, the specimens dealt with in this paper basically fall into two groups: wide tripinnate pinnae with broad primary racheis; and distally tapered, tripinnate pinnae. These are interpreted as proximal and distal fragments of the frond, respectively, and are most conveniently described separately.

Proximal frond fragments (Figs 1, 2, 26 and 27a). The most proximal part of the frond preserved in these specimens (Fig. 1) shows a primary rachis, 2·5 cm wide, that extends for 1·5 cm before branching dichotomously. The resulting branches lie at 90° to each other near the fork, but then gradually curve inwards towards each other. This curvature is achieved, at least in part, by a series of kinks occurring at about the points of attachment of each secondary pinna on the outward-facing side of the primary rachis (Fig. 2). The primary racheis above the dichotomy are 1·2–1·5 cm wide, tapering to *c.* 0·5 cm wide in the most distal part of the specimens (Figs 1, 2).

The overall shape of the two primary pinnae produced by the dichotomous primary rachis is not shown in these specimens, but they appear to taper proximally, at least on their inward-facing side. Each primary pinna is markedly asymmetrical, although they are essentially symmetrical to each other about the long axis of the frond (Fig. 1). On the outward-facing side of the primary rachis branches, robust secondary pinnae with racheis 0·5–0·6 cm wide are attached at 60°–70°, at intervals of 8–10 cm. Very little of these secondary pinnae is preserved, the longest fragment being only 15 cm long and clearly very incomplete, but they appear to be bipinnate (Fig. 1). Their shape cannot be determined from the fragments preserved. In between these large bipinnate secondary pinnae are much shorter (3–4 cm long) monopinnate intercalated pinnae spaced at 2–3 cm intervals (Fig. 2). They are tapered and terminated by a single rhomboidal apical pinnule.

On the inward-facing side of each primary rachis branch, secondary pinnae are inserted at intervals of 3–5 cm, usually at an angle of 70°–90°. They are 3 cm long and monopinnate near the base of the primary rachis branch (Fig. 1), becoming 30 cm long and bipinnate in the more distal parts (Fig. 2). Adjacent secondary pinnae overlap slightly in the middle of the frond. They appear tapered for much of their length, except in the longer ones which are parallel-sided in their proximal part, and are terminated by a single rhomboidal apical pinnule. There is little evidence of marked differentiation in development of the secondary pinnae, such as is seen on the outward-facing side of the primary racheis, but when they start to become bipinnate (some 20 cm from the base of the specimen), alternate secondary pinnae become shorter and less divided.

Another specimen with an apparently curved primary rachis is shown in Figs 3 and 27b. The primary rachis is *c.* 1·5 cm wide, tapering distally to 1·0 cm wide. Bipinnate

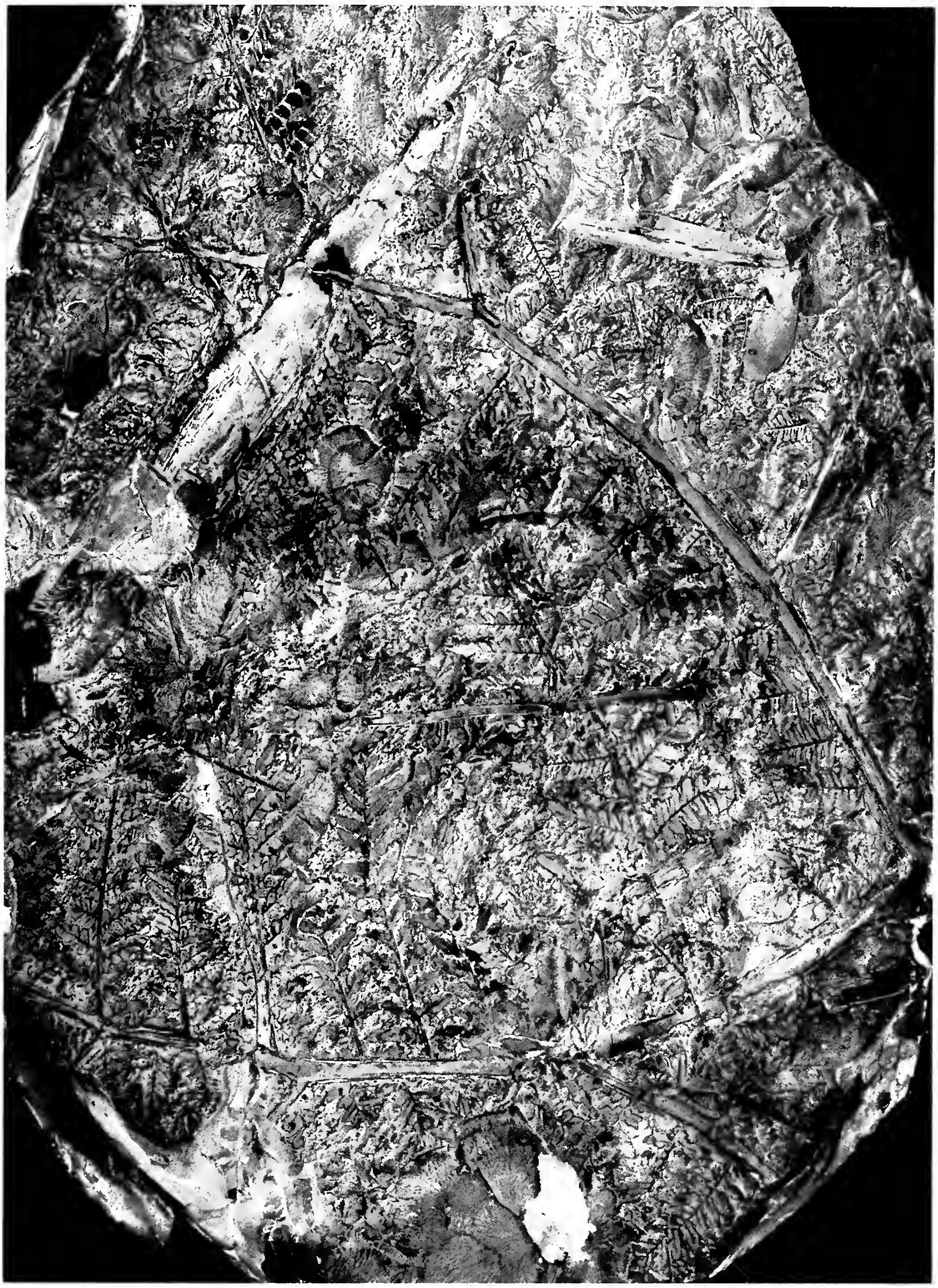


Fig. 1 *Neuropteris heterophylla.* Basal part of frond, showing dichotomy of primary rachis, photographed with crossed-polar filters. V.1797, × ⅓. See also Fig. 26.

econdary pinnae are attached at 60°–70° at *c.* 6 cm intervals n the right side of the specimen, but there is little evidence f secondary pinnae on the other side except for one short tump of secondary rachis. Short monopinnate pinnae are intercalated between the secondary pinnae, spaced at intervals of 1·5–2·0 cm. (In the middle of the specimen is a detached pinna of *Neuropteris semireticulata* Josten, unconnected with the *N. heterophylla* frond fragment.) If this was

Fig. 2 *Neuropteris heterophylla*, photographed with crossed-polar filters. Fig. 2a, primary rachis immediately above the dichotomy near base of frond. (The pinna fragment shown at the top is of the fern *Senftenbergia plumosa* (Artis) Zeiller.) V.1872, × ⅔. Figs 2b–d, details of Fig. 2a showing range of form of lateral pinnules, × 1. See also Fig. 27a.

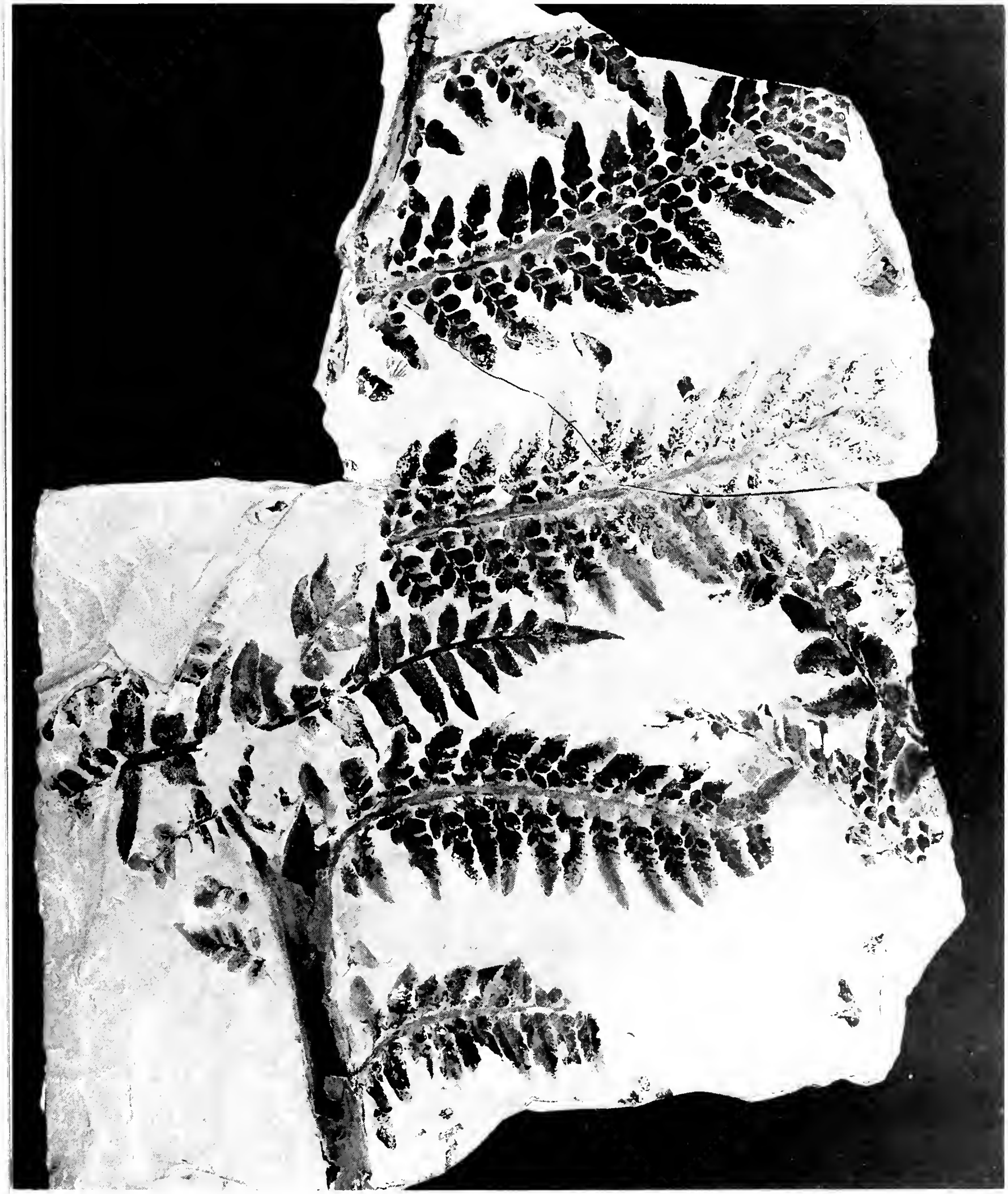
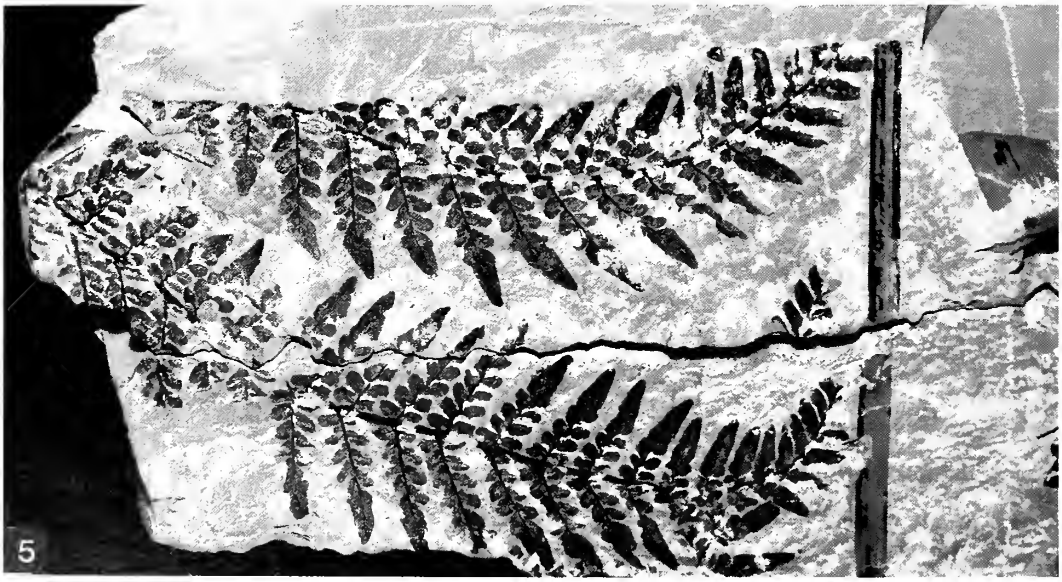


Fig. 3 *Neuropteris heterophylla.* Primary rachis probably just above dichotomy near base of frond, together with a detached fragment of a *N. semireticulata* Josten pinna, photographed with crossed-polar filters. V.63152, × ⅔. See also Fig. 27b.



Figs 4, 5 *Neuropteris heterophylla*, photographed with crossed-polar filters. Fig. 4, distal part of primary pinna branch. V.1867, × ⅔. See also Fig. 28c. Fig. 5, two bipinnate pinnae. V.1871, × ⅔. See also Fig. 28e.

part of a primary rachis from just above the main dichotomy, the greater width of the rachis and spacing of the secondary racheis suggest that it must have originated from a significantly larger frond than the specimens in Figs 1 and 2.

Distal frond fragments (Figs 4, 6–8, 28). These are distal segments of tripinnate pinnae, which are markedly asymmetrical about the primary rachis. The secondary pinnae on one side of the primary rachis are both longer and more pinnately divided than on the other. It is probable that the longer and more divided secondary pinnae were facing outwards from the frond, in which case Figs 4, 6 and 7 show left-hand primary pinna branches, and Fig. 8 a right-hand primary pinna branch. The primary rachis in most of the specimens is more or less straight, except that in Fig. 8, where curvature is accompanied by apparent distortion of the secondary pinnae, and may thus be a taphonomic effect. The widest primary racheis in these distal primary pinna fragments are 6 mm wide (Figs 6–7), and thus overlap with the width of the most distal preserved part of the primary pinnae in Fig. 1.

Fig. 6 *Neuropteris heterophylla.* Near distal part of primary pinna, photographed with crossed-polar filters. V.1868, × ⅔. See also Fig. 28b.

Secondary pinnae are attached at 60°–90° (most usually . 70°) on either side of the primary rachis. They are parallel-ided for much of their length, but are gently tapered in their listal part and terminated by a small, rhomboidal apical innule, *c.* 1 cm long. The secondary racheis are 0·5–3 mm vide. In the distal part of the frond the secondary pinnae are nonopinnate and oppositely arranged at intervals of 1–3 cm; ower in the frond they become bipinnate and alternately rranged at intervals of up to 5 cm. Where the secondary pinnae are bipinnate, one or two short, monopinnate pinnae are intercalated on the primary rachis between them. They are up to 2 cm long with a rhomboidal apical pinnule, and are spaced at intervals of *c.* 1 cm.

Tertiary pinnae are attached to the secondary racheis at 80°–90°, except near the secondary pinna apex where they are more oblique (*c.* 60°). They are spaced at intervals of 0·4 cm for the shorter pinnae, increasing to 0·8 cm in the longest preserved pinnae, and are oppositely or sub-oppositely

Fig. 7 *Neuropteris heterophylla.* Distal part of primary pinna, photographed with crossed-polar filters. V.2727, × ⅔. See also Fig. 28a.

arranged. They are parallel-sided for most of their length, and terminated by a single, rhomboidal apical pinnule, *c.* 1 cm long.

Pinnule morphology

Typical pinnules are shown in Figs 2b–d. They vary from 3 to 15 mm long and are 3–6 mm wide. The smallest pinnules are round to oval, about as broad as long; but the larger ones are more elongate, parallel-sided to linguaeform with a round apex. The longest pinnules are sometimes subtriangular with a bluntly acuminate apex. An acroscopic and sometimes a basiscopic swelling occurs near the base of the larger pinnules. In the largest pinnules the former becomes more prominent, until it eventually develops into a discrete, subsidiary order pinnule. Except near the pinna apex, the

Fig. 8 *Neuropteris heterophylla.* Distal part of primary pinna, photographed with crossed-polar filters. V.63153, × ⅔. See also Fig. 28d.

pinnules are at least partially constricted at the base. The degree of constriction is often more pronounced on the acroscopic side, with the pinnule being partially fused to the rachis on the basiscopic side. Only the largest pinnules tend to be equally constricted on both acroscopic and basiscopic sides. The angle of attachment of the pinnules to the rachis is usually 70°–80°. High in the pinna it sometimes appears to be as low as 60°, but this may be due to taphonomic distortion.

In the smallest pinnules there is little or no evidence of a midvein. In most pinnules, however, a thin midvein arises from the rachis at a low angle on the basiscopic side of the pinnule. It then curves and lies along the long axis of the pinnule. In most pinnules, the midvein is restricted to the

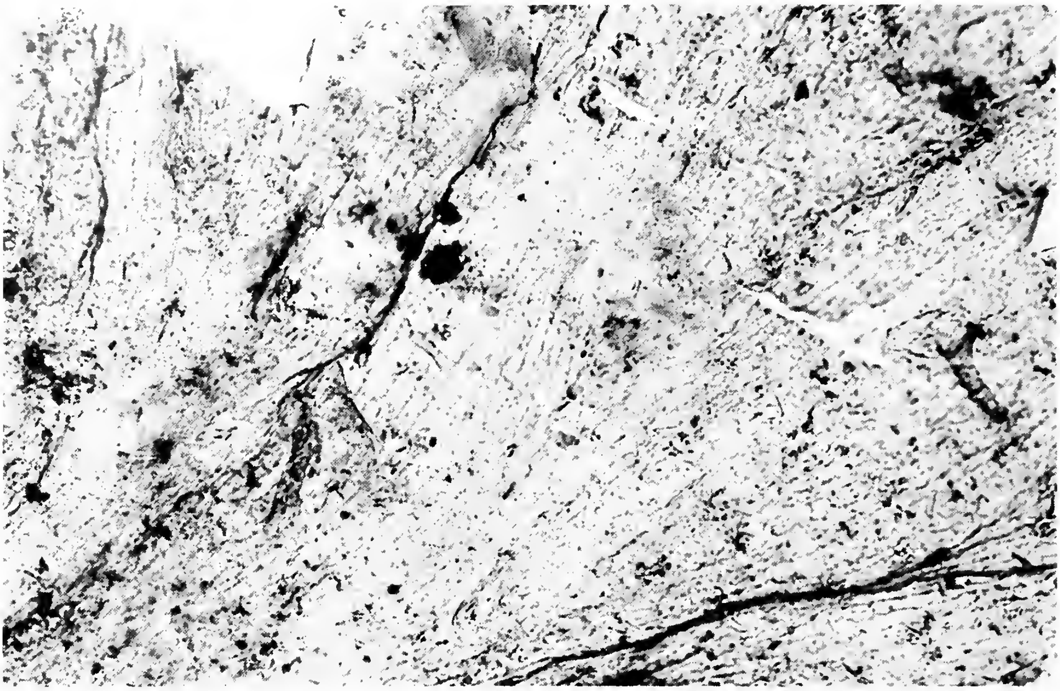


Fig. 9 *Neuropteris heterophylla.* Cuticle from adaxial surface of pinnule showing differentiation of cells in costal and intercostal fields, photographed using bright field illumination. V.2727$1, × 125.

lower half of the pinnule, but in the largest forms it may extend for up to two-thirds of the pinnule length. This decurrent midvein is never very pronounced, being only slightly wider than the lateral veins.

Lateral veins occur alternately on either side of the midvein, attached at intervals of 0·5–1·0 mm. They initially lie at a low angle to the midvein, extend for a short distance in an approximately straight line, and then arch to meet the pinnule margin at 80°–90°. They may branch up to four times, depending on the width of the pinnule. The angle of branching is usually 20°–30°, which often gives the veining a somewhat flexuous appearance. The vein density along the pinnule margin may vary from 40 to 55 per cm, but is usually between 48 and 52 per cm.

Cuticles

The adaxial cuticles from the pinnules appear robust, but have weakly developed intercellular flanges (Fig. 9). There is some differentiation in cell structure in the costal and intercostal fields. In the costal fields, the cells are elongate and subrhomboidal, up to 150 µm long × 20 µm wide (Fig. 17). Their long axes are aligned approximately parallel to the veins. In the intercostal fields the intercellular flanges are very weak, but there is a faint impression of shorter and more irregularly polygonal cells, up to 50 µm long × 20 µm wide (Fig. 18). Again, their long axes are aligned more or less parallel to the veins.

The abaxial cuticles are significantly thinner, and only small fragments could be prepared. Intercellular flanges, although not prominently developed, are clearly visible. Costal cells are elongate, parallel-sided and approximately 15 µm wide. It was impossible to determine their length. The intercostal cells are irregularly polygonal, 40–60 µm long and 12–18 µm wide, with their long axes aligned parallel to the nervation (Figs 10 and 20).

Stomata are restricted to the intercostal fields of the abaxial surface (Figs 10–11 and 19–22). They are anomocytic, with their polar axes approximately parallel to the veins. Their guard cells are 20–25 µm long and 5 µm wide. They do not seem to be significantly sunken.

Papillae occur in the costal fields of the abaxial epidermis (Fig. 10). They are 30–40 µm wide at their base and 25–35 µm high. Smaller papillae, 15–25 µm wide at their base and 10–20 µm high, also occur in the intercostal fields of the abaxial epidermis (Figs 19–20). They are less densely distributed than in the costal fields, and are mainly on the stomatal neighbour cells, where they appear to over-arch the guard cells (Figs 10–11 and 21–22).

Multicellular trichomes are also restricted to the abaxial epidermis, occurring mainly in the intercostal fields (Figs 12–14 and 23). They are 25–30 µm in diameter at their base, tapering to 20 µm. They consist of a uniseriate string of cells 25–35 µm long, and there is a slight constriction of the trichome at the junction of each cell (Fig. 12). The longest preserved fragment is 130 µm long, but is clearly incomplete (Fig. 12). Other examples are only 100 µm long, but seem to be entire and terminated by a swollen cell 35 µm in diameter, resembling a glandular structure (Figs 13–14). When viewed by SEM, these terminal structures appear to have ruptured, and situated on and near the apex of the trichome is an amorphous mass (Fig. 23; see also Fig. 13 for a view using light microscopy). Similar amorphous masses observed on these cuticles using light microscopy could be seen to have taken the safranin dye, and are almost certainly organic in origin. Being consistently associated with the trichome apices, they are, in our view, probably the remains of exudate produced by the trichomes. However, the volume of this

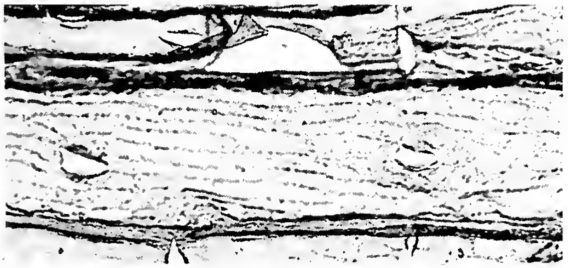
10

12

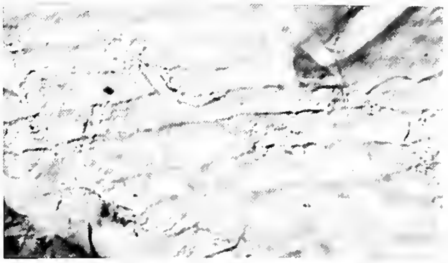
11

14

13

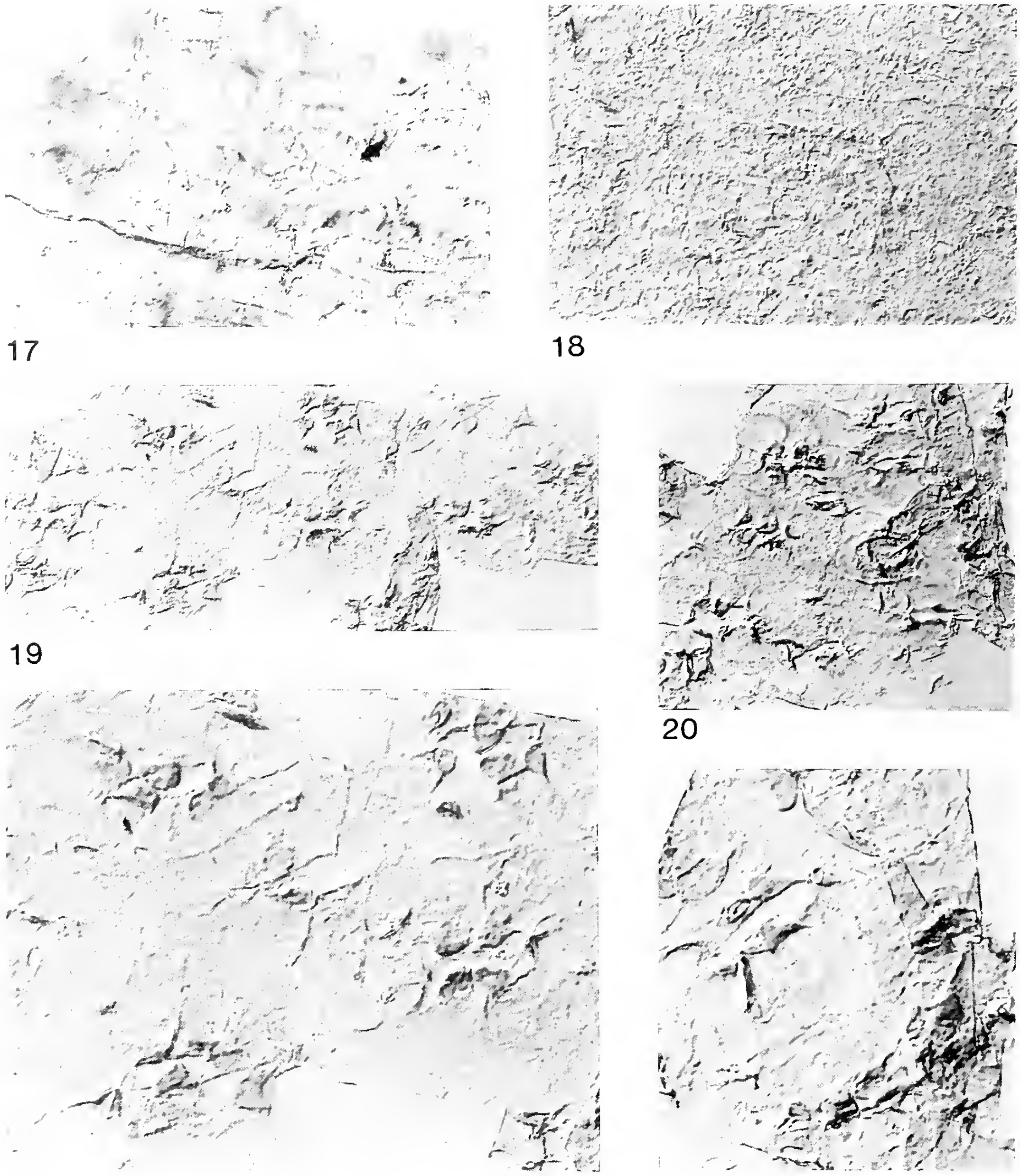


15



16

igs 10–16 *Neuropteris heterophylla.* Cuticles photographed using Normarski contrast (except Fig. 15). Figs 10–11, cuticles from abaxial surface of pinnule, showing papillate stomata, × 500. Fig. 10, V.1867$2. Fig. 11, V.1867$1. Figs 12–14, multicellular trichomes from abaxial surface of pinnule, × 500. Figs 12–13, V.63152$2. Fig. 14, V.2727$8. Fig. 15, cuticle from rachis, using bright field illumination. V.2727$8, × 125. Fig. 16, cuticle from rachis. V.2727$9, × 500.



Figs 17–22 *Neuropteris heterophylla.* Cuticles photographed using Normarski contrast. Fig. 17, cuticle from costal field on adaxial surface of pinnule. V.2727$1, × 250. Fig. 18, cuticle from intercostal field on adaxial surface of pinnule. V.1867$1, × 250. Figs 19–20, cuticles from abaxial surface of pinnule, showing parallel alignment of stomatal polar axes. V.1867$1, × 250. Figs. 21–22, details of papillate stomata. V.1867$1, × 500.

exudate often seems larger than could be contained in just the apical cell (e.g. Fig. 23d). This suggests that either the entire trichome functioned as a gland, in which case the transverse cell walls must have broken down when the trichome had become fully developed; or the exudate originated from a superficial cell within the body of the pinnule, and was channelled through the trichome to its apex.

Associated miospores

Attached to many of the cuticles prepared during this study were numerous miospores, mostly *c.* 25 µm in diameter (Figs 24–25). Dr B. Owens has kindly examined SEM photographs of some of them and concluded that they are a mixed assemblage, dominated by ?*Lycospora*, ?*Densosporites* and ?*Granulatisporites*. These trilete form-genera are believed to have been mostly produced by lycophytes and ferns (Smith & Butterworth 1967) and are quite different from the monolete prepollen produced by most medullosans (Stidd 1981). The only possible medullosan male reproductive organ to produce trilete prepollen is *Potoniea* (Halle 1933, Florin 1937), which Millay & Taylor (1979) have interpreted as an early offshoot from the main medullosan stock (see also Stidd 1978, 1981). In

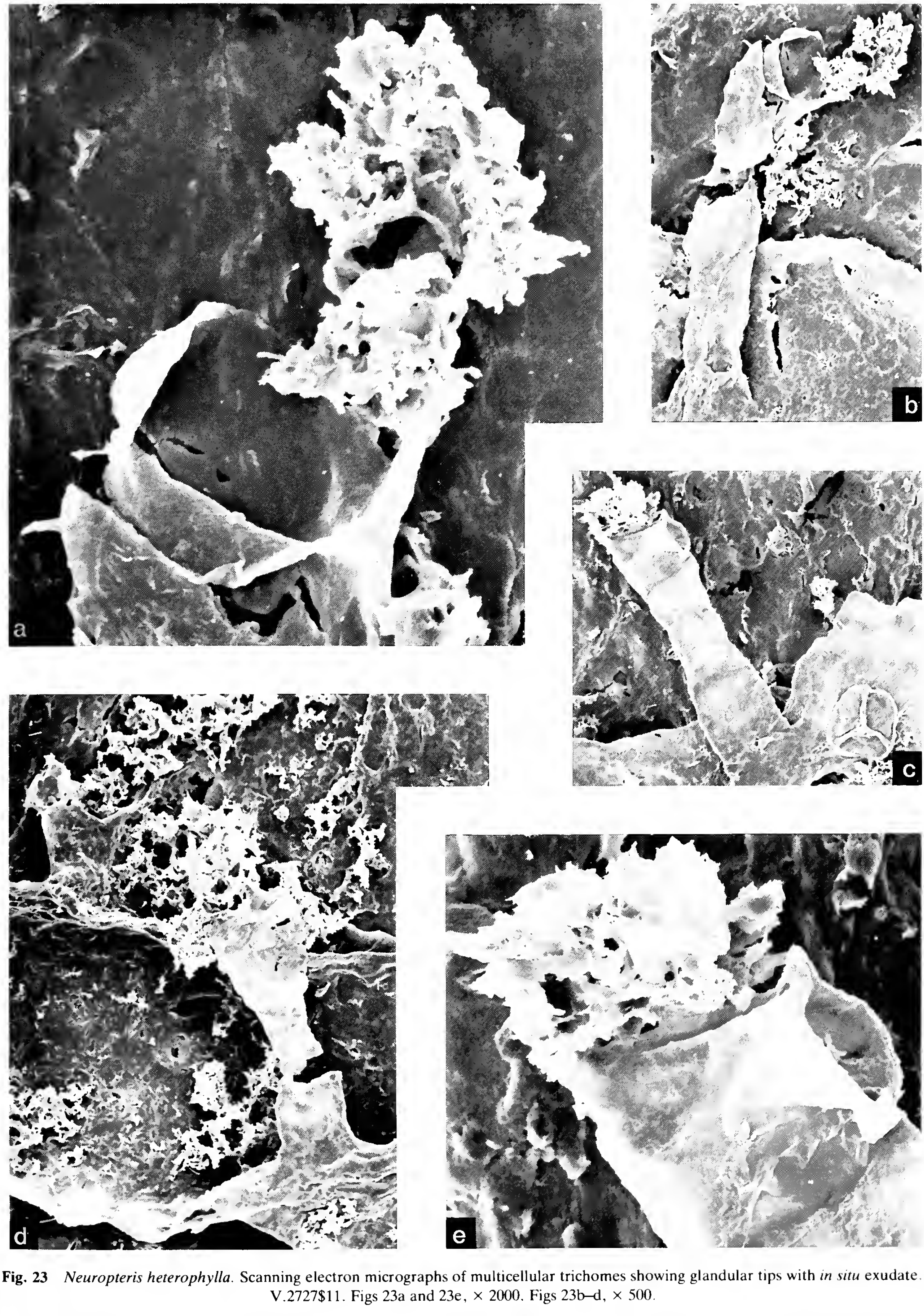


Fig. 23 *Neuropteris heterophylla*. Scanning electron micrographs of multicellular trichomes showing glandular tips with *in situ* exudate. V.2727$11. Figs 23a and 23e, × 2000. Figs 23b–d, × 500.

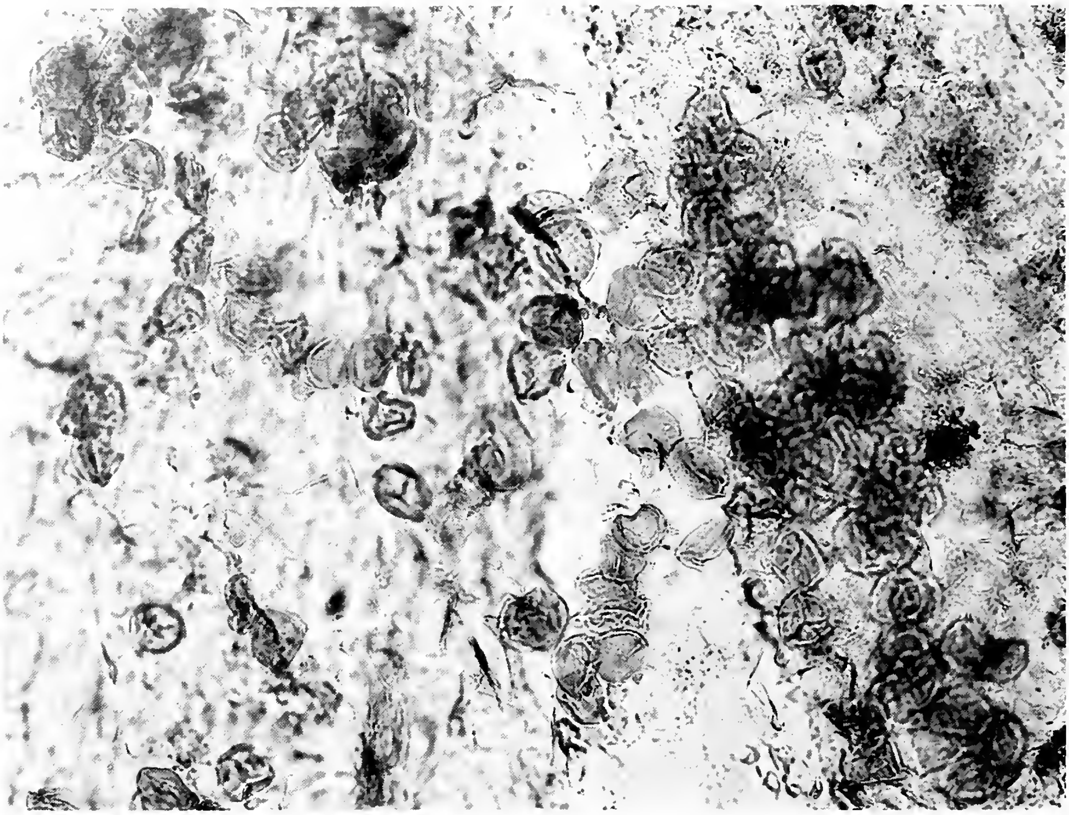


Fig. 24 *Neuropteris heterophylla.* Cuticle from abaxial surface of pinnule, photographed using bright field illumination, showing numerous spores attached. V.2727$2, × 250.

any case *Potoniea* prepollen is significantly larger (40–90 µm in diameter), has a less prominent tetrad mark than the miospores attached to our cuticles, and displays a distal sulcus. In our view, therefore, the miospores are unlikely to have anything to do with the plant which produced the *N. heterophylla* fronds. They probably only reflect the general spore/pollen rain in these lycophyte-dominated forests.

DISCUSSION

Reconstruction of frond

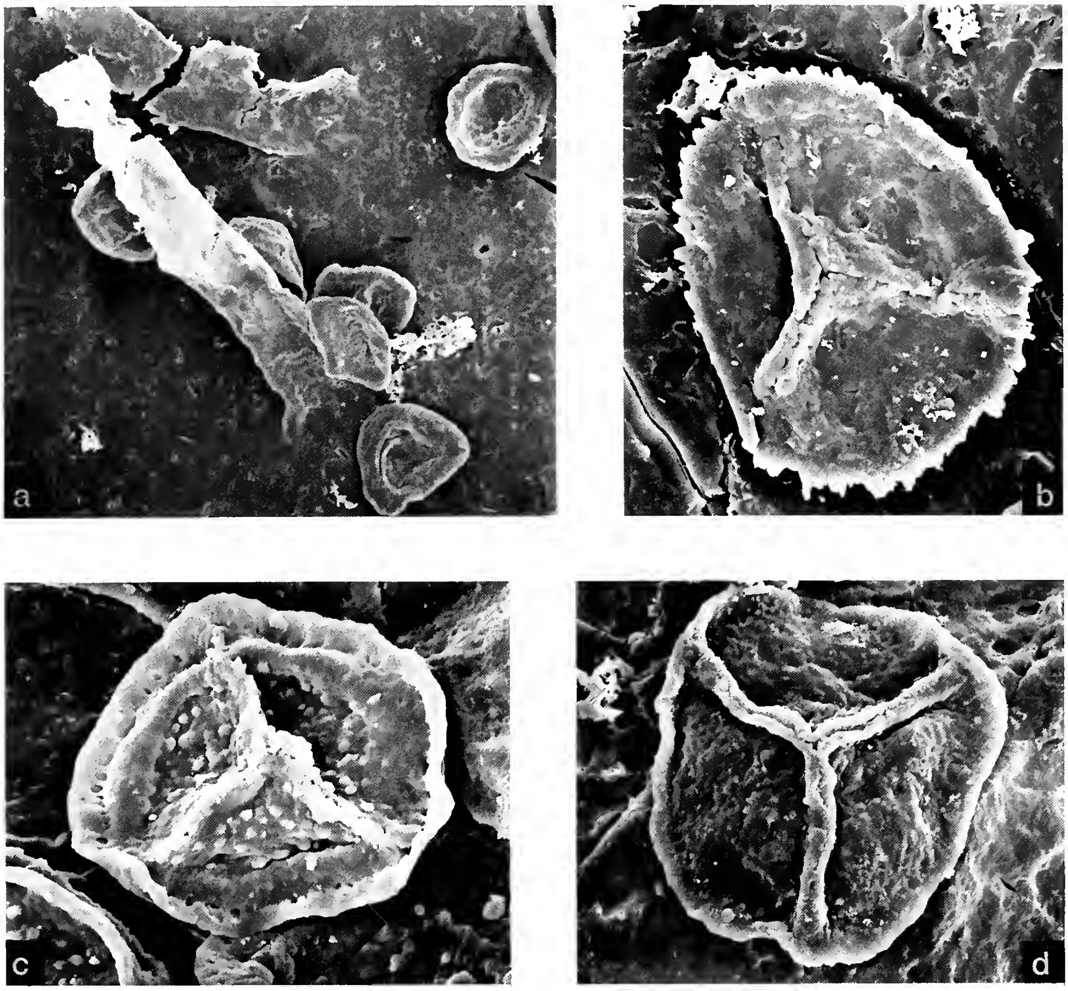
Based mainly on the specimens from Clay Cross described in this paper, we propose a reconstruction of the *N. heterophylla* frond, shown in Fig. 29. For convenience, the specimens have been reproduced at a unified scale as drawings (Figs 26–28), and the following discussion will refer to these rather than the photographs illustrated earlier in the paper. The reconstructed frond shows the following key features.

Dichotomy of primary rachis. This is particularly well seen in Fig. 26. The dichotomy is wide-angled and the resulting branches curve distally towards one another. It is also shown by the specimen figured by Brongniart (1831: pl. 71). Brongniart's drawing of this specimen suggests that the fork was a lateral branch, but Laveine's (1967: pl. A) photograph clearly shows that the right-hand side of the frond fragment is distorted. Taking this distortion into account, Brongniart's specimen shows the same pattern of branching as our Fig. 26, and differs only in having a narrower primary rachis and closer-spaced secondary pinnae (see comments below on estimated frond sizes).

Another, but less complete specimen figured by Laveine (1967: pl. M, fig. 1), part of which is also figured by Zeiller (1886: pl. 44), shows part of the frond just above the dichotomy. The two primary pinna branches lie at *c.* 80° to each other, although the dichotomy itself is not preserved.

Architecture below dichotomy. The specimen in Fig. 26 shows little of the frond below the dichotomy, but some evidence about this part of the frond is supplied by the specimen figured by Brongniart (1831: pl. 71). A 4-cm length of the main rachis below the dichotomy is preserved, and has monopinnate pinnae attached on either side. The only other specimen which probably shows this part of the frond is that illustrated by Crookall (1959: pl. 33, fig. 2), which has a rachis 0·9 cm wide, bearing short monopinnate pinnae. It compares favourably with the structure and dimensions of that part of the Brongniart (1831) specimen lying below the dichotomy, and it is difficult to see where else it could have occurred in the frond. The Crookall specimen is 13 cm long, and this is thus the minimum distance below the dichotomy that these monopinnate pinnae could have been attached.

There is no evidence of orbiculoid cyclopterid pinnules being attached to the primary rachis near the dichotomy, as in *Laveineopteris loshii* (Brongniart) Cleal *et al.* (von Roehl,



ig. 25 *Neuropteris heterophylla*. Scanning electron micrographs of spores attached to cuticle from abaxial surface of pinnule, V.2727$11. Fig. 25a, cluster of spores near base of multicellular trichome, × 500. Fig. 25b, unidentified azonate spore with equatorial ornamentation. Fig. 25c, ?*Densosporites* sp. Fig. 25d, ?*Granulatisporites* sp. Figs 25b–d, × 2000.

868: pl. 17), *Laveineopteris rarinervis* (Bunbury) Cleal *et al.* Carpentier, 1930: pl. 8; Gothan, 1953: text-fig. 8; Laveine, 967: pl. 41, fig. 3; pl. 45, fig. 3; pl. O, fig. 1). The specimen dentified as *N. heterophylla* with possible cyclopterids attached (Gothan, 1953: text-fig. 6) has been re-identified as *L. loshii* by Laveine (1967). The architecture seen in *N. heterophylla* is nearer to that of *N. obliqua* (Gothan, 1953: text-fig. 7) and *N. ovata* Hoffmann (Zodrow & Cleal 1988). Neither V.1797 nor the specimen figured by Brongniart 1831: pl. 71) show any evidence of the type of enlarged pinnules present in the lower part of the *N. ovata* and *N. obliqua* fronds (sometimes referred to as forma *impar* pinnules). However, the specimen of *N. heterophylla* illustrated by Laveine (1967: pls 11–12), which is probably part of a left-hand primary pinna just above the basal dichotomy, eems to have large, subtriangular pinnules, similar in shape o the forma *impar* pinnules from the base of the *N. obliqua* ronds.

Primary pinna branches immediately above dichotomy. A distinctive feature of *N. heterophylla* is the way that the primary pinna branches compensate for the reduced space available on their inward-facing side, due to the curvature of the primary rachis. It is achieved by the secondary pinnae being alternately long and short along that part of the primary rachis showing maximum curvature. It has not been demonstrated in any other neuropteroid species, nor in related fronds such as *Odontopteris* (Zeiller 1906) or *Callipteridium* (Wendel 1980). It can be clearly seen in Figs 26 and 27a.

Primary pinna terminals. These are well shown in Figs 28a–d. Another example was figured by Zeiller (1879: pl. 164, fig. 1; refigured by Zeiller, 1886: pl. 43, fig. 1). They become tripinnate at only a short distance from the pinna apex, and are normally distinctly asymmetrical about the primary rachis. This asymmetry is almost certainly a continuation of the asymmetry of the lower part of the primary pinna, with the side with the longer secondary pinnae facing outwards from the frond.

The small specimen shown in Fig. 28e may also have come from near a primary pinna terminal. However, bipinnate pinnae are also known attached to the inward-facing side of the primary pinna, lower in the frond (e.g. *c.* 40 cm above the dichotomy in Fig. 26). Since only two pinnae are shown in

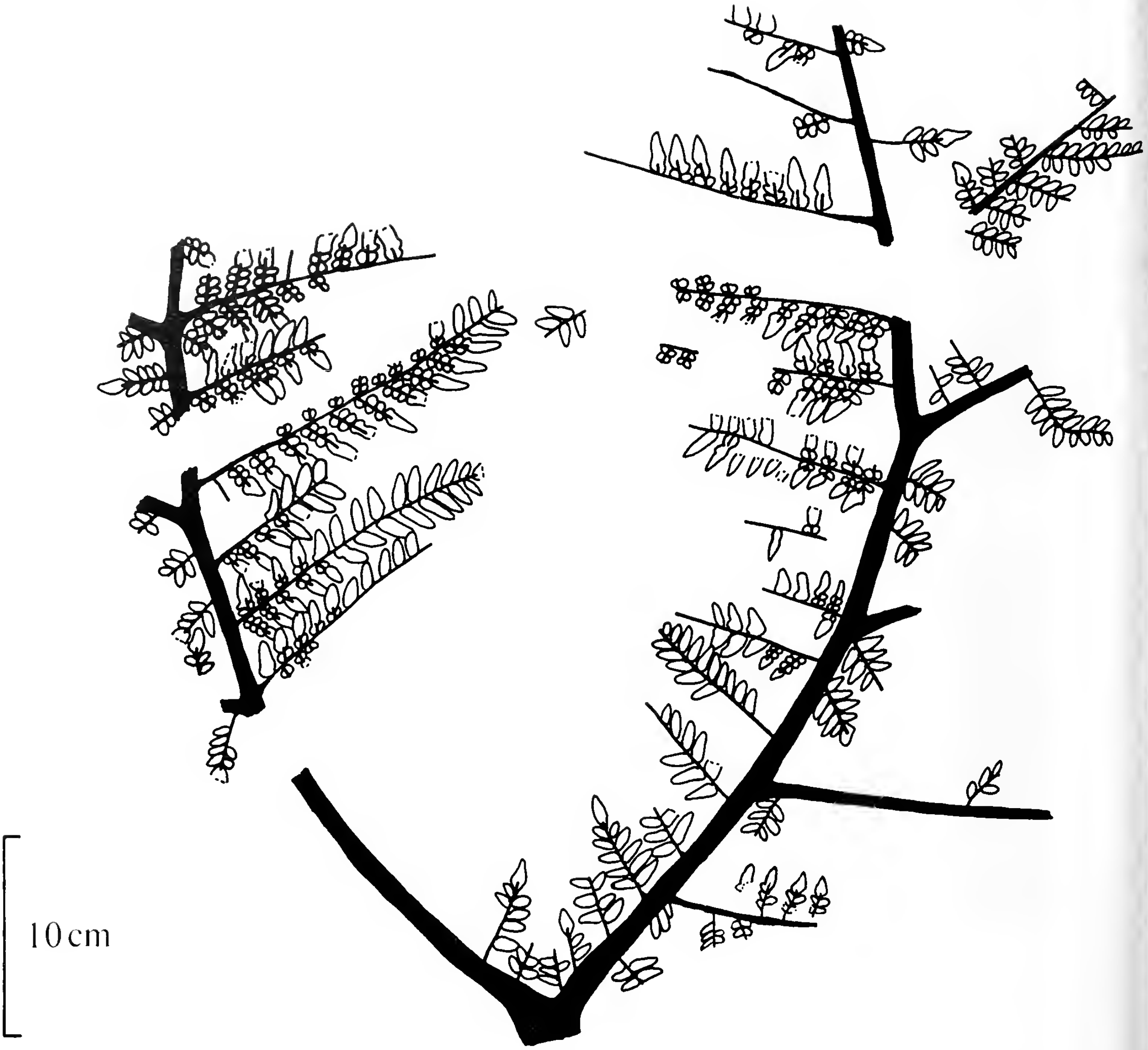


Fig. 26 *Neuropteris heterophylla*. Drawing of specimen shown in Fig. 1, showing dichotomy of primary rachis near the base of the frond. V.1797, × 0.3.

Fig. 28e, it is impossible to determine whether they are alternating long and short, as is characteristic of the lower part of the frond. This demonstrates the difficulty of positioning such small specimens within so complex a structure as the *N. heterophylla* frond.

Size and degree of pinnation of secondary pinnae. No complete secondary pinnae have been found attached to the outward-facing sides of the primary pinnae in the basal part of the frond. The longest known examples are 13 cm long (Fig. 26; see also Laveine, 1967: pl. 11, fig. 1), but are clearly very incomplete. The longest detached example is probably that shown in Crookall (1959: pl. 25, figs 1–2). It is a 17-cm long near terminal fragment of a bipinnate pinna. It is more or less symmetrical about the penultimate rachis, and is thus quite different from the asymmetrical terminals of the primary pinnae (discussed above). In nearly all of the known specimens, these outward-facing secondary pinnae are bipinnate. Just one (Laveine, 1967: pls 11–12) shows a tendency to become tripinnate.

Size of frond. None of the specimens described in this study, or documented in the literature, are complete enough to give a very reliable estimate of the overall size of the frond. However, using the largest available specimen (Fig. 26) it is possible to assess the approximate distance from the dichotomy to the frond apex (hereafter referred to as the DAD). Assuming that the two primary pinna branches, which curve distally in towards one another, did not overlap significantly at the frond apex, then the DAD in this frond was about 1 m. Using this as a base-line, it is possible to estimate the DAD of fronds in other, less complete specimens, using the assumption that frond size is broadly correlated with primary rachis width (PRW) and the spacing

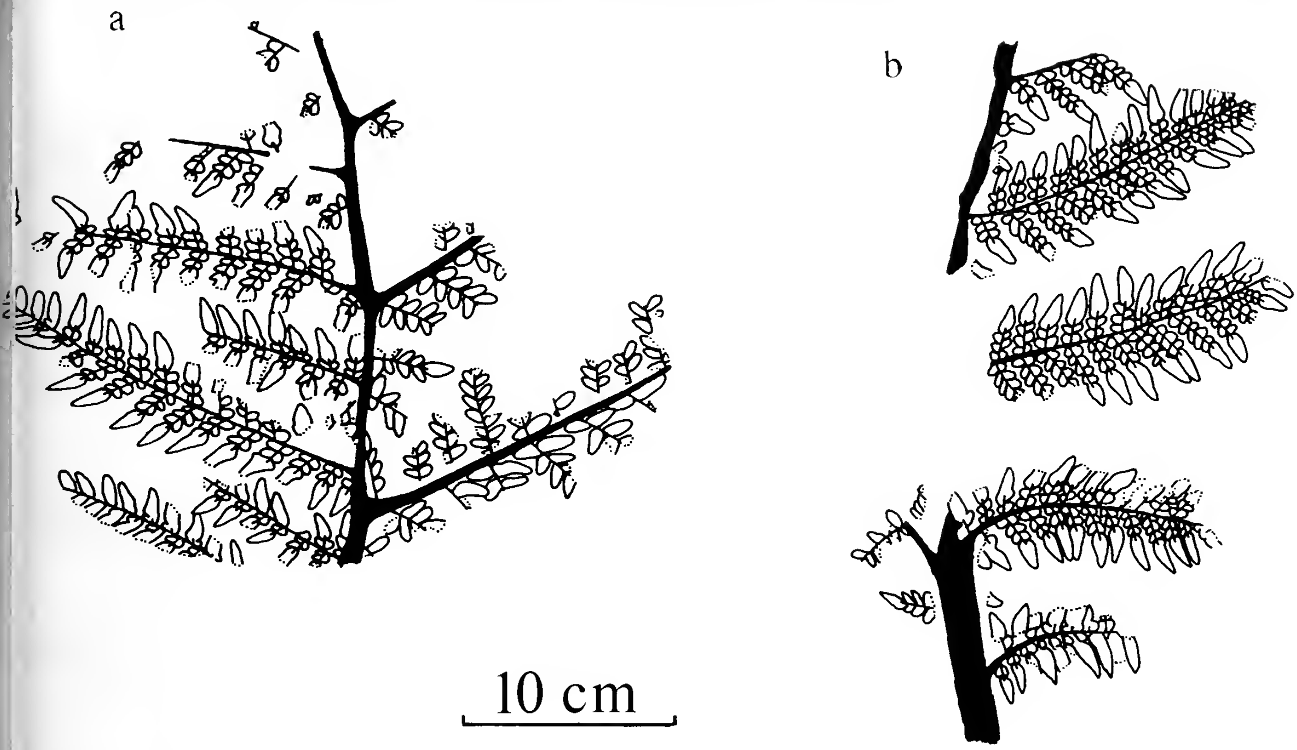


Fig. 27 *Neuropteris heterophylla.* Drawings of specimens shown in Figs 2–3, showing parts of primary rachis near the main dichotomy of the frond. Fig. 27a, V.1872. Fig. 27b, V.63152. Both × 0.3.

between secondary racheis (SRS) in comparable parts of the frond.

a. The smaller fragment shown in Fig. 27a has PRW and SRS dimensions comparable to a position about 35 cm above the dichotomy in Fig. 26. Consequently, it is also probably from a frond with a DAD of *c.* 1 m.

b. The specimen figured by Zeiller (1886: pl. 44) and Laveine (1967: pl. M, fig. 1) also has PRW and SAS dimensions similar to that in our Fig. 26. Its DAD is therefore again estimated to be *c.* 1 m.

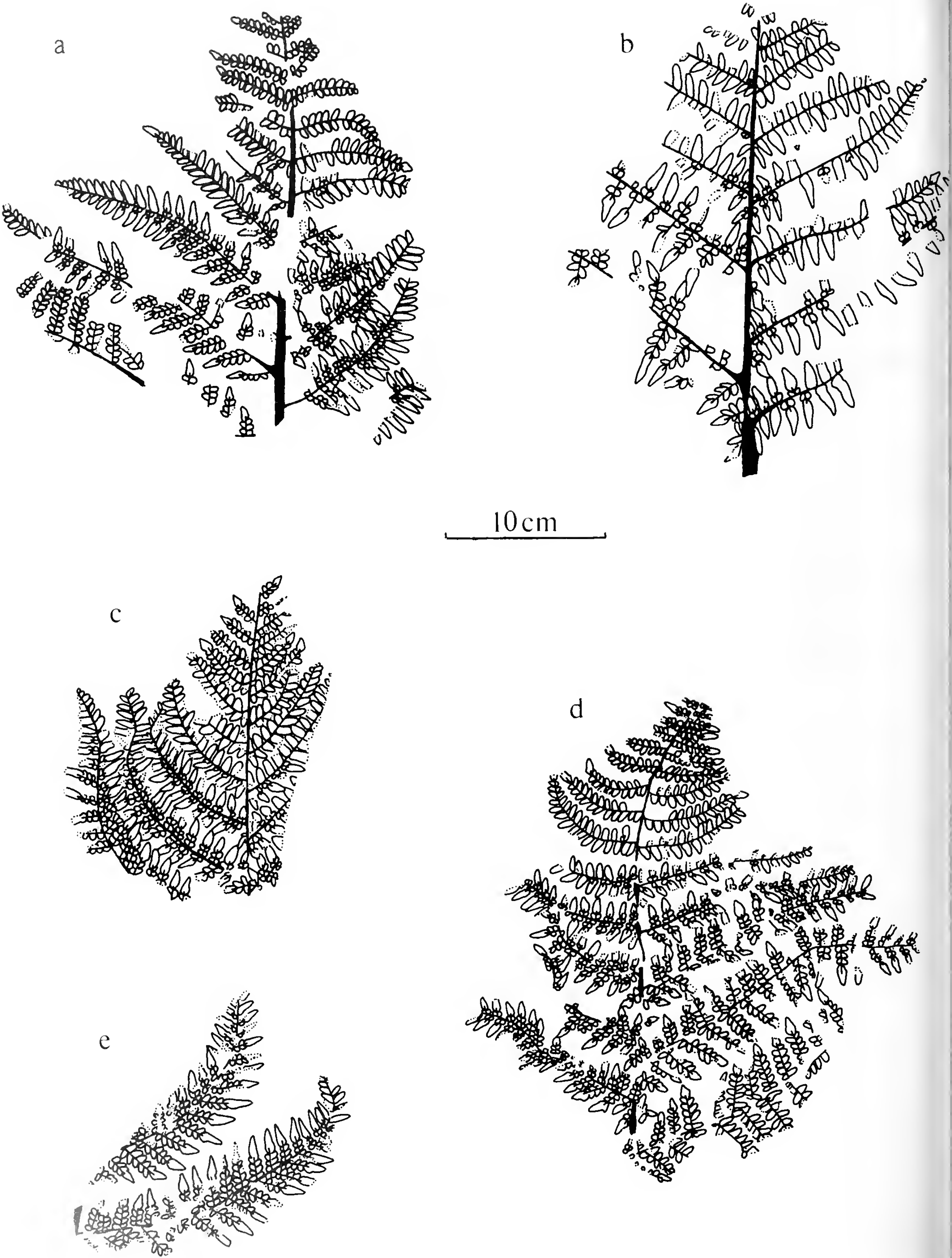
c. The specimen figured by Brongniart (1831: pl. 71) has a PRW immediately below the dichotomy of 1·4 cm, and a SAS on the outward-facing side of the frond just above the dichotomy of 4–5 cm. These dimensions are about half those in Fig. 26, and so the DAD is estimated as *c.* 0·5 m.

d. Fig. 27b shows a curved primary rachis with a PRW 1·5–1·0 cm and a SAS of *c.* 6 cm. If this was the proximal part of a primary pinna branch, then the PRW is approximately twice that in Fig. 26, and consequently the DAD would be *c.* 2 m. It is true that Fig. 27b does not show the alternating long and short secondary pinnae normally characterizing the proximal part of the frond, but this may simply be because the secondary pinnae were more widely spaced, reducing the competition for space in this part of the frond. The only alternative position for such a specimen would be below the dichotomy, but the marked tapering of the primary rachis, and the presence of bipinnate secondary pinnae (only monopinnate secondaries have been otherwise found in this part of the frond) tend to argue against this.

From the above evidence, it appears that the DAD of the fronds was normally 0·5–1·0 metres, possibly sometimes reaching 2·0 metres. To translate this into an estimate of the total length of the foliage-bearing part of the frond, it would be necessary to know how far the foliage extended below the dichotomy. There is little unequivocal evidence on this. The specimen figured by Brongniart (1831: pl. 71) shows 4 cm of frond below the dichotomy. However, if the specimen figured by Crookall (1959: pl. 33, fig. 2) has been correctly interpreted as part of a primary rachis below the dichotomy (see p. 166), then there was at least 13 cm of foliage below the dichotomy in a small frond. This suggests that there may have been at least 30 cm of foliage below the dichotomy in one of the fronds with a DAD of 1 metre, and perhaps 60 cm or more in the largest fronds. Combining this evidence, we suggest that the overall length of the foliage-bearing part of the frond may have varied from 0·7 m to 2·6 m, the most commonly found probably being about 1·3 m long. There is no evidence available as to the length of the petioles, and so it is impossible to estimate the complete length of the frond, from its point of attachment to the stem to the apex.

No complete outward-facing secondary pinnae are preserved, so the width of the frond cannot be determined. Fig. 26 shows a width of 0·6 m, but the secondary pinnae are clearly very incomplete, and the total frond width may have been 1·0 m or more. If this estimate is correct, then that part of the frond lying above the primary pinna dichotomy must have been as wide as it was long.

General comments on frond architecture. The type of bipartite frond reconstructed in Fig. 29 broadly reflects the


a
b
10 cm
c
d
e

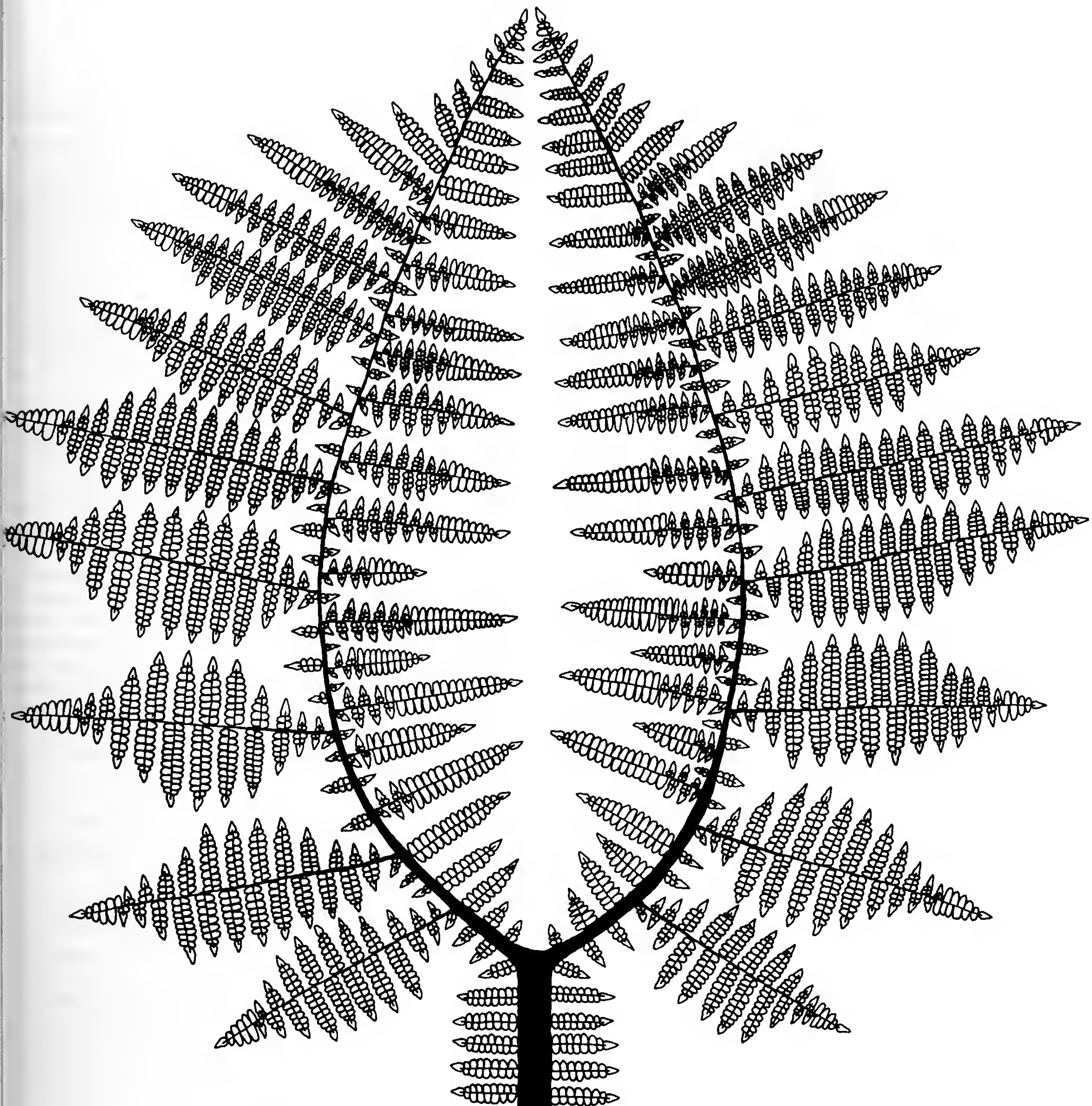


Fig. 29 *Neuropteris heterophylla.* Proposed reconstruction of average-sized frond. About one seventh natural size.

---

ig. 28 *Neuropteris heterophylla.* Drawings of specimens shown in Figs 4–8, showing near terminal parts of primary pinnae. Fig. 28a, V.2727. Fig. 28b, V.1868. Fig. 28c, V.1867. Fig. 28d, V.63153. Fig. 28e, V.1871. All × 0.3.

structure envisaged by Gothan (1941) for *Neuropteris* (syn. *Imparipteris*), except for the absence of orbicular cyclopterid pinnules at the base. Although varying in detail, such a bipartite structure is extremely common in Palaeozoic pteridosperm fronds, occurring in the Calamopityales, Callistophytales and Lyginopteridales, as well as the Trigonocarpales (Daber 1980, Gastaldo 1988); only the Peltaspermales fronds are normally characterized by exclusively pinnate branching (Kerp 1986). It thus occurs in both classes of Palaeozoic pteridosperms (the Ginkgoopsida and Cycadopsida *sensu* Meyen, 1987), which are believed to have evolved independently from the progymnosperms. Consequently, the bipartite frond structure also probably developed independently in the two classes. Its function is at present unclear, but may have maximized the width of each frond without developing excessively long racheis, particularly those of the second order. For structural reasons, the longer a rachis becomes, the wider it must be, particularly in its proximal part. Since the racheis probably had no photosynthetic function (they show no evidence of stomata), minimizing the rachis:lamina bulk ratio would help increase the efficiency of the frond as a whole.

Significance of epidermal structures

Based mainly on cuticle evidence, Cleal & Zodrow (1989) divided *Neuropteris* into four main groups. Elucidating the epidermal structure of *N. heterophylla* has had important consequences for the nomenclature of this group of foliage, since it has allowed the four groups to be made the basis of a formal taxonomy. Full details of the revised nomenclature are presented by Cleal *et al.* (1990), but the results may be summarized as follows.

Group 1 = *Laveineopteris* Cleal, Shute & Zodrow 1990
Group 2 = *Neuropteris* (Brongniart) Sternberg *emend.* Cleal, Shute & Zodrow 1990
Group 3 = *Macroneuropteris* Cleal, Shute & Zodrow 1990
Group 4 = *Neurocallipteris* Sterzel *emend.* Cleal, Shute & Zodrow 1990

From the preconceptions of earlier authors (e.g. Bertrand, 1930) *N. heterophylla* might be expected to fall into Group 1 of this classification (i.e. with *'N.' loshii*, *'N.' tenuifolia* and *'N.' rarinervis*). However, the epidermal characters found in the present study place it clearly in Group 2 (i.e. with *N. ovata* and *N. flexuosa*). These are: the cell structure in the costal and intercostal fields are clearly differentiated on the adaxial surface; the stomata are anomocytic; cell structure is clearly visible on the abaxial cuticle; and there are both papillae and multicellular trichomes on the abaxial cuticle.

Although multicellular trichomes are present in other neuropteroid species (Barthel 1961, 1962, Cleal & Zodrow 1989), this is the only one reported to have glandular-tipped hairs. In some of the specimens, what appear to be the remains of the exudate produced by the glands are preserved. To the best of our knowledge, this is the oldest evidence of *in situ* exudate preserved in the fossil record. It seems to have been a sticky, resinous substance, which also covered at least part of the abaxial surface of the frond, causing numerous miospores to adhere to it. Whether this condition was the result of taphonomic breakdown of the glandular tips, causing the exudate to become spread over the frond surface, or whether the exudate covered the frond surface in life, is not clear. Its function is also not certain, although a protective role against herbivorous insect attack would seem possible. It has been noted elsewhere that there is little direct evidence of insect attack in medullosan foliage and that they must have had some defence against it (Cleal & Laveine 1988, Cleal & Zodrow 1989). The sticky exudate produced by the hairs of *N. heterophylla* could well have been a deterrent to such attack, although it seems strange that this is the only neuropterid known to adopt such a strategy. On the other hand, Beerbower *et al.* (1987) argued that herbivory was not a significant feeding mode for Carboniferous arthropods, in which case the exudate may have had an alternative, perhaps excretory function.

Taxonomy

Laveine (1967) has reported that the type specimen of *N. heterophylla* figured by Brongniart (1822) is lost. He therefore nominated a specimen figured by Brongniart (1831: pl. 71) as neotype, and illustrated a photograph of it.

In the absence of direct evidence of reproductive organs or stem/rachis anatomy, the taxonomic position of *N. heterophylla* can only be determined from circumstantial evidence. We have provisionally placed it in the pteridosperm order Trigonocarpales Meyen based on its similarity, in both frond architecture and epidermal structure, to *Neuropteris ovata*, which Beeler (1983) has reported attached to *Medullosa noei* Steidtmann stems. As with most species of trigonocarpalean foliage, the identification of *N. heterophylla* has traditionally depended on the shape and nervation of the pinnules, and we have been able to add little to the description of these features given by Laveine (1967). We have, however, been able to add details of its epidermal structure, which require the diagnosis to be enlarged. The taxonomy may be summarized as follows.

Division **PINOPHYTA** Meyen, 1987
Order **TRIGONOCARPALES** Meyen, 1987

Form-genus ***NEUROPTERIS*** (Brongniart) Sternberg
emend. Cleal *et al.* 1990

Neuropteris heterophylla (Brongniart) Sternberg

1822 *Filicites (Nevropteris) heterophyllus* Brongniart: 239; pl. 2, fig. 6.
1825 *Neuropteris heterophylla* (Brongniart) Sternberg: xvi.
1967 *Neuropteris heterophylla* (Brongniart) Sternberg; Laveine: 140; pl. A; pl. B, fig. 1; pls 11–13 (q.v. for synonymy).
1990 *Neuropteris heterophylla* (Brongniart) Sternberg; Cleal *et al.*: 487.

DIAGNOSIS. Ultimate pinnae oval and imparipinnate. Pinnules oval, sometimes somewhat triangular, generally with round apex. Pinnule base cordiform in proximal part of pinna; towards pinna apex becoming attached to rachis by up to half of its catadromic side. Apical pinnules usually broad with round apex, and length:breadth ratio 1–2; on short pinnae, more elongate with an obtuse apex. Nervation dense. Midvein visible for about half of the pinnule length and rather strong at base. Thick, somewhat flexuous lateral veins arise from midvein at acute angles, dichotomize two to four times, and reach pinnule margin at oblique angles. Adaxial cuticle thicker than abaxial. Adaxial epidermal cells subrhomboidal, more elongate in costal fields. Papillae and glandular multi-cellular trichomes abundant on abaxial epidermis. Stomata anomocytic, only on intercostal fields of abaxial epidermis; polar axes more or less parallel to veins.

Comparison with other species

Neuropteris heterophylla is most similar to *N. obliqua* (Brongniart) Zeiller and isolated fragments are easily confused. However, the former has rounder lateral pinnules, attached more narrowly to the rachis; and broader, more deltoid apical pinnules with a rounder apex. Also, it does not have the large subtriangular pinnules (known as forma *impar*) that characterize the basal part of the *N. obliqua* frond. The epidermal features of *N. obliqua* are at present unknown (cuticles identified as this species by Barthel, 1962, in fact belong to *Laveineopteris loshii* (Brongniart) Cleal *et al.* – see Laveine, 1967).

Also very similar is the holotype of *Neuropteris grangeri* Brongniart, which originated from the Pennsylvanian of Ohio, USA (Laveine 1967: pl. H, fig. 2). The American specimen has pinnules with a more obtuse apex than is typical for *N. heterophylla*, and lateral veins that meet the pinnule margin at a less oblique angle. However, not enough material has been described from the type area of *N. grangeri* to determine the range of its morphological variation, and so a full comparison with *N. heterophylla* is impossible.

Many of the European records of *N. grangeri* were transferred to *Neuropteris ghayei* Stockmans & Willière by Stockmans & Willière (*in* Pastiels & Willière, 1954). *N. ghayei* is very similar to *N. heterophylla*, but has rather larger, rounder, thicker-limbed pinnules. Furthermore, the midvein of *N. ghayei* is only well developed near the base of the pinnule and the lateral veins are more flexuous, sometimes pseudoanastomosed. It also tends to have more tapered ultimate pinnae. The epidermal structure of *N. ghayei* is unknown.

It can be difficult to distinguish the smaller pinnules of *N. heterophylla* and *Laveineopteris loshii* (Brongniart) Cleal *et al.*, which are more or less oval in both species. However, the larger pinnules of the latter are more linguaeform and have a more prominent midvein extending for at least ⅔ of the pinnule length. Also, *L. loshii* has more broadly arched lateral veins, which meet the pinnule margin at a less oblique angle and are never flexuous. There is also a significant difference in the cuticles. The adaxial epidermal cells of *L. loshii* do not differ significantly between the costal and intercostal fields; the abaxial cuticle shows little evidence of cell structure, other than the stomatal guard cells, and there are neither papillae nor the glandular hairs as found in *N. heterophylla*.

Laveineopteris tenuifolia (Sternberg) Cleal *et al.* could be confused with the larger pinnules of *N. heterophylla*, but are generally more linguaeform, have a more prominent midvein extending for up to ¾ of the pinnule length, and non-flexuous lateral veins. The epidermal structure of *L. tenuifolia*, which is essentially identical to that of *L. loshii*, also serves to distinguish it from *N. heterophylla* (see previous paragraph).

The specimens described by Wills (1914) as *N. heterophylla* are difficult to assess. Only one figured specimen shows features of the gross morphology, and this is a single, small pinnule, probably from a near-terminal position in a pinna. It shows none of the characters necessary to place it in a particular species. The cuticles figured by Wills are quite different from those of *N. heterophylla*, lacking the prominent papillae on the abaxial surface, and having cyclocytic stomata with a ring of significantly thickened subsidiary cells. Based on the epidermal characters, Wills' specimens are closest to *Macroneuropteris scheuchzeri* (Hoffmann) Cleal *et al.*, but it would be difficult to reconcile such an identification with the small size of the pinnules.

ACKNOWLEDGEMENTS. Thanks go to Dr C. R. Hill (Natural History Museum) for reading the manuscript and making many constructive suggestions. We are also grateful to Dr Bernard Owens (British Geological Survey) for advice on the spores attached to the cuticles prepared during this study. The macro-photographs in this paper were taken by Mr Harry Taylor (Photographic Studio, Natural History Museum).

REFERENCES

Barthel, M. 1961. Der Epidermisbau einiger oberkarbonischer Pteridospermen. *Geologie*, Berlin, **10**: 828–849.

—— 1962. Epidermisuntersuchungen an einigen inkohlten Pteridospermenblättern des Oberkarbons und Perms. *Geologie*, Berlin, **11**: 1–140.

—— 1976. Die Rotliegendflora Sachsens. *Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden*, **24**: 1–190.

Beeler, H. E. 1983. Anatomy and frond architecture of *Neuropteris ovata* Hoffmann and *N. scheuchzeri* Hoffmann from the Upper Pennsylvanian of the Appalachian Basin. *Canadian Journal of Botany*, Ottawa, **61**: 2352–2368.

Beerbower, R., Scheckler, S. E. & Valkenburgh, B. van 1987. An entangled bank – The Smithsonian Conference on the Evolution of the Terrestrial Ecosystem. *Palaios*, Tulsa, **2**: 526–527.

Bertrand, P. 1930. Bassin Houiller de la Sarre et de la Lorraine. I. Flore Fossile. 1. Neuroptéridées. *Études des Gîtes Minéraux de la France*, Paris. 58 pp., 30 pls.

Brongniart, A. 1822. Sur la classification et la distribution des végétaux fossiles en général, et sur ceux des terrains de sédiment supérieur en particulier. *Mémoires du Muséum d'Histoire Naturelle*, Paris, **8**: 203–240.

—— 1828. *Prodrome d'une histoire des végétaux fossiles*. viii + 223 pp. Paris.

—— 1831. *Histoire des végétaux fossiles*. **1** (5): 209–248, pls 61–74 + 61 *bis*. Paris.

Carpentier, A. 1930. Notes paléophytologiques. *Annales de la Société Géologique du Nord*, Lille, **54**: 186–189.

Cleal, C. J. & Laveine, J.-P. 1988. The juvenile frond of the Middle Carboniferous pteridosperm *Paripteris* Gothan. *Géobios*, Lyon, **21**: 245–250.

——, **Shute, C. H. & Zodrow, E. L.** 1990. A revised taxonomy for Palaeozoic neuropterid foliage. *Taxon*, Berlin, **39**: 486–492.

—— **& Zodrow, E. L.** 1989. Epidermal structure of some medullosan *Neuropteris* foliage from the middle and upper Carboniferous of Canada and Germany. *Palaeontology*, London, **32**: 837–882.

Crookall, R. 1959. Fossil plants of the Carboniferous rocks of Great Britain. Part 2. *Memoirs of the Geological Survey of Great Britain, Palaeontology*, London, 4: 85–216.

Daber, R. 1980. Zum Problem der Gabelwedelformen des Karbons und Perms – eine Übersicht. *Schriftenreihe für Geologische Wissenschaften*, Berlin, **16**: 15–48.

Florin, R. 1937. On the morphology of the pollen-grains in some Palaeozoic pteridosperms. *Svensk Botanisk Tidskrift*, Stockholm, **31**: 307–338.

Gastaldo, R. A. 1988. The frond architecture of *Sphenopteris pottsvillea* (White) Gastaldo and Boersma. *Journal of Paleontology*, Tulsa, **62**: 982–988.

Gothan, W. 1941. Paläobotanische Mitteilungen. 5. Die Unterteilung der karbonischen Neuropteriden. *Paläontologische Zeitschrift*, Berlin, **22**: 421–428.

—— 1953. Die Steinkohlenformation der westlichen paralischen Steinkohlenreviere Deutschlands. Lief. 5. *Beihefte zum Geologischen Jahrbuch*, Hannover, **10**: 1–83.

Halle, T. G. 1933. Observations sur la structure de quelques échantillons carbonisés de *Potoniea* du terrain houiller de la Lorraine. *Annales de la Société Géologique du Nord*, Lille, **58**: 193–206.

Havlena, V. 1953. Neuropteridy českého karbonu a permu. *Rozpravy Ústředniho Ústavu Geologického*, Prague, **16**: 1–168.

Kerp, J. H. F. [1986]. *On* Callipteris *Brongniart from the European Rotliegend basins*. PhD thesis, Rijksuniversiteit te Utrecht (unpubl.).

Kryshtofovich, A. 1944. The mode of preservation of plant fossils and its bearing on the problem of coal. *American Journal of Science*, New Haven, 242: 57–73.

Laveine, J.-P. 1966*a*. Remarques sur quelques frondes ptéridospermophytiques paléozoïques. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences*, Paris, (D) **262**: 1625–1628.

—— 1966*b*. À propos de la classification des Neuroptéridées. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences*, Paris, (D) **262**: 1680–1683.

—— 1967. Les Neuroptéridées du Nord de la France. *Études Géologiques pour l'Atlas de Topographie Souterraine*, Lille, **1** (5): 1–344, pls A–P, 1–84.

—— 1987. Importance of understanding of the architecture of frond for systematics of Neuropteridae and Callipteridiaceae and its stratigraphic implications. *Acta Palaeontologica Sinica*, Beijing, **26**: 71–79.

—— **& Brousmiche, C.** 1982. Documents pour servir à la reconstitution de la fronde chez certaines Neuroptéridées. *Géobios*, Lyon, **15**: 243–247.

Meyen, S. V. 1987. *Fundamentals of palaeobotany*. 432 pp. London.

Millay, M. A. & Taylor, T. N. 1979. Paleozoic seed fern pollen organs. *Botanical Review*, Lancaster, Pa, **45**: 301–375.

Pastiels, A. & Willière, Y. 1954. Étude géologique du Bassin houiller de Charleroi. La concession Trieu-Kaisin. *Publication, Association pour l'Étude de la Paléontologie et de la Stratigraphie Houillères*, Brussels, **20**: 1–196.

Reichel, W. & Barthel, M. 1964. Das 'Schweinsdorfer Flöz' des Döhlener Beckens. Neue Flözaufschlüsse und Florenfunde. *Jahrbuch des Staatliches Museum für Mineralogie und Geologie*, Dresden, **1964**: 203–247.

Roehl, E. von 1868. Fossile Flora der Steinkohlenformation Westphalens, einschliesslich Piesberg bei Osnabrück. *Palaeontographica*, Stuttgart, **18**: 1–191.

Smith, A. H. V. & Butterworth, M. A. 1967. Miospores in the coal seams of the Carboniferous of Great Britain. *Special Papers in Palaeontology*, London, **1**: 1–324.

Sternberg, K. von 1825. *Versuch einer Geognostisch-botanischen Darstellung der Flora der Vorwelt*, Leipzig, 4. xlii + (8) + 48 pp., pls 40–59, A–E.

Stidd, B. M. 1978. An anatomically preserved *Potoniea* with *in situ* spores from the Pennsylvanian of Illinois. *American Journal of Botany*, Lancaster, Pa, **65**: 677–683.

—— 1981. The current status of the medullosan seed ferns. *Review of Palaeobotany and Palynology*, Amsterdam, **32**: 63–101.

Stockmans, F. 1933. Les Neuroptéridées des bassins houillers belges. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, Brussels, **57**: 1–61.

Wendel, R. 1980. *Callipteridium pteridium* (Schlotheim) Zeiller im Typusgebiet des Saaletrogs. *Schriftenreihe für Geologische Wissenschaften*, Berlin, **16**: 107–169 (incl. 18 pls).

Wills, L. 1914. Plant cuticles from the Coal Measures of Britain. *Geological Magazine*, London, (6) **1**: 385–390, pls 30–31.

Zeiller, R. 1879. Végétaux fossiles du terrain houiller de la France. *Explication de la Carte géologique de la France*, Paris, **4** (2): 1–185, atlas pls 159–176.

—— 1886. Bassin houiller de Valenciennes, description de la flore fossile. *Études des Gîtes Minéraux de la France*, Paris. Atlas of 94 pls.

—— 1906. Bassin Houiller et Permien de Blanzy et du Creusot. Fasc. II. Flore fossile. *Études des Gîtes Minéraux de la France*, Paris. 265 pp., 51 pls.

Zodrow, E. L. & Cleal, C. J. 1988. The structure of the Carboniferous pteridosperm frond *Neuropteris ovata* Hoffmann. *Palaeontographica*, Stuttgart, (B) **208**: 105–124.

Bull. Br. Mus. Nat. Hist. (Geol.) **46** (2): 175–270 Issued 31 January 1991

Tertiary Ostracoda from the Lindi area, Tanzania

MANZOOR AHMAD

Customs Co-operation Council, Rue de l'Industrie 26–38, B-1040 Brussels, Belgium
(on secondment from the Central Board of Revenue, Islamabad, Pakistan).

JOHN W. NEALE

Department of Geology, The University, Hull, England, HU6 7RX

QADEER A. SIDDIQUI

Department of Geology, St Mary's University, Halifax, Nova Scotia, Canada, B3H 3C3

CONTENTS

SYNOPSIS. Ostracods from the Upper Eocene–Lower Miocene of the Lindi area of Tanzania, East Africa, are described. 114 species and 2 subspecies are recognized, of which 51 species and 2 subspecies are new. A new genus, *Crenaleya*, is proposed.

The stratigraphical distribution of the ostracod faunas indicates a close relationship with regional geological events, the faunas becoming less diverse during the Oligocene regression and more diverse during the Miocene transgression. The sedimentation rate deduced from valve/carapace ratios shows a higher rate of sedimentation for the Upper Eocene and Lower Miocene than for the Oligocene. The faunas, in general, are indicative of warm shallow shelf-seas with nearby reefs, with temperatures varying between 10°–25° C and water depths of about 50 m. Three ostracod biozones are recognized; the presence of a deep water fauna in the Lower Miocene of the South Mtwero region is also recorded.

The Tanzanian ostracods show affinities with those of India, Pakistan and South Africa; there are a few species in common with the Mediterranean, Caribbean and Indo-Pacific regions.

INTRODUCTION

The fossil ostracods described in this paper come from the Lindi area, which lies in the Southern Province of Tanzania and is bounded by latitudes 9° 50′ S and 10° 05′ S, and longitudes 39° 40′ E and 39° 45′ E. The position of the area relative to the remainder of coastal East Africa is shown in Fig. 1. Cretaceous to Pliocene marine sediments are known from the area, but the present study is concerned only with those ranging from Upper Eocene to Lower Miocene. These Palaeogene beds are in continuity with, or sometimes rest with slight unconformity on, the Upper Cretaceous rocks and have been laid down continuously from late Eocene times into the overlying Oligocene. A small break in deposition during the Chattian was followed by transgression, resulting in widespread deposition of Lower Miocene beds, a wide occurrence recognized by Eames & Kent (1955). The Pliocene is not well known in this area though farther north in the synclinal areas and seaward of the Dar-es-Salaam embayment, post-Miocene sediments amount to thousands of feet in thickness.

The whole succession dips gently to the ENE, the dip not exceeding 10°. According to Eames *et al.* (1962), the late Eocene to early Miocene was a time of low tectonic activity and the region seems to have undergone gentle overall subsidence with no apparent violent movement; the whole sequence of Cretaceous–Tertiary sedimentation seems to have been associated with the various cycles of broad gentle warping. Kent (*in* Burk & Drake 1974) mentions a period of peneplanation, occupying most of the Cretaceous and

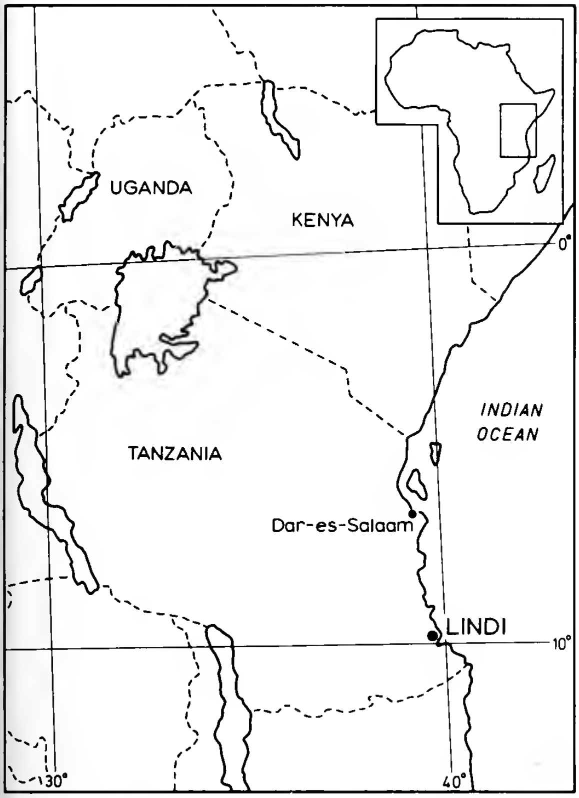


Fig. 1 Map of East Africa, showing the position of Lindi.

alaeocene, which was disturbed by activation of the Lindi ault system during Oligocene and early Miocene times.

TRATIGRAPHY

he marine Cretaceous succession in the Lindi area consists general of clay with subordinate sandstones and limetones. There was no break in deposition between the retaceous and the Palaeocene but there was a change in nvironment.

(a) *Palaeocene.* Outcrops of Palaeocene deposits are umerous but small and frequently disturbed. At the base lies rown sandy detrital limestone followed by a chain of reef-nolls, the lithology of which varies considerably. Formation f reef-knolls was followed by a series of silts, clays and npersistent thin limestones.

(b) *Upper Eocene.* Sandy reef limestones with interbedded yers of soft marly clays lie at the base and are overlain by ndy reef limestones in a series of interbedded buff-grey lays, buff siltstones and thin, hard, sometimes siliceous, raminiferal limestones. The thickness is estimated to be lmost 70 m.

(c) *Oligocene.* Distribution of Oligocene deposits is limited, epresenting a further stage in the early Tertiary regression. he rocks are generally impersistent, being rubbly and silty mestones, soft marly limestones, buff-grey marly clays and uff silts. The estimated thickness is about 80 m.

(d) *Lower Miocene.* The early Lower Miocene is represented by about 5 m of soft buff silty sandstones, which become increasingly calcareous upwards and contain some lenses of gypsiferous clay. In the area immediately to the east of Lindi Town (Kitunda Cliff) the silty sandstones pass upwards into massive reef limestones, but north of Lindi Bay clays and silts appear to replace part of the limestones.

BP-Shell surveys have shown that Lower Miocene beds are brought in on the downthrow side of the Lindi Fault in Lindi Bay, showing evidence of large-scale contemporaneous movement of the fault. At Ras Tapuri a breccia of very large blocks of Miocene limestone is developed 400 m from the easternmost Eocene limestones.

PREVIOUS WORK ON TANZANIAN OSTRACODS

The earliest description of ostracods from Tanzania was given by Sars (1910), who described 29 Recent species belonging to seven genera, all from the fresh-water Lake Tanganyika. Rome (1962) monographed the Lake Tanganyika fauna, establishing two new genera, one new subgenus and 47 new species. Short papers by Vavra, Klie, Lowndes and others also deal with the Recent ostracods of this general area. Ramsay (1968) described three late Cretaceous species of *Cytherelloidea* from the Mikaramu Stream, Tanzania. A year later, Bate (*in* Bate & Bayliss 1969) described 22 new species from Cretaceous sediments and later Bate (1975) described 52 species of which 24 were new, and four new genera, from the Middle Jurassic sediments of Tanzania. The first Tertiary species described from the Lindi area (sample FCRM 1648, Upper Eocene) was *Phalcocythere* cf. *spinosa* Siddiqui, compared with *P. spinosa* Siddiqui 1971 from the Upper Eocene of Pakistan. The only other Tertiary ostracod described from Tanzania, the *Triebelina* cf. *howei* (Stephenson, 1946) of Keij (1976), is from the mid-Oligocene sample FCRM 1576 and is here regarded as identical with *T. howei* from the Caribbean region: see p. 191.

SYSTEMATIC DESCRIPTIONS

All type and figured specimens mentioned in this paper are deposited in the collections of the Palaeontology Department of the British Museum (Natural History); register number prefix OS. Reference is made to other material held at the BP Research Centre, Sunbury-on-Thames.

Subclass **OSTRACODA** Latreille, 1806
Order **PODOCOPIDA** Müller, 1894
Suborder **PLATYCOPA** Sars, 1866
Family **CYTHERELLIDAE** Sars, 1866

Genus ***CYTHERELLA*** Jones, 1849

TYPE SPECIES. *Cytherina ovata* Roemer, 1840.

Cytherella lindiensis sp. nov. Pl. 1, figs 4–9

NAME. After the Lindi area, the type locality in Tanzania.

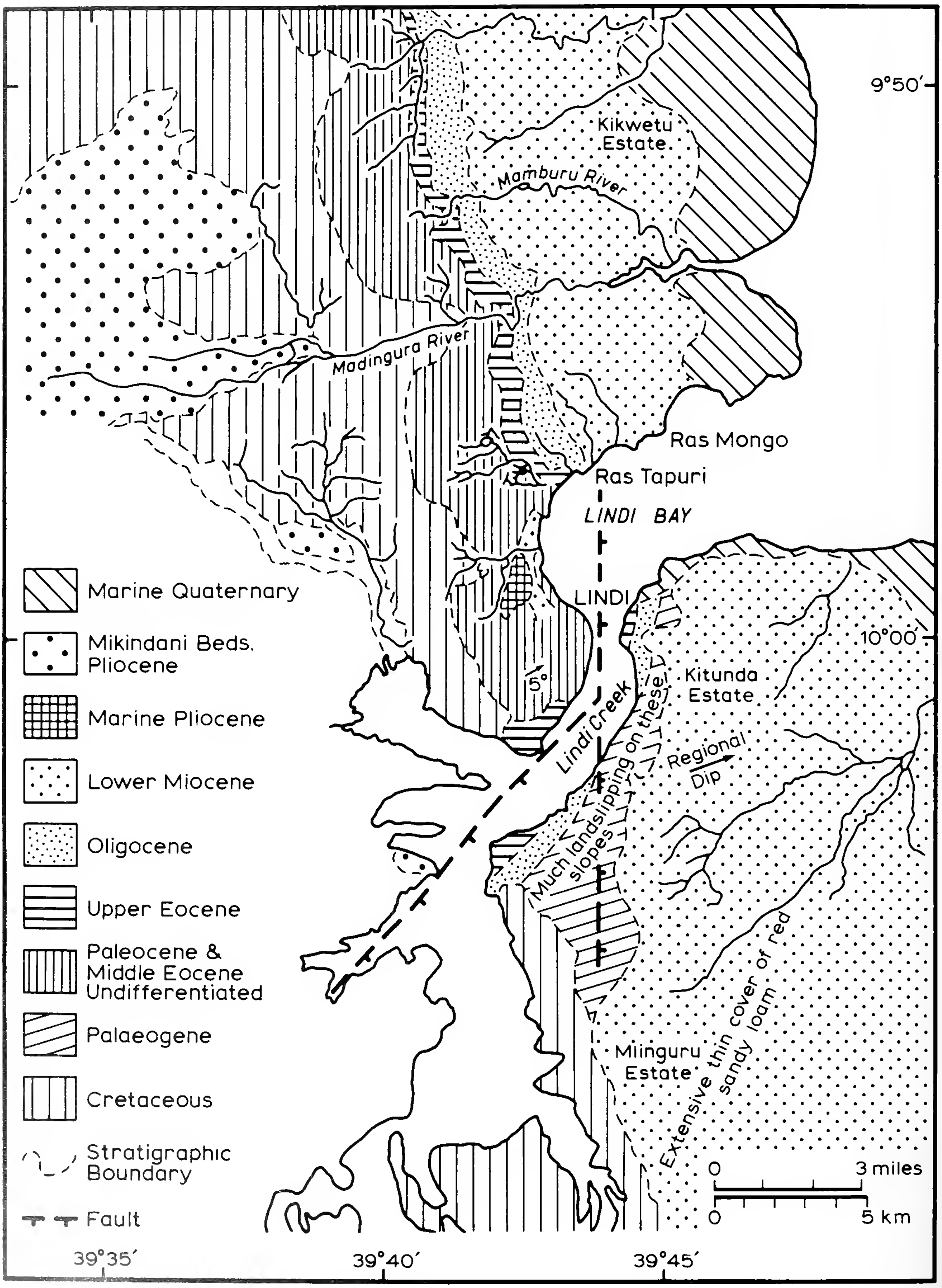


Fig. 2 Geological map of the Lindi area, Tanzania (after Kent *et al.*, 1971).

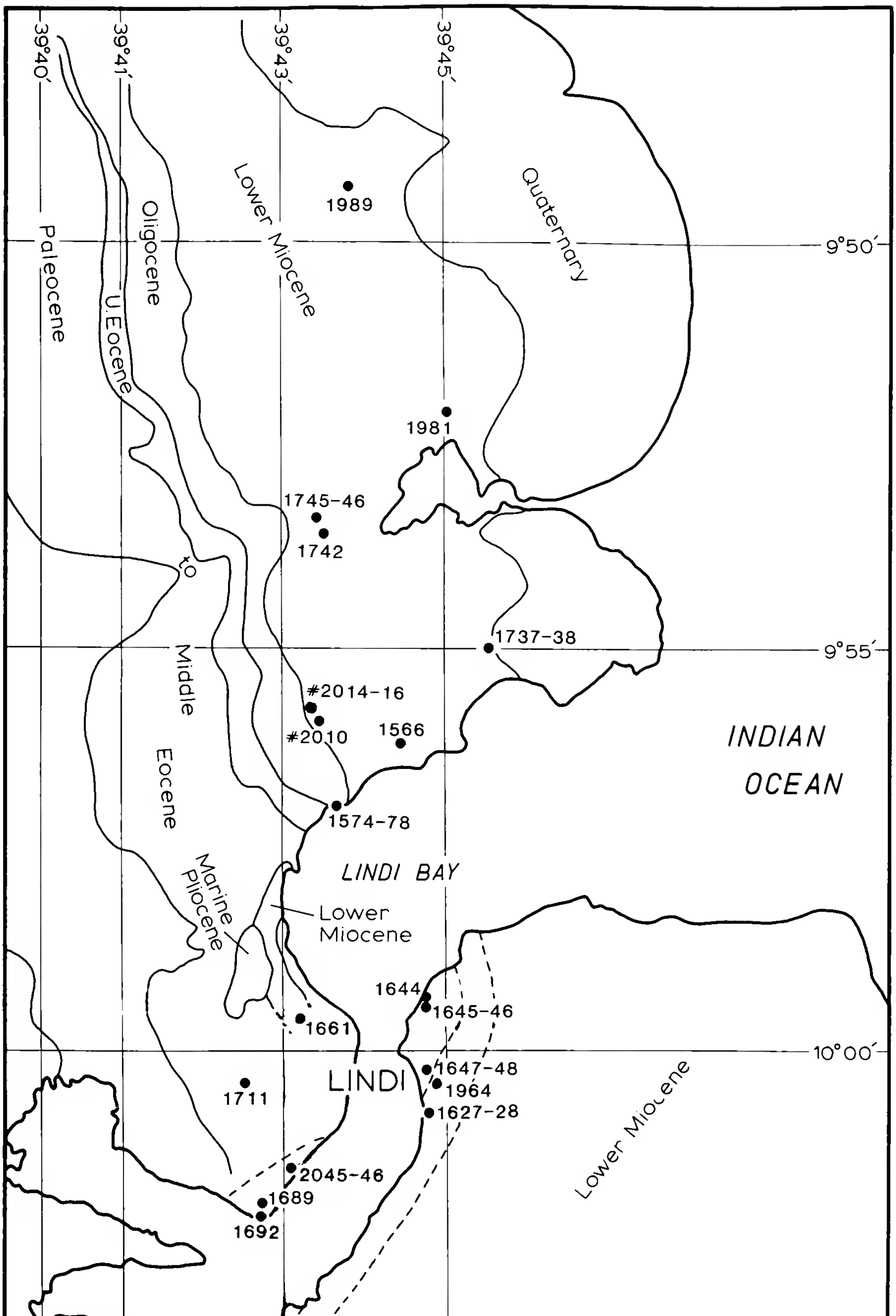


Fig. 3 Sample location map, Lindi, Tanzania. #approx. position only. FCRM 1963 lies off the south-east corner of the map.

DIAGNOSIS. A species of *Cytherella* with females egg-shaped and males subovate in lateral view. Surface completely smooth. Sexual dimorphism pronounced.

HOLOTYPE. A female right valve, OS 8025. Ten paratypes, OS 8026–35. Sample FCRM 2033, Lindi Creek, east shore; Upper Eocene.

OTHER MATERIAL. 50 specimens, from FCRM 1711, 2033, 2034, 2045.

DESCRIPTION. Carapace medium-sized with greatest width just behind the mid-length and greatest height in the anterior half of the valve. Sexual dimorphism pronounced; presumed females more egg-shaped, males more elongate. Dorsal margin convex, ventral margin slightly concave. Anterior margin broadly rounded, posterior comparatively narrowly rounded. Right valve overlaps left. External lateral surface smooth.

Internally, central muscle scars form a pinnate impression with 14 elongate scars in the anterior row and 10 in the posterior; the axis slopes from dorsal to posteroventral in females and is almost perpendicular to the length in males. The scars are at approximately mid-length in males, posterior to mid-length in females.

DIMENSIONS (µm).	L	H	W
Holotype, female right valve OS 8025	550	370	170
Paratype, male carapace OS 8027	710	415	275
Paratype, male right valve OS 8026	690	410	170

REMARKS. *C. ovata* (Roemer, 1840) and *C. tumidosa* Alexander, 1934 are the closest in shape to *C. lindiensis*. *C. ovata* differs in having the anterior and posterior margins more arched; *C. tumidosa* is larger than *C. lindiensis*, and has the greatest height posterior to the mid-length.

Cytherella mediocalva sp. nov. Pl. 1, figs 1–3

NAME. Latin *medio*, middle + *calvus*, bald; with reference to the smooth central area of the valves.

DIAGNOSIS. Elongate, subquadrate in lateral view. Dorsal margin gently arched, ventral almost straight. Anterior symmetrically rounded, posterior rather narrowly rounded. Carapace strongly pitted except for an inverted T-shaped smooth central area.

HOLOTYPE. A carapace, OS 7994. 10 paratypes, OS 7995–8004. Sample FCRM 1745, Mbanja River; Lower Miocene.

OTHER MATERIAL. 28 specimens, from FCRM 1566 (e.g.

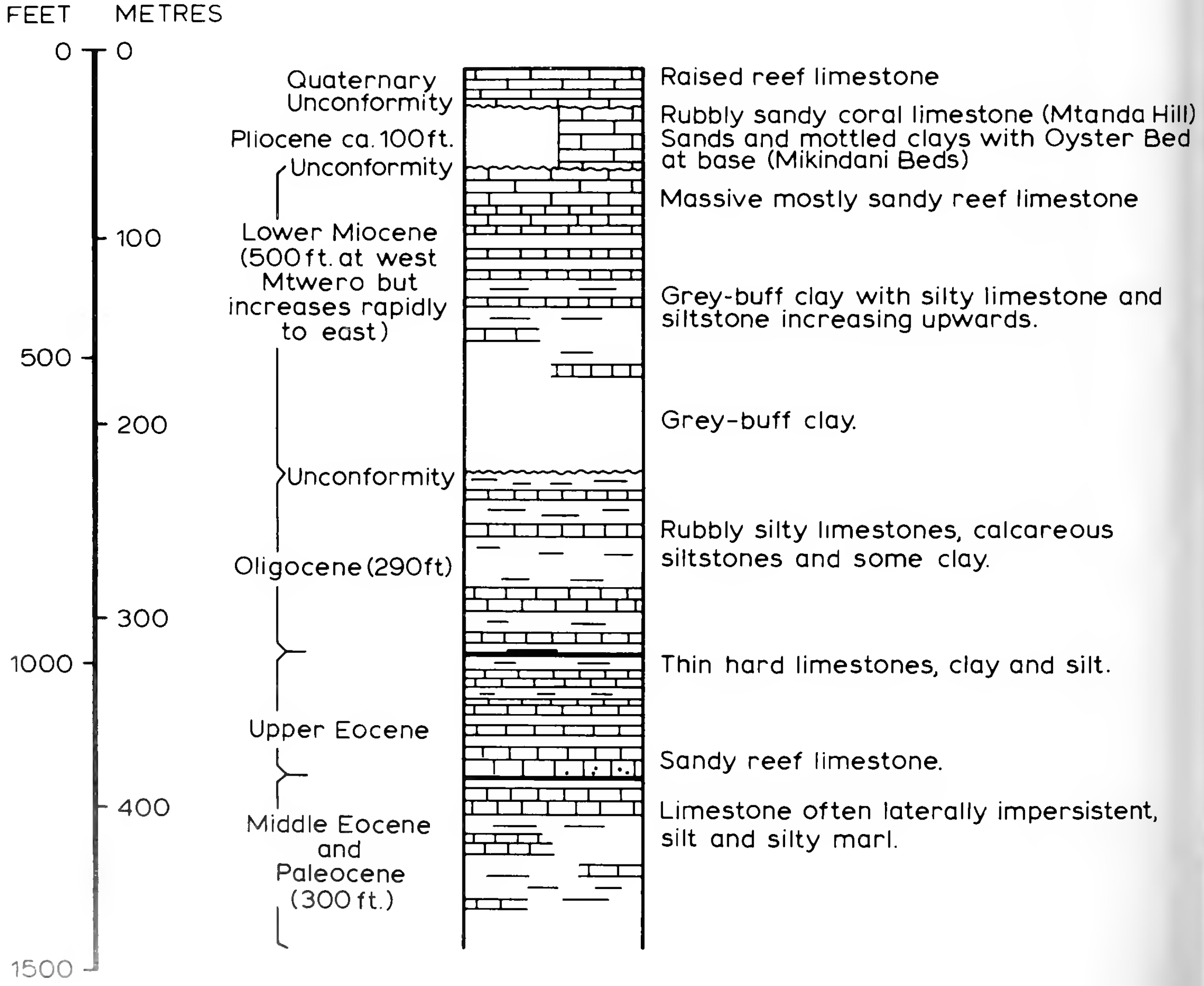
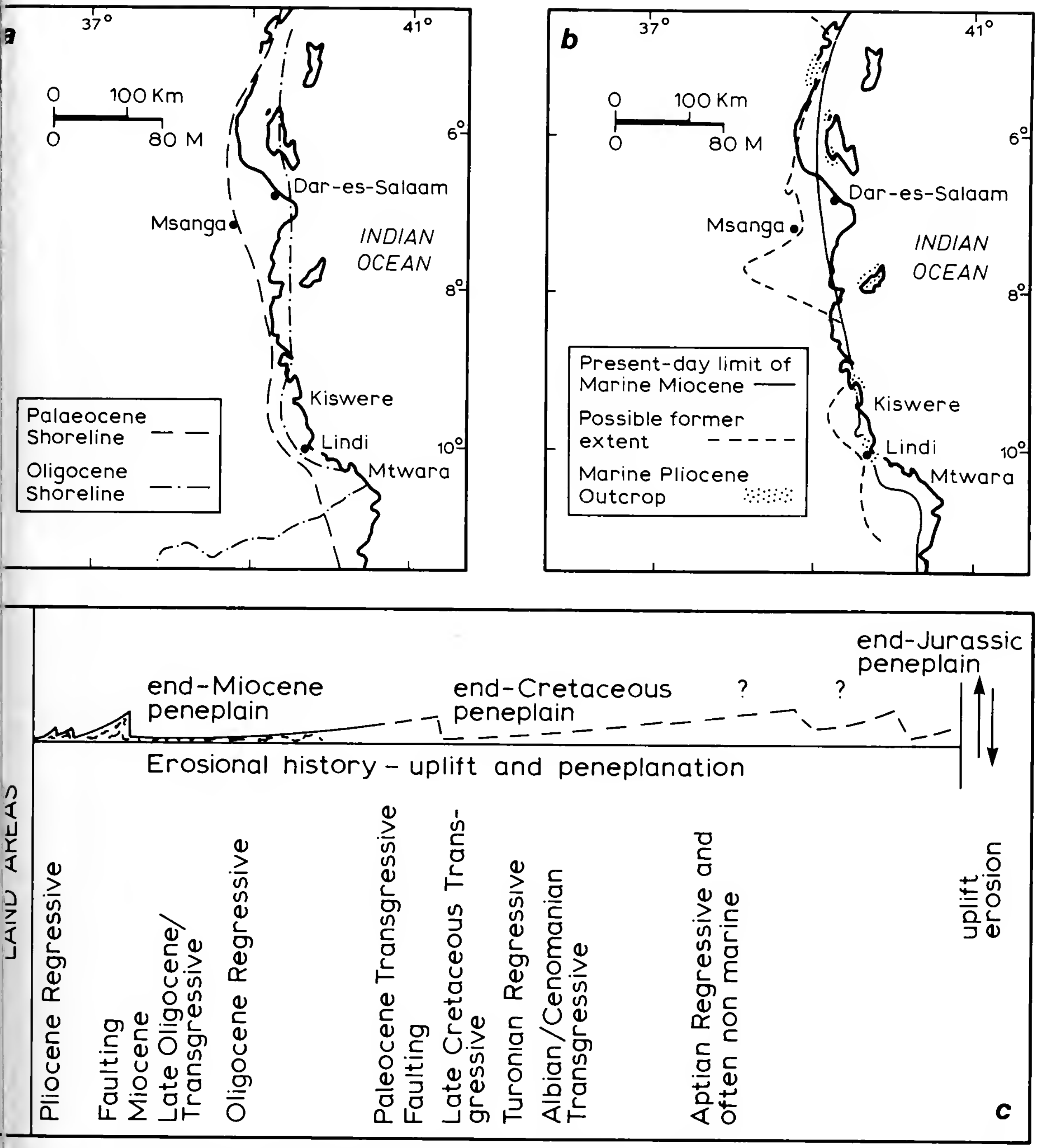


Fig. 4 Stratigraphical succession in the Lindi area (from unpublished BP-Shell report, 1957).



ig. 5 Tanzania, coastal region. a, positions of early Tertiary shorelines. b, distribution of Neogene rocks. c, geological history of the area. (a, b from Kent *et al.*, 1971; c from Kent, *in* Burke & Drake 1974.)

S 8005–17), 1746 (e.g. OS 8076–83), 1989 (e.g. OS 8024), 10 (e.g. OS 8018–24).

ESCRIPTION. Shell medium to thick; shape elongate, sub- adrate to subovate, with greatest height in the middle d widest just behind the mid-length. Sexual dimorphism esent, presumed males being more elongate than females. Anterior margin symmetrically rounded, posterior comparatively narrower but the carapace is thicker here than at the anterior margin. Dorsal margin arched, passing smoothly into anterior and posterior margins; ventral margin almost straight. Right valve larger than left and overlaps it all round. Surface ornamentation consists of circular pits concentrated in anterior and posterior portions and along ventral

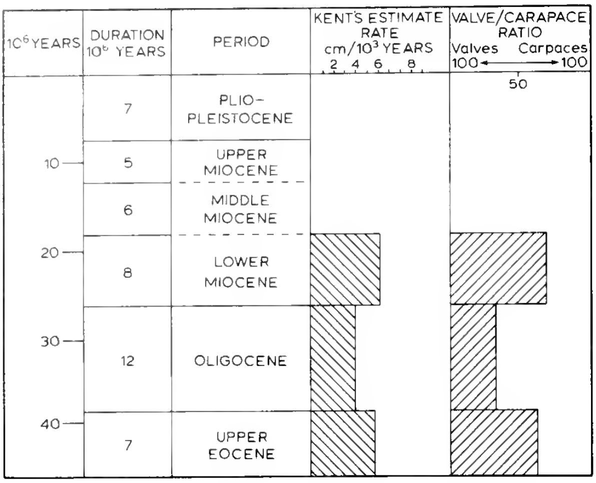


Fig. 6 A comparison of the valve/carapace ratio with the sedimentation rate. (Estimated by Kent *et al.*, 1971.)

margin. There is a smooth central area in the form of an inverted T.

DIMENSIONS (μm).	L	H	W
Holotype, male carapace OS 7994	835	515	360

REMARKS. *C. mediocalva* differs from *C. cretensis* Sissingh 1972 in its dorsal view and in not being pitted over its entire lateral surface. Also, the anterior margin of *C. cretensis* is more conspicuously raised. *C. vandenboldi* Sissingh is more quadrate than *C. mediocalva* and the slope of its postero-dorsal margin is different.

Genus *CYTHERELLOIDEA* Alexander, 1929

TYPE SPECIES. *Cythere williamsoniana* Jones, 1849.

Cytherelloidea gemellata sp. nov. Pl. 2, figs 9–10

NAME. 'Paired' or 'double', with reference to the pair of longitudinal ridges on the lateral surface.

DIAGNOSIS. A species of *Cytherelloidea* characterized by a strong marginal ridge and two longitudinal ridges running parallel to the dorsal and ventral margins, from the posterior margin to just behind the anterior margin.

HOLOTYPE. A carapace, OS 8088. A right valve, OS 8089, is a paratype. No other material. Sample FCRM 2033, Lindi Creek, east shore; Upper Eocene.

DESCRIPTION. Carapace medium-sized, subrectangular, with greatest height behind anterior margin and greatest width in posterior half. Anterior margin symmetrically rounded, posterior not so symmetrical, being obliquely inclined towards the ventral margin. Dorsal margin straight in anterior half, then sloping down posteriorly. Ventral margin slightly concave. Right valve overlaps left, the overlap being conspicuous along mid-dorsal and mid-ventral borders. Externally a strong ridge runs along all margins. Two longitudinal ridges, parallel to the dorsal and ventral margins, run from the posterior margin to just before the anterior end. Entire surface finely reticulate.

DIMENSIONS (μm).	L	H	W
Holotype, carapace OS 8088	500	280	160
Paratype, right valve OS 8089	540	300	105

REMARKS. The two lateral ridges in *C. gemellata* are longer than in any other Tanzanian *Cytherelloidea* species. However, the present species resembles *Cytherelloidea* sp. B, and it is possible that *C. gemellata* is the male and *Cytherelloidea* sp. B the female dimorph of the same species. *C. gemellata* also resembles *C. andersoni* and *C. wayensis*, both described by Sexton (1951); however, the upper ridge in *C. andersoni* bends at an obtuse angle just before the mid-length, and that of *C. wayensis* is concave, while the upper ridge of *C. gemellata* is comparatively straight.

Cytherelloidea patagiata sp. nov. Pl. 2, figs 1–4

NAME. 'Ornamented with a border'.

DIAGNOSIS. A species of *Cytherelloidea* with an almost entire marginal ridge. Two short ridges run from the posterior end towards the middle. Two more short ridges originate from the dorsal margin; the anterior one runs more or less parallel to the anterior margin and the median one runs obliquely towards the middle of the anterior margin. Left valve with a distinct hinge tooth.

HOLOTYPE. A male left valve, OS 8085. Two female left valves, OS 8086–7, are paratypes. Sample FCRM 2033, Lindi Creek, east shore; Upper Eocene. No other material.

DESCRIPTION. Left valve elongate, subrectangular with greatest height at anterior cardinal angle and greatest width near posterior end. Sexual dimorphism is extremely pronounced, presumed females being swollen ventrolaterally, and males being comparatively slender. Anterior margin symmetrically rounded; posterior rounded in the upper half but obliquely inclined towards ventral border in the lower half. Dorsal margin concave anteriorly but uniformly convex from mid-length to posterior end; ventral margin convex. There are five external ridges; the longest, a strong marginal ridge, runs subperipherally along the anterior margin, becomes peripheral ventrally, is inflated posteriorly and is reduced along the dorsal margin. A short median ridge originates from the inflated posterior end, runs for about one-third of

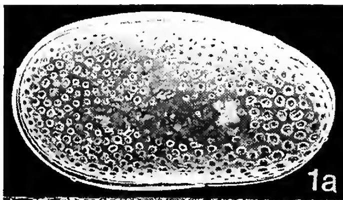
---

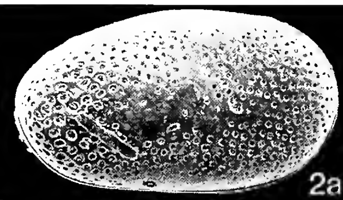
PLATE 1

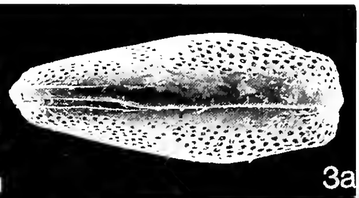
Figs 1–3 *Cytherella mediocalva* sp. nov. **Holotype**, male carapace, OS 7994; 1, lateral view from left, ×54; 2, lateral view from right, ×54; 3, dorsal view, ×56.

Figs 4–9 *Cytherella lindiensis* sp. nov. Figs 4–6, **holotype**, female right valve, OS 8025; 4, muscle scars, ×350; 5, external lateral view, ×72; 6, internal lateral view, ×69. Fig.7, paratype, male carapace, OS 8027, ×66. Figs 8, 9, paratype, male right valve, OS 8026; 8, external lateral view, ×62; 9, internal lateral view, ×64.

Figs 10–12 *Paranesidea fracticorallicola* Maddocks, 1969. Right valve, OS 8114; 10, external lateral view, ×57; 11, muscle scar pattern, internal lateral view, ×140; 12, internal lateral view, ×59.


1a

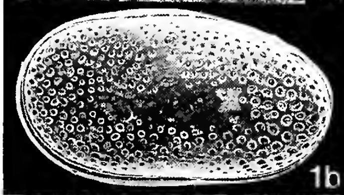

2a


3a

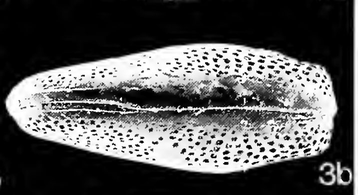

4a


5a

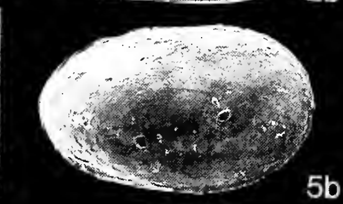

6a


1b


2b


3b

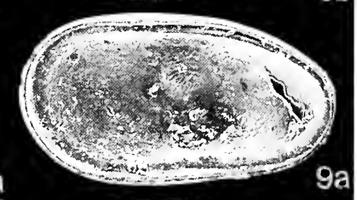

4b

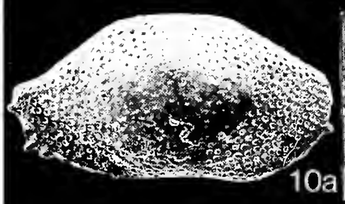

5b


6b


7a


8a


9a


10a

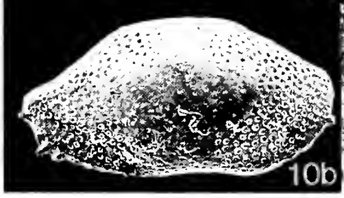

11a

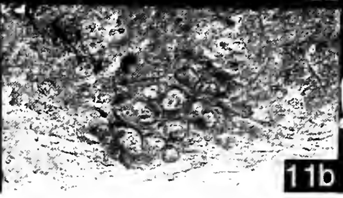

12a


7b


8b


9b


10b


11b


12b


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

the length and disappears into the ventral swelling. Above this, a slightly longer ridge runs parallel to the dorsal margin, and ends just above the muscle scars. Starting slightly behind mid-length, another ridge runs obliquely from the dorsal margin to slightly in front of the muscle scar pit. The fifth ridge runs along the anterior part of the dorsal margin for a short distance, then bends almost at a right angle ventrally, where it disappears about the middle of the valve. Entire surface reticulate, most of the fossae being secondarily pitted. Fossae more elongate and larger along the free margins than in the central and dorsal areas. Muscle scars visible externally in a depressed area. Line of concrescence, inner margin and marginal zone cannot be differentiated. Muscle scars raised, forming two rows with a central axis between them, in a feather-shaped pattern. There are five scars anterior to the axis, one at the tip, four posterior to the axis and one at the bottom. Hinge adont as in other *Cytherelloidea* but the selvage of the left valve grows out just behind the anterior end to form a distinct tooth. Keij (1953), van Morkhoven (1963) and Al-Sheikhly (personal discussion) have observed a similar tooth in some Tertiary–Recent species.

DIMENSIONS (μm).	L	H	W
Holotype, male left valve OS 8085	450	260	085
Paratype, female left valve OS 8086	425	250	085

REMARKS. *Cytherelloidea patagiata* is very similar to *C. beckmanni* Barbieto-Gonzales (1971: 262; pl. 2, figs 1c, 2c, 3c; pl. 45, figs 14, 15) first reported from Naxos (Cyclades) and later by Sissingh (1972) from Crete (Calabrian age), the differences between the two being in the degree of development of the ridges. The anterior marginal ridge is stronger in the Tanzanian species, while the lower posterolateral ridge is shorter in *C. patagiata* than in *C. beckmanni*. The outline of the posterior margin also differs slightly.

Cytherelloidea sp. A Pl. 2, figs 5–8

FIGURED SPECIMEN. A carapace, OS 8084. The only specimen, which is not well preserved. Sample FCRM 2034, Lindi Creek, east shore; Upper Eocene.

DESCRIPTION. A *Cytherelloidea* with a strong rim along the anterior and posterior margins; the entire lateral surface is weakly reticulate. Carapace rectangular, compressed, with greatest width just in front of mid-length. Anterior and posterior margins symmetrically rounded, dorsal margin straight to slightly concave, ventral margin convex. A strong marginal ridge occurs along the anterior and posterior margins; another strong short ridge occurs just in front of the posterior end and parallel to it. No interior details could be seen because there were no single valves.

DIMENSIONS (μm).	L	H	W
Carapace OS 8084	730	370	170

REMARKS. The present species differs from all other Tanzanian *Cytherelloidea* in not having any lateral ridges.

Cytherelloidea sp. B Pl. 2, figs 11–12; Pl. 3, fig. 1

FIGURED SPECIMEN. A carapace, OS 8090. Sample FCRM 2033, Lindi Creek, east shore; Upper Eocene. The only specimen.

DESCRIPTION. A species of *Cytherelloidea* with a comparatively inflated posterior end, and having a strongly developed marginal rim along the anterior and dorsal margins. Two short parallel ridges run from the posterior to about one-quarter the length; another ridge runs along the mid-dorsal border. Carapace elongate, subrectangular, with greatest height near anterior margin and greatest width near posterior end. Anterior margin symmetrically rounded, with about thirty denticles along the edge; posterior margin inflated. Dorsal margin wavy because of the strong marginal rim, ventral margin straight to very slightly convex. Left valve overlaps right. Surface ornamentation consists of a rounded sub-peripheral ridge running along anterior and dorsal margins. Two short parallel ridges run forward from the inflated posterior margin for about a quarter of the length; another lateral ridge runs along the middle third of the carapace. Entire surface reticulate.

DIMENSIONS (μm).	L	H	W
Carapace OS 8090	540	270	190

REMARKS. In general shape, *Cytherelloidea* sp. B resembles Sexton's (1951) two species *C. wayensis* and *C. andersoni*, from the Miocene and Mid-Oligocene of North America. The only difference is that *Cytherelloidea* sp. B has shorter lateral ridges, which run for only about a third of the length; in fact this feature differentiates this species from all other *Cytherelloidea*. For more discussion see remarks on *C. gemellata*, p. 184.

Suborder **PODOCOPA** Sars, 1866
Superfamily **BAIRDIACEA** Sars, 1888
Family **BAIRDIIDAE** Sars, 1888

Genus ***BAIRDIA*** M^cCoy, 1844

TYPE SPECIES. *Bairdia curta* McCoy, 1844.

Bairdia amygdaloides (Brady) ***oblongata*** van den Bold, 1946 Pl. 3, fig. 12; Pl. 4, figs 1–3

1946 *Bairdia amygdaloides* (Brady) var. *oblongata* van den Bold: 70; pl. 1, fig. 5.

PLATE 2

Figs 1–4 *Cytherelloidea patagiata* sp. nov. Figs 1, 2, **holotype**, male left valve, OS 8085; 1, external lateral view, ×108; 2, internal lateral view, ×105. Figs 3, 4, paratype, female left valve, OS 8086; 3, external lateral view, ×102; 4, muscle scar pattern, external lateral view, ×670.

Figs 5–8 *Cytherelloidea* sp. A. Carapace, OS 8084; 5, lateral view from left, ×62; 6, details of surface ornamentation, ×700; 7, dorsal view, ×62; 8, lateral view from right, ×62.

Figs 9, 10 *Cytherelloidea gemellata* sp. nov. **Holotype**, carapace, OS 8088; 9, dorsal view, ×93; 10, lateral view from left, ×92.

Figs 11, 12 *Cytherelloidea* sp. B. Carapace, OS 8090; 11, lateral view from right, ×82; 12, dorsal view, ×86. See also Pl. 3, fig 1.

Figured specimens. A carapace, OS 7925 (FCRM 1578); a right valve, OS 7927 (FCRM 2033).

Localities and horizons. Sample FCRM 1578, 1628, 1711, 2033; Palaeocene to Middle Oligocene.

Remarks. This species, originally described from the Miocene of Cuba and Guatemala, is widespread in Tanzania. The Tanzanian specimens have a slightly more upturned posterior margin than van den Bold's material but are otherwise very similar. They also resemble some specimens (BM(NH) In.37118) from the Palaeocene of the Salt Range, Pakistan, named by Latham (1938: text-fig. 1) as *Bairdia subdeltoidea* (Münster).

Dimensions (µm).	L	H	W
Carapace OS 7925.	1045	690	520
Right valve OS 7927.	1050	610	350

Bairdia cf. ***attenuata*** Brady, 1880 Pl. 3, fig. 10

cf. 1880 *Bairdia attenuata* Brady: 59; pl. 11, fig. 3a–c.

Figured specimen. A carapace, OS 7934. Sample FCRM 1989, Likonga bridge; Lower Miocene. No other material.

Remarks. The original locality is given as dredgings at depths of 40 fathoms off the reefs at Honolulu, Hawaii, and 155 fathoms at lat. 11° 35′ S, long. 144° 3′ E, in Torres Strait, between Australia and Papua. The Tanzanian specimens have a more acuminate posterior end and are slightly smoother. In this respect they are closer to *Bairdoppilata planolata* Holden, 1976, but Holden's species has a more upturned and produced posterior margin.

Dimensions (µm).	L	H	W
Carapace OS 7934.	760	490	370

Bairdia cf. ***schulzi*** (Hartmann, 1964) Pl. 4, figs 4, 5

cf. 1964 *Triebelina schulzi* Hartmann: 44; pls 4, 5, figs 14–22.
cf. 1966 Species BA of Maddocks: 47, fig. 2.
cf. 1969 *Neonesidea schulzi* (Hartmann) Maddocks: 20–22.
cf. 1976 *Neonesidea schulzi* (Hartmann); Holden: 12; pl. 7, figs 9–11.

Figured specimen. A carapace, OS 7933. Sample FCRM 1989, Likonga bridge; Lower Miocene.

Other material. 14 carapaces, including juveniles, from samples FCRM 2033 (Upper Eocene) and FCRM 1746, 1792, 1989, 2015 (Lower Miocene).

Remarks. The Tanzanian specimens are much smaller, but otherwise compare well with *Triebelina schulzi* Hartmann from El Salvador, and sp. BA of Maddocks, 1966, from Madagascar. Holden has described the species from the Lower and Upper Miocene of the Midway area, Hawaiian Islands.

Dimensions (µm).	L	H	W
Carapace OS 7933.	590	370	315

Genus ***PARANESIDEA*** Maddocks 1969

Type species. *Paranesidea fracticorallicola* Maddocks, 1969.

Paranesidea fracticorallicola Maddocks, 1969 Pl. 1, figs 10–12

1969 *Paranesidea fracticorallicola* Maddocks: 43; pl. 1, figs 5, 6; text-figs 16–18.

Figured specimen. A right valve, OS 8114. Sample FCRM 2033, Lindi Creek, east shore; Upper Eocene. There is one other specimen from the same sample.

Remarks. Maddocks' species, from the Recent of Nossi-Bé, Madagascar, is larger than the Tanzanian specimens but they are otherwise identical.

Dimensions (µm).	L	H	W
Right valve OS 8114	795	430	285

Paranesidea nigrescens (Ruggieri, 1962) Pl. 3, figs 6–7

1962 *Bairdia nigrescens* Ruggieri: 11; text-figs 4, 4a; pl. 1, figs 7, 8.
1972 *Neonesidea nigrescens* (Ruggieri) Sissingh: 77; pl. 2, fig. 14.

Figured specimen. A carapace, OS 7923. Sample FCRM 2033, Lindi Creek, east shore; Upper Eocene. The only specimen.

Dimensions (µm).	L	H	W
Carapace OS 7923	840	500	480

Remarks. Ruggieri (1962), who described this species from the Miocene (Tortonian) of central Sicily, placed it in *Bairdia*. Based on his material from the Early Tortonian Tefeli Formation of central Crete, Sissingh (1972) transferred it to *Neonesidea*. As the species is coarsely punctate, rotund, and has a tight spiral muscle scar pattern (as illustrated by Ruggieri), it is here transferred to *Paranesidea*.

Paranesidea cf. ***fortificata*** (Brady, 1880) Pl. 3, figs 4, 5, 9, 11

cf. 1880 *Bairdia fortificata* Brady: 50.

Figured specimens. A left valve, OS 7953, and a carapace, OS 7951; both from FCRM 1989.

PLATE 3

Fig. 1 *Cytherelloidea* sp. B. Carapace, OS 8090; lateral view from left, ×82. See also Pl. 2, figs 11–12.

Figs 2, 3 *Triebelina howei* (Stephenson, 1946). Left valve, OS 7968; 2, external lateral view, ×72; 3, internal lateral view, ×75.

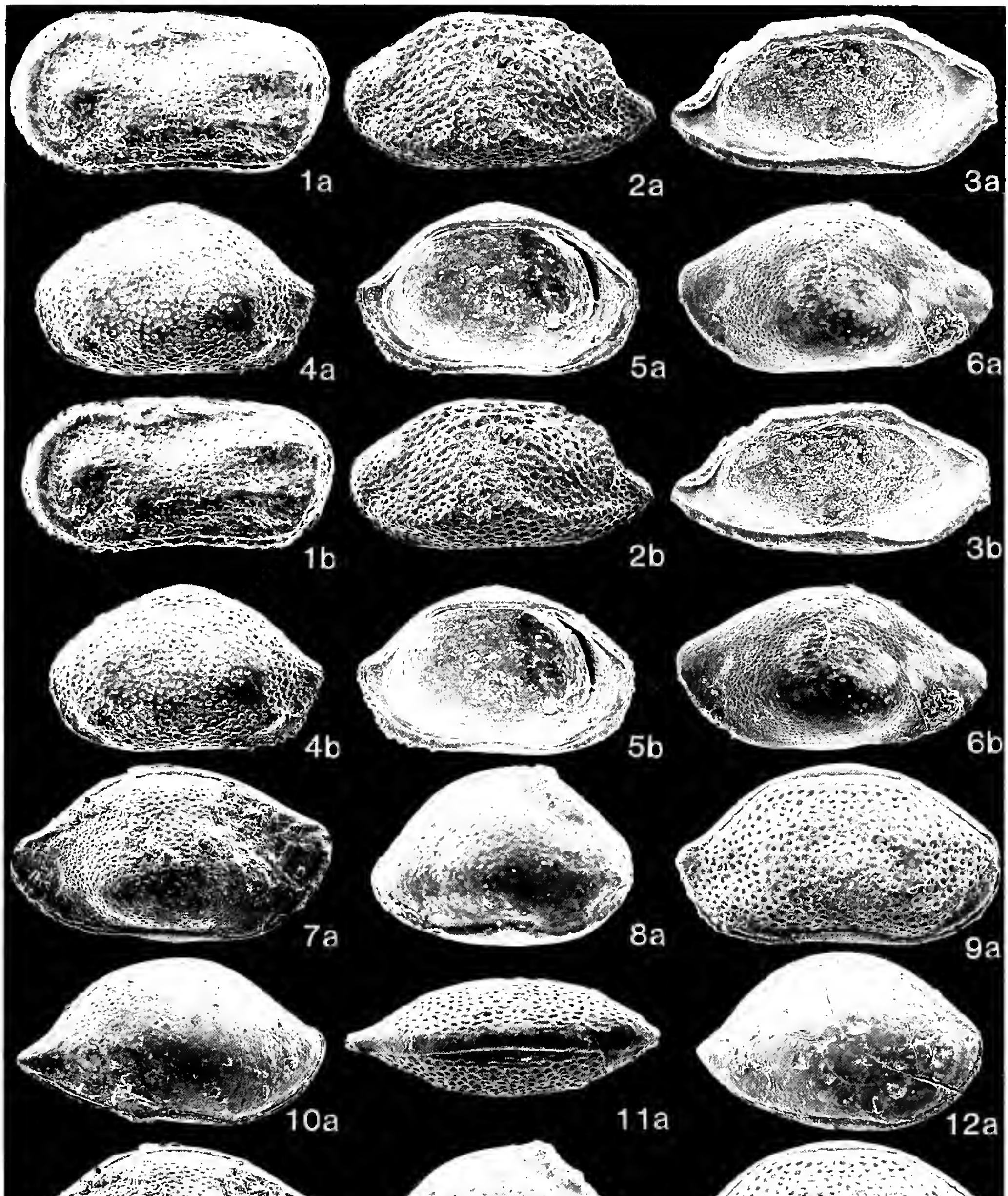
Figs 4, 5, 9, 11 *Paranesidea* cf. *fortificata* (Brady, 1880). Figs 4, 5, left valve, OS 7953; 4, external lateral view, ×58; 5, internal lateral view, ×58. Figs 9, 11, carapace, OS 7951; 9, lateral view from right, ×79; 11, dorsal view, ×76.

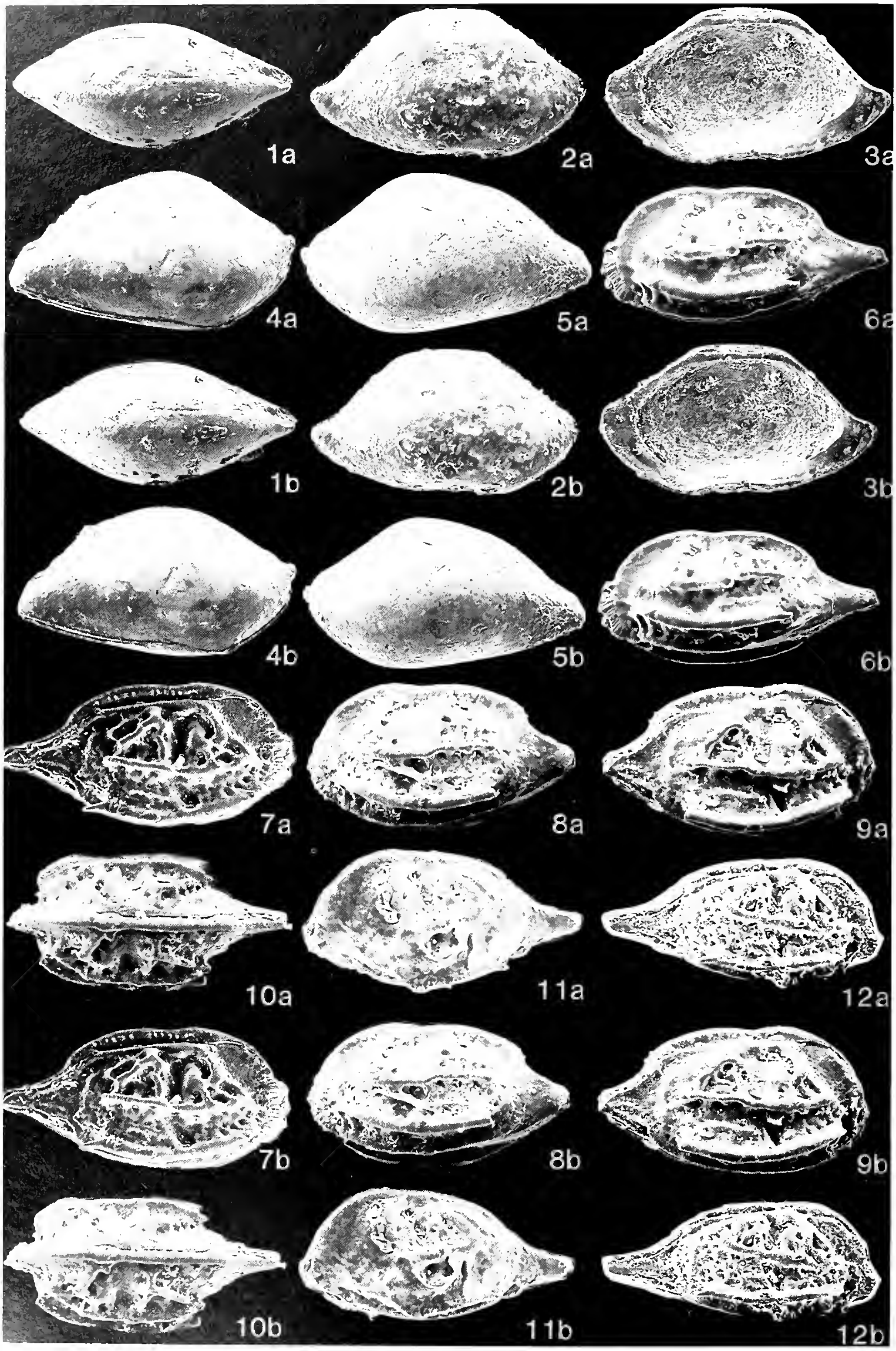
Figs 6, 7 *Paranesidea nigrescens* (Ruggieri, 1962). Carapace, OS 7923; 6, lateral view from left, ×54; 7, lateral view from right, ×55.

Fig. 8 *Paranesidea* sp. A. Carapace, OS 7924; lateral view from right, ×60.

Fig. 10 *Bairdia* cf. *attenuata* Brady, 1880. Carapace, OS 7934; lateral view from right, ×58.

Fig. 12 *Bairdia amygdaloides* (Brady) *oblongata* van den Bold, 1946. Carapace, OS 7925; lateral view from right, ×39. See also Pl. 4, fig. 1.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

OTHER MATERIAL. Eight specimens from samples FCRM 1989 (e.g. OS 7951, 7953); 2033, 2046 (e.g. OS 7952); Upper Eocene to Lower Miocene.

DIMENSIONS (µm).	L	H	W
Left valve OS 7953	690	450	190
Carapace OS 7951	590	350	240

REMARKS. The Tanzanian specimens are identical in shape with Brady's from the Recent of Booby Island, south of New Guinea, but are only slightly more than half the size.

Paranesidea sp. A Pl. 3, fig. 8

FIGURED SPECIMEN. A carapace, OS 7924. Sample FCRM 1711, east flank of Kitulo Hill; probably Palaeocene. The only specimen.

DESCRIPTION. Carapace subovoid, with the greatest height slightly more than two-thirds of the greatest length. The greatest height lies almost at mid-length whilst the greatest length is subventral. Dorsal margin strongly arched, sloping steeply towards both anterior and posterior margins; ventral margin concave in the middle with convex anteroventral and posteroventral ends. Left valve larger than right and overlaps it all round. Lateral surface finely punctate in the centre to almost smooth along the margins.

DIMENSIONS (µm).	L	H	W
Carapace OS 7924	620	460	360

REMARKS. The Tanzanian specimen strongly resembles *Bairdia subdeltoidea* (Münster) var. *rotunda* Alexander, 1927, but the anterior margin is higher and the posterior more produced in that species.

Genus *TRIEBELINA* van den Bold, 1946

TYPE SPECIES. *Triebelina indopacifica* van den Bold, 1946.

Triebelina howei (Stephenson, 1946) Pl. 3, figs 2, 3

1946 *Glyptobairdia howei* Stephenson: 347; pl. 42, figs 5–6; text-figs 1–2.
1947 *Triebelina howei* (Stephenson) Stephenson: 578.
1974 *Triebelina howei* (Stephenson); Poag: 42; pl. 1, fig. 3.
cf. 1976 *Triebelina howei* (Stephenson); Keij: 41–42; pl. 2, figs 8–9.

FIGURED SPECIMEN. A left valve, OS 7968. Sample FCRM 1578, coastal cliff west of Ras Tapuri; Middle Oligocene.

OTHER MATERIAL. A specimen from sample FCRM 1576.

DIMENSIONS (µm).	L	H	W
Left valve OS 7968	620	325	180

REMARKS. Keij (1976) also found six valves of this species in sample FCRM 1576, from approximately the same locality as 1578. While comparing his specimens with *T. howei*, he remarked that the two are practically identical except that the East African specimens have a much weaker ornamentation. He mentions that, while the ornamentation of the right valves is very similar, there are major differences in the ornamentation of the left valves. The semicircular dorsal carina of the nominal species is absent in his African specimens, except for weak indications of its ends; also, the ventrolateral carina with the flattened triangular area around its mid-length is barely indicated in the African specimens though well developed in those from the Caribbean. He also noted that the length/height ratio was 1·75 for the Caribbean form and 2·0 for the East African.

Our left valve does not show any of the differences mentioned by Keij; the ornamentation is as strongly developed as in Caribbean specimens, and the length/height ratio is 1·93. Van den Bold's figures (1974: pl. 1, figs 5–6) show the ratio of 1·75 for the left valve to 2·0 for the right valve, almost the same as we calculated from Keij's figures (1976: 41).

Keij's suggestion that the African forms may be older than the American, and have weaker ornamentation because they are closer to the supposed ancestral genus *Paranesidea,* is therefore not supported. His other conclusion, that Tanzanian specimens demonstrate that Tertiary to Recent shallow-water tropical marine ostracods sometimes had, and have, a wide geographical distribution, remains valid.

Superfamily **CYTHERACEA** Baird, 1850
Family **CYTHERIDAE** Baird, 1850
Subfamily **CYTHERINAE** Baird, 1850
Tribe **PAIJENBORCHELLINI** Deroo, 1966

Genus *PAIJENBORCHELLA* Kingma, 1948

TYPE SPECIES. *Paijenborchella iocosa* Kingma, 1948.

The genus comprises two subgenera, *Paijenborchella* s. str. and *Eopaijenborchella* Keij, 1966.

Subgenus *PAIJENBORCHELLA* Kingma, 1948

Paijenborchella (*Paijenborchella*) cf. *iocosa* Kingma, 1948 Pl. 5, fig. 4

cf. 1948 *Paijenborchella iocosa* Kingma: 86; pl. 8, fig. 12.

PLATE 4

Figs 1–3 *Bairdia amygdaloides oblongata* van den Bold, 1946. Fig. 1, carapace, OS 7925; dorsal view, ×43; see also Pl. 3, fig. 12. Figs 2, 3, right valve, OS 7927; 2, external lateral view, ×42; 3, internal lateral view, ×43.

Figs 4, 5 *Bairdia* cf. *schulzi* (Hartmann, 1964). Carapace, OS 7933; 4, lateral view from right, ×72; 5, lateral view from left, ×72.

Figs 6–10 *Paijenborchella* (*Eopaijenborchella*) *quasimalaiensis* sp. nov. Figs 6, 7, paratype, male carapace, OS 7722; 6, lateral view from left, ×83; 7, lateral view from right, ×85. Figs 8–10, **holotype**, female carapace, OS 7721; 8, lateral view from left, ×93; 9, lateral view from right, ×95; 10, dorsal view, ×100.

Figs 11, 12 *Paijenborchella* (*Eopaijenborchella*) *quasimalaiensis dilata* subsp. nov. Female? carapace, OS 7733 (specimen lost); 11, lateral view from left, ×96; 12, lateral view from right, ×97. See also Pl. 5, figs 1, 3.

Figured specimen. A carapace, OS 7740. Sample FCRM 1566, Mongo Stream, Lindi; Lower Miocene.

Other material. Two specimens: samples FCRM 1738 (right valve, specimen lost); FCRM 1989 (left valve, OS 7739).

Dimensions (µm).	L	H	W
Carapace OS 7740	550	210	300

Remarks. Except for the less developed alar spines, and especially the fact that the upper spine is missing, the Tanzanian specimens agree with *P. iocosa* Kingma. On the other hand, the ventrolateral spine and the lateral, upper, bridge-like ridge are better developed in the Tanzanian specimens than in *P. solitaria* Ruggieri. Probably the Tanzanian specimens represent a form intermediate between the Far Eastern *P. iocosa* and the Italian *P. solitaria*.

Subgenus *EOPAIJENBORCHELLA* Keij, 1966

Type species. *Paijenborchella lomata* Triebel, 1949.

Paijenborchella (*Eopaijenborchella*) *quasimalaiensis* sp. nov. Pl. 4, figs 6–10

Name. Like *malaiensis* Kingma, 1948.

Diagnosis. Species of subgenus *Eopaijenborchella* with three prominent ridges; the lower two lie in the ventral half, the upper one almost at mid-height of the valve. Median sulcus prominent.

Holotype. A female carapace, OS 7721. Four other specimens, OS 7722–5, are paratypes. Sample FCRM 2034, Lindi Creek, east shore; Upper Eocene.

Other material. Three specimens from samples FCRM 2033 (2) and 2034 (OS 7720).

Description. Carapace subovate to almost pear-shaped in lateral view. Anterior margin slightly modified by a flange, but otherwise rounded; posterior margin produced into a caudal process. Dorsal margin straight to slightly arched, except for a small constriction above the median sulcus. Ventral margin is strongly modified by the ventral ridges and appears convex in lateral view. Sexual dimorphism present, presumed males being more elongate and slightly less wide than females. The difference can be seen most clearly in dorsal view, when females look distinctly bulbous. Left valve overlaps right, the overlap being especially obvious along the dorsal margin. Surface ornament consists of three prominent longitudinal ridges, the most ventral of which is weakly developed and slightly longer than the others. Middle ridge well developed and ends in a short blunt spine; top ridge weakly developed and about the same length as the middle one. Median sulcus well developed, running from the middle ridge to the dorsal margin, with a triangular ridge behind it and a hook-shaped projection in front of it. Inner margin and line of concrescence coincide throughout and run parallel to the outer margin. Marginal pore canals straight, simple and almost equally spaced. Anterior marginal pore canals number about 12; only two could be seen passing through the caudal process. The hinge in the right valve consists of a bifid anterior tooth followed by a coarsely serrated groove terminated by a narrow posterior tooth.

Dimensions (µm).	L	H	W
Holotype female carapace OS 7721	460	280	260
Paratype male carapace OS 7722	550	290	280

Remarks. *P. malaiensis* Kingma, *P. cymbula* Ruggieri, 1951, and *P. geoffreyi* Anderson, 1964, are all closely related to this Tanzanian species. The most obvious differences are in the patterns of ornamentation, especially the outlines of the small ridges in the dorsal part; also, the caudal process is shorter in the Tanzanian species than in the others. *P. quasimalaiensis* differs from both *P. cymbula* and *P. malaiensis* in not having a well developed secondary ridge running along the median ridge from the sulcus towards the posterior. Unlike any other *Paijenborchella* species from Tanzania, this one has three lateral ridges almost equal in length.

Paijenborchella (*Eopaijenborchella*) *quasimalaiensis dilata* subsp. nov. Pl. 4, figs 11–12; Pl. 5, figs 1–3

Name. 'Spread, expanded', with reference to the two median ridges broadening out towards the posterior.

Holotype. A male right valve, OS 7732. A female carapace, OS 7733, is a paratype (lost). Sample FCRM 2014, stream SW of Mtwero; Lower Miocene.

Other material. One specimen from sample FCRM 1745.

Dimensions (µm).	L	H	W
Holotype, male right valve OS 7732	475	190	120
Female carapace OS 7733 (spec. lost)	465	220	230

Remarks. The subspecies differs from the typical subspecies in having three subequal longitudinal ridges, the length decreasing from the ventral one to the dorsal. The small kink

---

PLATE 5

Figs 1–3 *Paijenborchella* (*Eopaijenborchella*) *quasimalaiensis dilata* subsp. nov. Figs 1, 3, Female? carapace, OS 7733 (specimen lost); 1, dorsal view, ×98; 3, ventral view, ×96; see also Pl. 4, figs 11, 12. Fig. 2, **holotype**, male right valve, OS 7732, external lateral view, ×95.

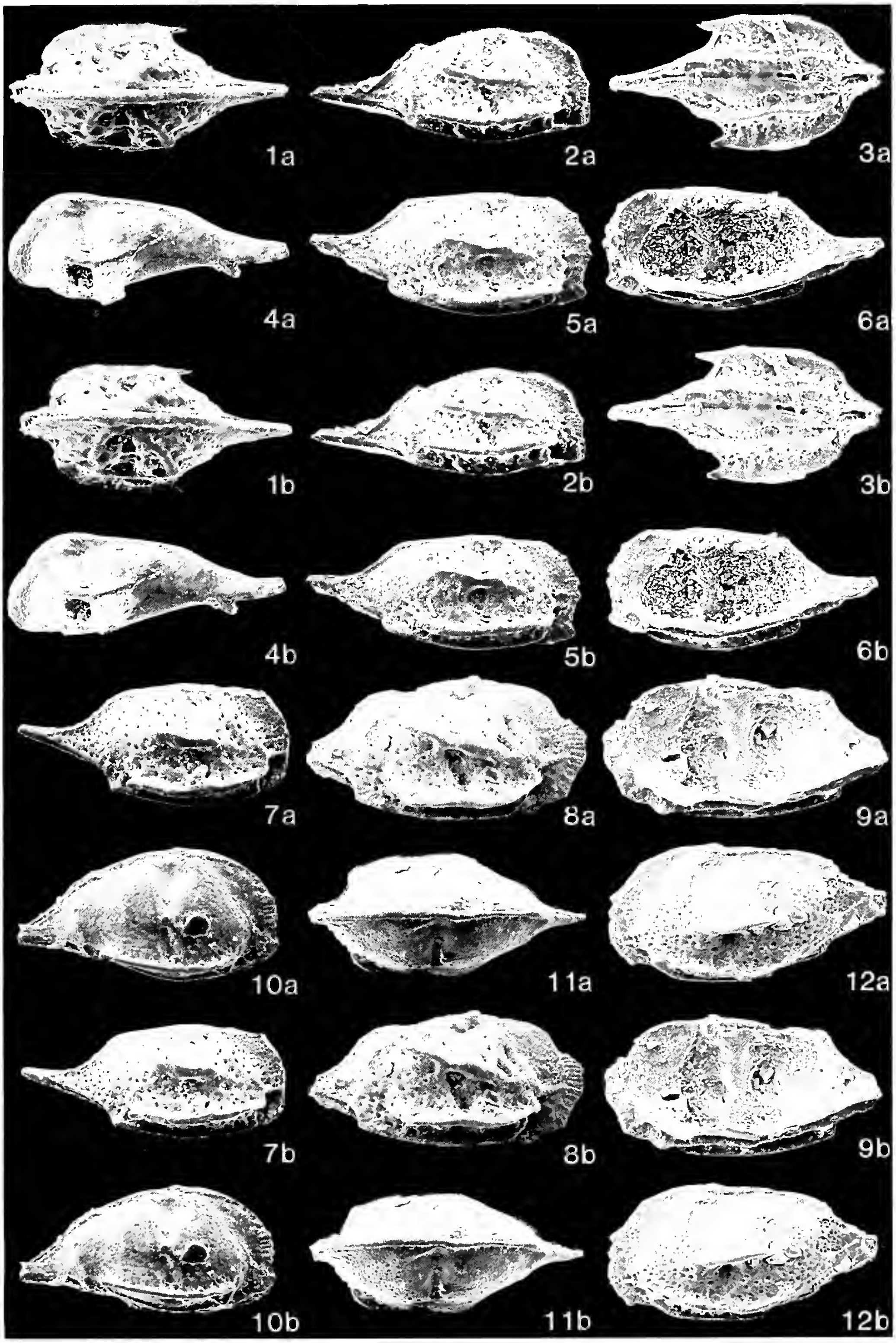
Fig. 4 *Paijenborchella* (*Paijenborchella*) cf. *iocosa* Kingma, 1948. Carapace, OS 7740, slightly oblique lateral view from left, ×83.

Figs 5–7 *Paijenborchella* (*Eopaijenborchella*) *disadunca* sp. nov. Figs 5, 6, **holotype**, male right valve, OS 7727; 5, external lateral view, ×99; 6, internal lateral view, ×100. Fig. 7, paratype, female right valve, OS 7728, external lateral view, ×100.

Figs 8, 9 *Paijenborchella* (*Eopaijenborchella*) *disadunca*, Morphotype A. Right valve, OS 7726; 8, external lateral view, ×108; 9, internal lateral view, ×110.

Figs 10, 11 *Paijenborchella* (*Eopaijenborchella*) *disadunca*, Morphotype D. Carapace (juvenile), OS 7731; 10, lateral view from right, ×105; 11, dorsal view, ×114.

Fig. 12 *Paijenborchella* (*Eopaijenborchella*) *disadunca*, Morphotype B. Carapace OS 7729, lateral view from left, ×114. See also Pl. 6, fig. 1.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

in the mid-dorsal margin of *P. quasimalaiensis* s.str. is not present in the subspecies. In dorsal view the males of the subspecies do not widen posteriorly.

Paijenborchella (*Eopaijenborchella*) *disadunca* sp. nov.

Pl. 5, figs 5–7

NAME. 'Not hooked', with reference to the absence of a hook-like ridge in front of the sulcus.

DIAGNOSIS. Species of subgenus *Eopaijenborchella* having a comparatively sharp caudal process and no ridges above the upper longitudinal one.

HOLOTYPE. A male right valve, OS 7727. A female right valve, OS 7728, is a paratype. Sample FCRM 1742, Mbanja River; Lower Miocene.

OTHER MATERIAL. Five specimens, from samples FCRM 1742 and 1745.

DESCRIPTION. Carapace subtriangular to subquadrate in lateral view. Anterior margin symmetrically rounded, posterior produced into a sharp caudal process. Dorsal margin straight, ventral margin obscured by the ventral longitudinal ridge running parallel to it. Surface ornament consists of a subcentral sulcus and three longitudinal ridges. These ridges decrease in length from the ventral to the dorsal one. The upper ridge runs up towards the dorsal margin, the other two run parallel to the long axis. Intercostal areas pitted by numerous pores.

DIMENSIONS (µm).	L	H	W
Holotype, male right valve OS 7727	455	210	130
Paratype, female right valve OS 7728	440	210	130

REMARKS. This species differs from *P. quasimalaiensis* only in not having ridges on the dorsolateral surface and in the caudal process being more acutely pointed. Some specimens differ slightly in the number and distribution of pores, and in the arrangement of the longitudinal ridges; these are grouped as four morphotypes.

Morphotype A

Pl. 5, figs 8–9

FIGURED SPECIMEN. A right valve, OS 7726. Sample FCRM 1738, South Mtwero; Lower Miocene. The only specimen.

DIMENSIONS (µm).	L	H	W
Right valve OS 7726	420	235	145

REMARKS. This differs from typical *P. disadunca* in having the dorsal ridge comparatively strongly developed, diverging away from the lower ridges and ending in a blunt knob.

Morphotype B

Pl. 5, fig. 12; Pl. 6, fig. 1

FIGURED SPECIMEN. A carapace, OS 7719. Sample FCRM 1628, Kitunda; Middle Oligocene. The only specimen.

DIMENSIONS (µm).	L	H	W
Carapace OS 7719	395	200	185

REMARKS. The three lateral ridges are subparallel rather than divergent. Morphotype B is more densely punctate than any of the others.

Morphotype C

Pl. 6, figs 2–3

FIGURED SPECIMENS. A female carapace, OS 7730, and a male left valve, OS 7736. Sample FCRM 1742, Mbanja River; Lower Miocene.

OTHER MATERIAL. Two specimens, from FCRM 1738 and FCRM 2016.

DIMENSIONS (µm).	L	H	W
Female carapace OS 7730	415	230	220
Male left valve OS 7736	460	240	150

REMARKS. The upper lateral ridge is shorter and thicker, the median sulcus is deeper and the anterior margin is more symmetrically rounded than in *P. disadunca* s.str. The pores are concentrically arranged.

Morphotype D

Pl. 5, figs 10–11

FIGURED SPECIMEN. A juvenile carapace, OS 7731. Sample FCRM 2033, Lindi Creek, east shore; Upper Eocene. The only specimen.

DIMENSIONS (µm).	L	H	W
Carapace OS 7731	395	220	215

REMARKS. The median ridge of morphotype B is not developed in this form and the caudal process is set lower.

Family **LEPTOCYTHERIDAE** Hanai, 1957*a*

Genus ***LEPTOCYTHERE*** Sars, 1925

TYPE SPECIES. *Cythere pellucida* Baird, 1850.

Leptocythere amoena sp. nov.

Pl. 7, figs 5–11

NAME. 'Delightful, lovely', with reference to its beautiful ornamentation.

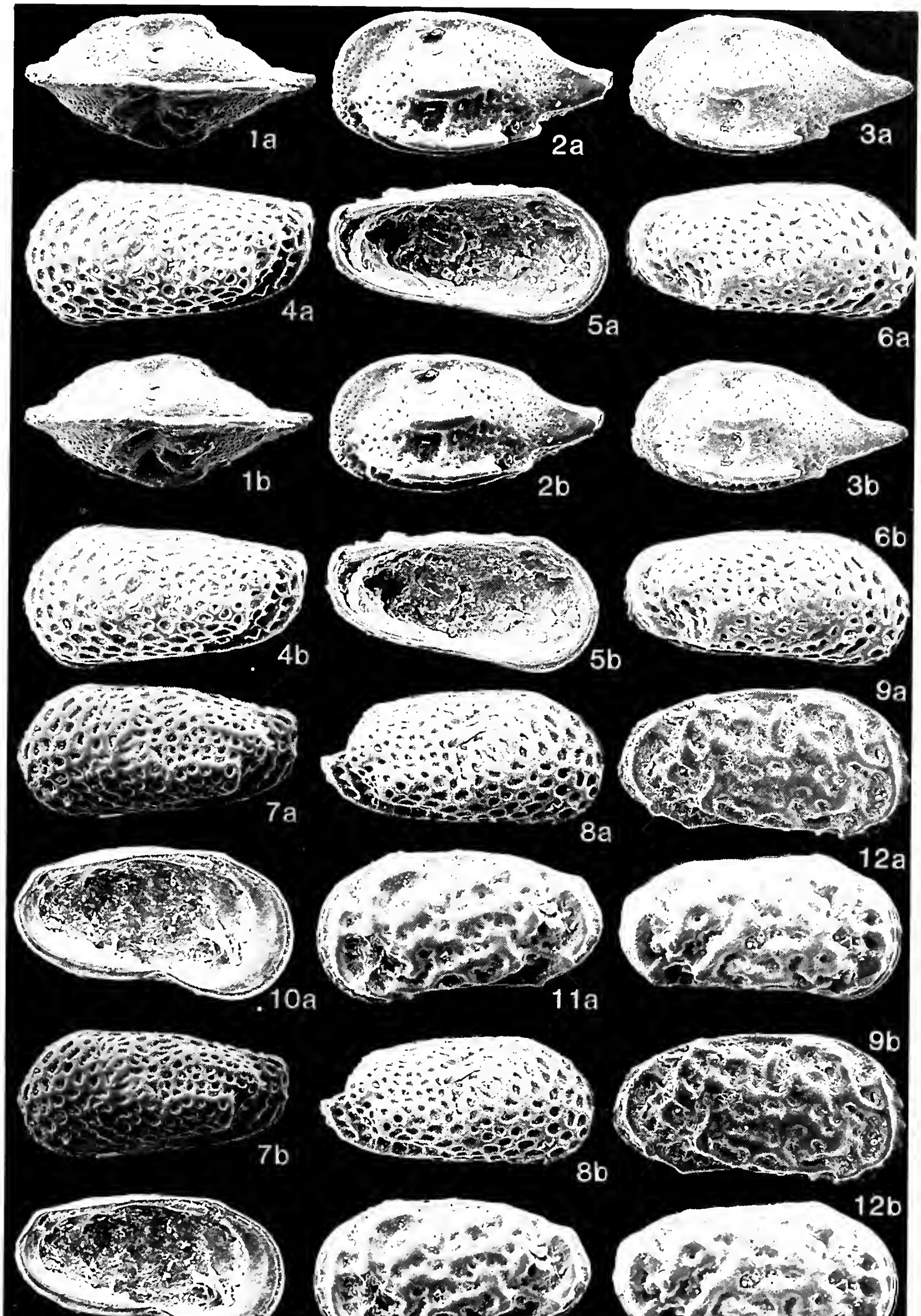
PLATE 6

Fig. 1 *Paijenborchella* (*Eopaijenborchella*) *disadunca*, Morphotype B. Carapace, OS 7729, dorsal view, ×118. See also Pl. 5, fig. 12.

Figs 2, 3 *Paijenborchella* (*Eopaijenborchella*) *disadunca*, Morphotype C. Fig. 2, Female carapace, OS 7730, lateral view from left, ×107. Fig. 3, Male left valve, OS 7736, external lateral view, ×98.

Figs 4–8 *Leptocythere fastigata* sp. nov. Fig. 4, **holotype**, left valve, OS 8132, external lateral view, ×124. Figs 5, 7, paratype, left valve, OS 8134; 5, internal lateral view, ×122; 7, external lateral view, ×120. Fig. 6, paratype, right valve, OS 8133, external lateral view, ×110. Fig. 8, right valve, OS 8136, external lateral view, ×129.

Figs 9–12 *Callistocythere jugosa* sp. nov. Fig. 9, **holotype**, right valve, OS 8140, external lateral view, ×135. Figs 10, 11, paratype, left valve, OS 8141; 10, internal lateral view, ×123; 11, external lateral view, ×125. Fig. 12, paratype, carapace, OS 8138, lateral view from right, ×106; see also Pl. 7, fig. 1.


1a
2a
3a
4a
5a
6a
1b
2b
3b
6b
4b
5b
9a
7a
8a
12a
10a
11a
9b
7b
8b
12b
10b
11b

DIAGNOSIS. Elongate, subrectangular, with a beautiful polygonal reticulation recalling honeycomb. Anterior and posterior with strong marginal rims.

HOLOTYPE. A carapace, OS 8150. Two other right valves, OS 8151–2, are paratypes (OS 8152 is broken). Sample FCRM 1578, coastal cliff west of Ras Tapuri; Middle Oligocene. No other material.

DESCRIPTION. Carapace medium-sized, subrectangular in lateral view with greatest height at the anterior cardinal angle and greatest width in front of the posterior end. Anterior margin rounded, with a marked anterior cardinal angle; posterior margin subrounded and narrower. Dorsal and ventral margins straight and subparallel, converging very slightly posteriorly. External surface with a beautiful reticulation reminiscent of a honeycomb, enclosing a raised central area with a surrounding groove. Along the posterior, anterodorsal and posteroventral margins there are deeper pits, numbering about nine posteriorly and five along the dorsal half of the anterior margin. There are strong anterior and posterior marginal rims. Eye tubercle very reduced and only present as an opaque spot. Duplicature moderately wide; inner margin very regular and slightly separated from the line of concrescence in the dorsal part of the anterior margin, leaving a narrow vestibule. Selvage very strongly developed, running halfway between inner and outer margins in the right valve; in the left valve it runs slightly nearer to the outer margin in the dorsal half and medially in the ventral half of the anterior margin. Marginal pore canals simple, short and parallel; they number 28–30, mostly concentrated in the anterior and anteroventral regions. Muscle scars consist of four adductor scars and a V-shaped frontal scar. Hinge weakly holamphidont. In the right valve, a small anterior tooth placed on an elongate platform, and an adjacent socket joined by a groove to the small conical posterior tooth. Left valve with complementary elements.

DIMENSIONS (μm).	L	H	W
Holotype, carapace OS 8150	745	345	315
Paratype, right valve OS 8151	600	270	135
Paratype, right valve OS 8152	720	355	160

REMARKS. Some specimens of *L. paracastanea* Swain 1955 have somewhat similar ornament, lateral outline and marginal pore canals, but the Tanzanian species can be easily distinguished by the conspicuous slope of its dorsal margin towards the posterior end. In addition, the anterior and posterior marginal rims do not seem to be present in Swain's species, which also has a more complicated hinge. *Leptocythere* (*Amnicythere*) *fallax* Devoto 1965 has a very similar ornament of polygonal meshes and also a similar outline, but it has a different hinge.

Leptocythere fastigata sp. nov. Pl. 6, figs 4–8

NAME. 'Rising to a point', with reference to its tapering to a point posteriorly.

DIAGNOSIS. A small ostracod, subrectangular in side view. Lateral surface coarsely pitted, with a weak posteroventral marginal ridge.

HOLOTYPE. A left valve, OS 8132. Three other valves, OS 8133–5, are paratypes. Sample FCRM 1566, Mongo Stream; Lower Miocene.

OTHER MATERIAL. Two specimens (OS 8126–7) from FCRM 1989, Lower Miocene.

DESCRIPTION. Carapace small, subrectangular, tapering posteriorly; highest at the anterior cardinal angle and widest slightly in front of the posterior end. Anterior margin rounded, posterior subrounded in the right valve and obliquely truncate in the left. Ventral margin almost straight, with a concave indentation anterior of mid-length when seen from inside. Dorsal margin straight, making a distinct cardinal angle at the posterior end. External surface coarsely reticulate, the fossae being larger in the anterior half than in the posterior. A weak marginal ridge is present along posterior and posteroventral margins. Internally, margin very narrow; line of concrescence and inner margin coincide except anteriorly, where there is a very narrow vestibule. Normal pores few, coinciding with the ridges of the reticulate ornament externally. Muscle scars cannot be seen; hinge typical of the genus.

DIMENSIONS (μm).	L	H	W
Holotype, left valve OS 8132	380	180	100
Paratype, left valve OS 8134	370	190	105
Paratype, right valve OS 8133	420	210	115
Right valve OS 8136	360	180	100

REMARKS. The small dimensions of the species, the very narrow duplicature, and the absence of sexual dimorphism suggest that the specimens may not be adult. However, since *Leptocythere* species tend to be small and the Tanzanian ostracods are rather small anyway, it seems more useful to name it than to leave it under open nomenclature. *L. crepidula* Ruggieri 1950 resembles the Tanzanian species somewhat, but the coarser reticulation and straight dorsal and ventral margins of *L. fastigata* easily differentiate the two.

Genus ***CALLISTOCYTHERE*** Ruggieri, 1953

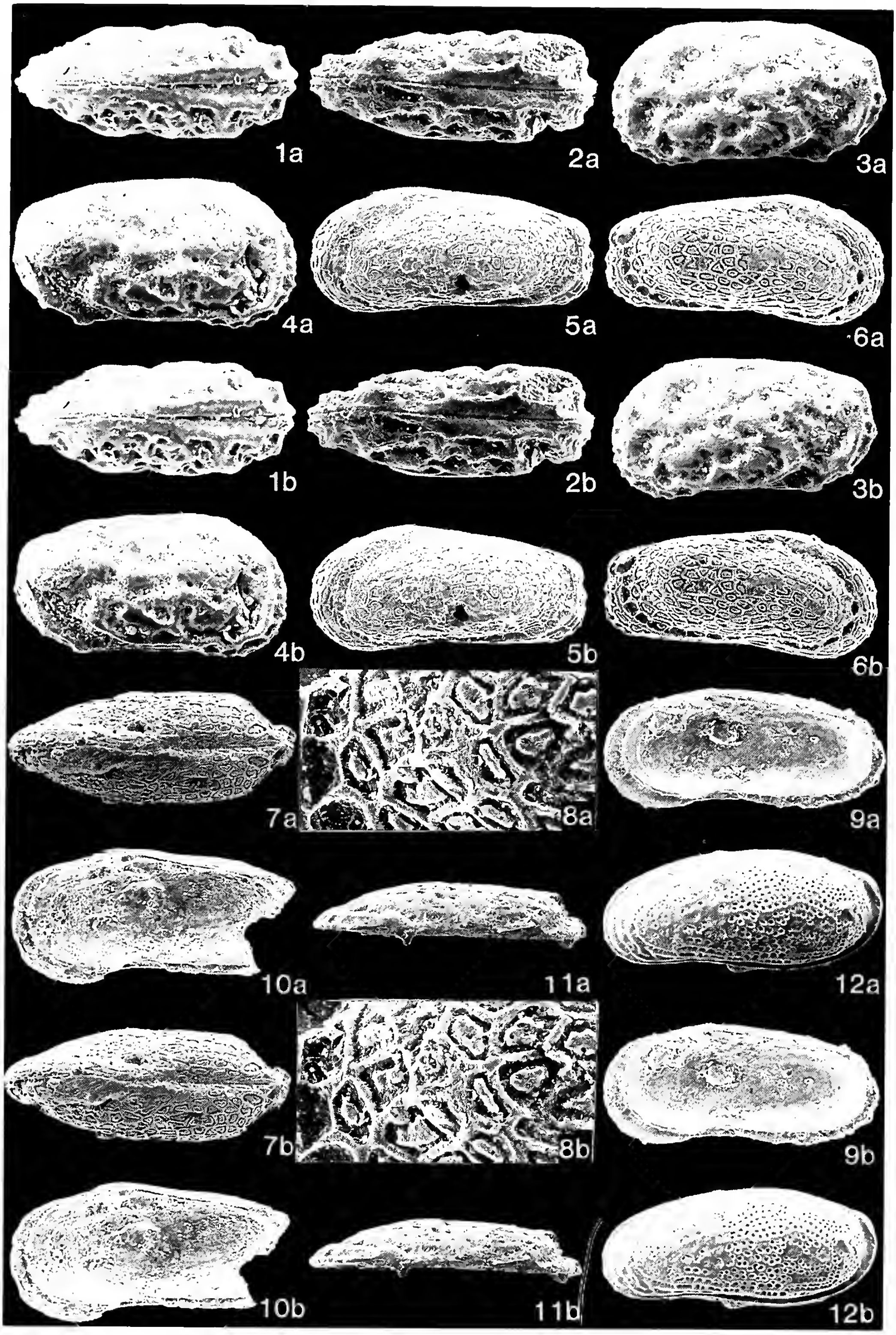
TYPE SPECIES. *Cythere littoralis* Müller, 1894.

PLATE 7

Figs 1–4 *Callistocythere jugosa* sp. nov. Fig. 1, paratype, carapace, OS 8138, dorsal view, ×108; see also Pl. 6, fig. 12. Figs 2–4, carapace, OS 7742; 2, dorsal view, ×129; 3, lateral view from left, ×125; 4, lateral view from right, ×128.

Figs 5–11 *Leptocythere amoena* sp. nov. Figs 5–8, **holotype**, carapace, OS 8150; 5, lateral view from left, ×62; 6, lateral view from right, ×61; 7, dorsal view, ×64; 8, details of surface ornament, ×300. Figs 9, 11, paratype, right valve, OS 8151; 9, internal lateral view, ×77; 11, dorsal view, ×75. Fig. 10, paratype, right valve (broken), OS 8152, internal lateral view, ×65.

Fig. 12 *Tanella* sp. B. Carapace, OS 8126, lateral view from left, ×105.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

Callistocythere jugosa sp. nov. Pl. 6, figs 9–12; Pl. 7, figs 1–4

NAME. 'Full of ridges', in reference to the many ridges on the lateral surface.

DIAGNOSIS. A species of *Callistocythere* with the lateral surface covered with undulating ridges; an anteroventral and another posteroventral ridge extend along the margins and slightly modify the lateral outline of the valves.

HOLOTYPE. A right valve, OS 8140. Five paratypes, OS 8141–5. Sample FCRM 1989, Likonga bridge; Lower Miocene.

OTHER MATERIAL. Ten specimens, including OS 7742 (FCRM 1575), pl. 7, figs 2–4, and OS 8138–9 (FCRM 1566). The latter are indicated as 'A' in Table 1, p. 260. Also occurs in FCRM 1575.

DESCRIPTION. Carapace small, subquadrate in lateral view, and highest anteriorly. Anterior margin rounded, posterior comparatively narrower. Dorsal margin, modified by the marginal ridge, is straight to slightly arched; ventral margin straight to slightly convex in internal view. In dorsal view, carapace almost lens-shaped. Left valve slightly larger than right but overlap inconspicuous. External surface covered with strong knotty ridges, elongated along the margins. The anteroventral ridge originates near the anterior cardinal angle, follows the anterior margin, then runs along the ventral margin as far as the middle, where it turns upwards and merges into other small posterior ridges. Posterodorsal ridge runs from the posteroventral area towards posterior and dorsal margins, curving slightly behind the anterior margin and ending just above the anteroventral area. The smaller lateral ridges are distributed haphazardly; no particular pattern could be observed. Eye tubercle absent. Duplicature moderately wide along the anterior and posteroventral margins; line of concrescence and inner margin coincide except in upper half of anterior margin, where there is a narrow vestibule. Selvage runs parallel to outer margins except anteriorly, where they coincide. Hinge in left valve consists of an anterior socket, followed by three individual small teeth and a crenulate bar with another socket posteriorly.

DIMENSIONS (μm).	L	H	W
Holotype, right valve OS 8140	340	180	095
Paratype, left valve OS 8141	365	200	080
Carapace OS 8138	425	235	195
Carapace OS 7742	360	200	145

REMARKS. There is a single carapace (OS 7742) from FCRM 1575 (Mid-Oligocene) which is more rectangular and has slightly different ornament, but is morphologically identical with this species. Some other specimens with reduced ridges are classified as Morphotype A. *Leptocythere kiata* Hornibrook 1953 has a very similar outline and ornament, but its truncated posterior margin and slightly different distribution of ridges easily distinguish it. *L. cranekeyensis* Puri 1960 has marginal denticles, a tuberculate posterior rim and very low ridges compared with *C. jugosa*. The Tanzanian species differs from *C. nipponica* Hanai 1957*a* in not having the second marginal rim and in being much smaller.

Genus *TANELLA* Kingma, 1948

TYPE SPECIES. *Tanella gracilis* Kingma, 1948.

***Tanella* sp. A** Pl. 8, figs 1–3

FIGURED SPECIMENS. A right valve, OS 8131; a left valve OS 8127. Sample FCRM 1661, near top of old garnet mine, north Lindi; Lower Miocene. The only material.

DESCRIPTION. Valves small, elongate in side view, ovate with greatest height in the middle. Dorsal margin gently convex, anterior symmetrically rounded, posterior very slightly curved in below. Ventral margin slightly concave before mid-length. External surface reticulate with fossae of varying shapes; muri mostly arranged longitudinally. Reticulation very faint along posterior, posteroventral and anterodorsal margins. Eye spot absent. Duplicature moderately wide; line of concrescence and inner margin separate anteriorly to form a very narrow vestibule. There are four adductor muscle scars and a U-shaped frontal scar. Hinge of right valve consists of a bar thickening at the anterior end to form a low anterior tooth and at the posterior end to give a better-developed posterior tooth. Left valve with complementary elements.

DIMENSIONS (μm).	L	H	W
Right valve OS 8131	380	170	090
Left valve OS 8127	400	205	090

***Tanella* sp. B** Pl. 7, fig. 12

FIGURED SPECIMEN. A carapace, OS 8126. Sample FCRM 1661, near top of old garnet mine, north Lindi; Lower Miocene. The only specimen.

DESCRIPTION. Elongate-ovate in side view, with greatest height in middle. Dorsal margin convex, anterior symmetrically rounded; posterior with marked cardinal angle and rounded posteroventrally; ventral margin concave in anterior half. Surface finely reticulate with low longitudinal ridges. Eye spot absent. No internal features were seen because there were no single valves.

DIMENSIONS (μm).	L	H	W
Carapace OS 8126	435	195	190

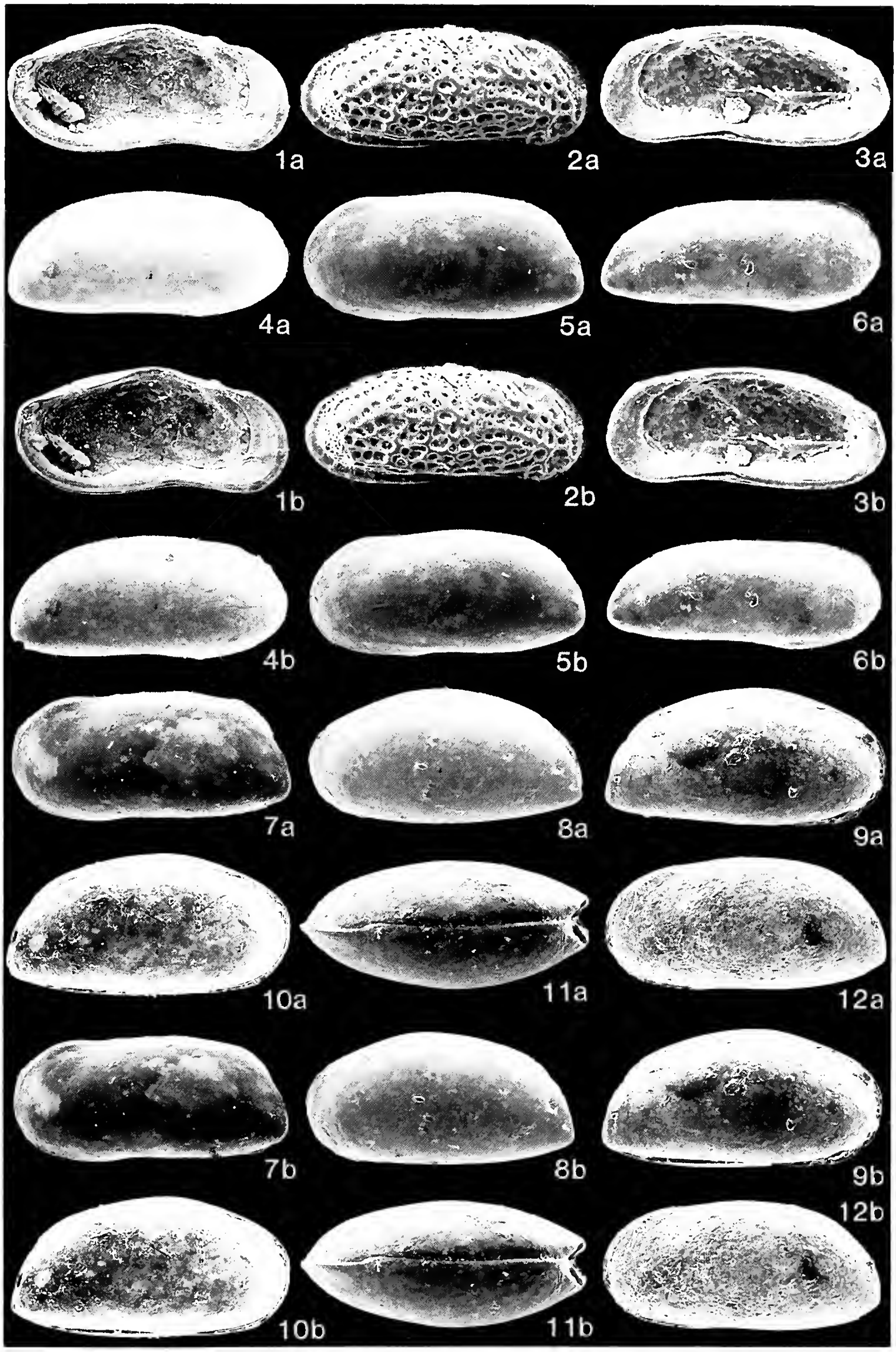
PLATE 8

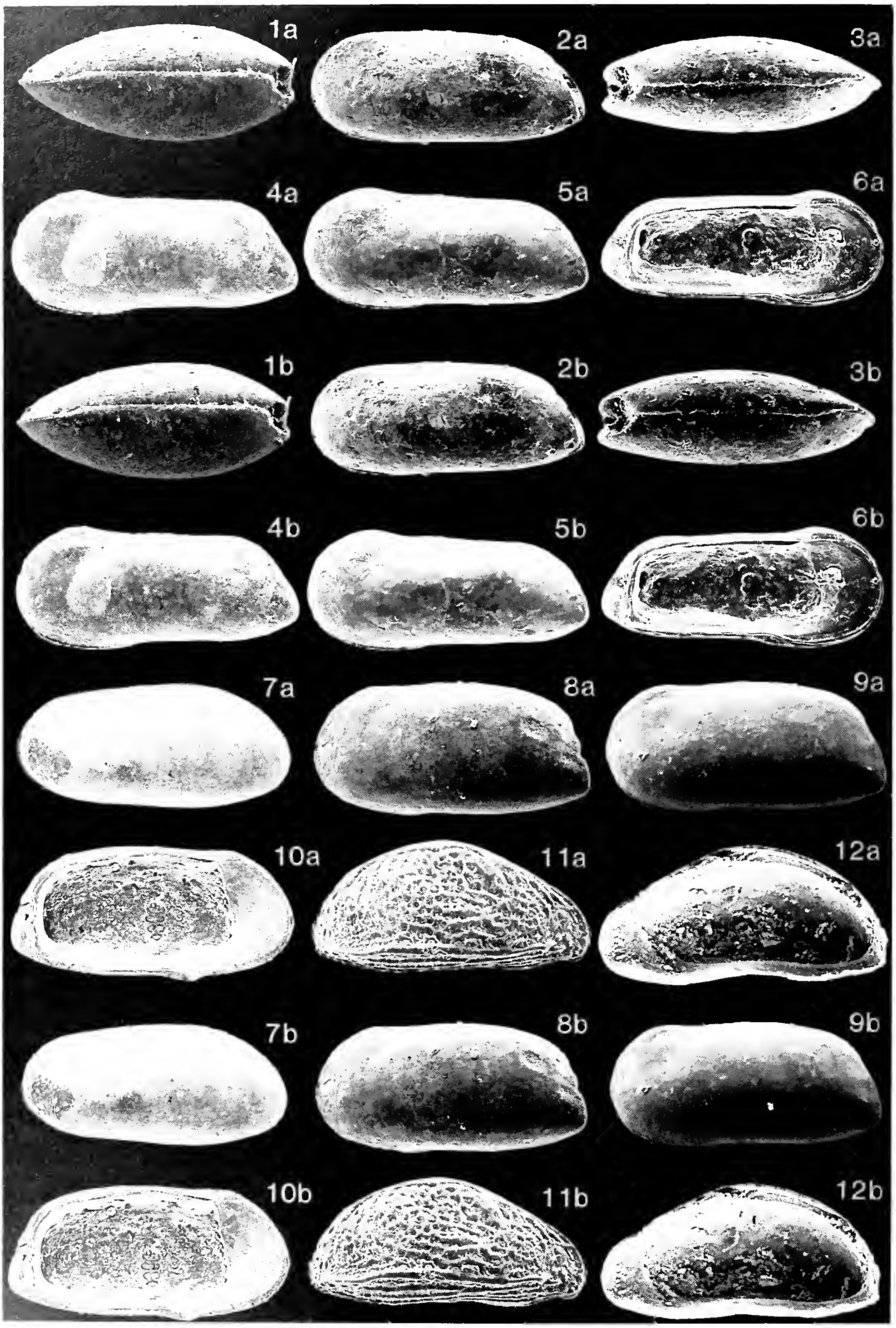
Figs 1–3 *Tanella* sp. A. Fig. 1, Left valve, OS 8127, internal lateral view, ×113. Figs 2, 3, right valve, OS 8131; 2, external lateral view, ×145; 3, internal lateral view, ×145.

Figs 4–7 *Krithe liebaui* sp. nov. Fig. 4, paratype, female right valve, OS 8161, external lateral view, ×65. Fig. 5, **holotype**, female left valve, OS 8322, external lateral view, ×60. Fig. 6, paratype, male right valve, OS 8323, external lateral view, ×70. Fig. 7, paratype, male left valve, OS 8324, external lateral view, ×60; see also Pl. 9, fig. 9 (slightly more oblique view).

Figs 8–11 *Krithe medioelata* sp. nov. Figs 8, 9, **holotype**, carapace, OS 8166; 8, lateral view from left, ×54; 9, lateral view from right, ×55. Figs 10, 11, paratype, carapace, OS 8167; 10, lateral view from right, ×58; 11, dorsal view, ×59.

Fig. 12 *Krithe burdigalia* sp. nov. Paratype, female carapace, OS 8164, lateral view from left, ×60. See also Pl. 9, fig. 1.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
12b
10b
11b


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

Family **CYTHERIDEIDAE** Sars, 1925
Subfamily **CYTHERIDEINAE** Sars, 1925

Genus ***CLITHROCYTHERIDEA*** Stephenson, 1936

TYPE SPECIES. *Cytheridea garretti* Howe & Chambers, 1935.

Clithrocytheridea*? *semiluna sp. nov.
Pl. 9, figs 11, 12; Pl. 10, figs 1, 2

NAME. 'Half moon'.

DIAGNOSIS. A more or less egg-shaped species of *Clithrocytheridea*? with carapace inflated ventrally; ventral surface almost flat with four longitudinal ridges in each valve.

HOLOTYPE. A carapace, OS 8154. Four paratypes, OS 8155–8. Sample FCRM 2033, Lindi Creek, east shore; Upper Eocene.

OTHER MATERIAL. Three specimens from the same sample. Also occurs in FCRM 2045.

DESCRIPTION. Carapace egg-shaped in lateral view, with greatest height almost in the middle and greatest width in the mid-ventral half. Anterior and posterior margins almost continuous with dorsal, each junction being marked by a slight angle. Dorsal margin symmetrically and broadly curved in front but sloping and almost straight posteriorly. Ventral margin straight to slightly concave in the middle while the ventrolateral surface is strongly concave. Lateral surface weakly reticulate. A thin, flexuous, sharply defined longitudinal ridge defines the boundary between the lateral and flattened ventral surfaces; the ventral ridge nearest to this is single anteriorly, dividing into two about mid-length; the next is single posteriorly, bifurcating towards the front. There are several more ridges on the ventral surface. Internally, the right hinge consists of crenulate anterior and posterior tooth plates separated by a smooth bar which has a distinct accommodation groove dorsal to it. Other internal features cannot be seen clearly.

DIMENSIONS (μm).	L	H	W
Holotype, carapace OS 8154	405	220	250
Paratype, right valve OS 8155	330	175	130

REMARKS. This Tanzanian species probably does not truly belong to *Clithrocytheridea* and may in fact represent a new genus. It is provisionally placed in it, however, because it resembles that genus in hinge details and general outline. It differs in the outline of its arched dorsal margin and in having ventral ridges; the muscle scars and other internal features are unknown.

Genus ***ROSTROCYTHERIDEA*** Dingle, 1969*a*

TYPE SPECIES. *Rostrocytheridea chapmani* Dingle, 1969*a*.

Rostrocytheridea? sp. Pl. 10, figs 3, 4

FIGURED SPECIMEN. A right valve, OS 7915. Sample FCRM 2033, Lindi Creek, east shore; Upper Eocene.

OTHER MATERIAL. Two valves (e.g. OS 7914) from the same sample.

DESCRIPTION. Right valve subovate to egg-shaped in outline, with greatest height equal to slightly more than half the length. Anterior margin symmetrically rounded, posterior incurved below. Dorsal margin convex, sloping both anteriorly and posteriorly from the greatest height, which is about two-fifths the length from the anterior margin. Ventral margin convex. Lateral surface smooth except for some punctation, mostly concentrated above the centre. Internally, marginal pore canals, muscle scars and hinge are typical of the genus.

DIMENSIONS (μm).	L	H	W
Right valve OS 7915	410	260	140

REMARKS. This Tanzanian species does not belong to *Rostrocytheridea* s. str. but shows an evolutionary intermediate stage between the Cretaceous genus *Rostrocytheridea*, with a pointed posterior margin, and the Miocene–Recent *Cyprideis*, with almost equally rounded posterior and anterior margins.

Family **KRITHIDAE** Brady, Crosskey & Robertson, 1874
Subfamily **KRITHINAE** Mandelstam, 1960

Genus ***KRITHE*** Brady, Crosskey & Robertson, 1874

TYPE SPECIES. *Ilyobates praetexta* Sars, 1866.

Krithe burdigalia sp. nov. Pl. 8, fig. 12; Pl. 9, figs 1–3

NAME. A reference to its occurrence in the Burdigalian (Lower Miocene).

DIAGNOSIS. A species of *Krithe* with marked sexual dimorphism. Presumed males subrectangular in lateral view; females are slightly higher behind the middle.

HOLOTYPE. A male carapace, OS 8163. Two female carapaces, OS 8164–5, are paratypes. Sample FCRM 1989, Likonga bridge; Lower Miocene.

OTHER MATERIAL. Four specimens from the same sample.

PLATE 9

Figs 1–3 *Krithe burdigalia* sp. nov. Fig. 1, paratype, female carapace, OS 8164, dorsal view, ×60; see also Pl. 8, fig. 12. Figs 2, 3, **holotype**, male carapace, OS 8163; 2, lateral view from left, ×60; 3, dorsal view, ×61.

Figs 4–6 *Ommatokrithe prolata* Ahmad, 1977*d*. Figs 4, 6, holotype, female left valve, OS 7768; 4, external lateral view, ×59; 6, internal lateral view, ×59. Fig. 5, paratype, male left valve, OS 7769, external lateral view, ×59.

Fig. 7 *Parakrithe cicatricosa* sp. nov. **Holotype**, female left valve, OS 8168, external lateral view, ×86.

Figs 8–10 *Krithe liebaui* sp. nov. Figs 8, 10, paratype, male left valve, OS 8326; 8, external lateral view, ×61; 10, internal lateral view, ×62. Fig. 9, paratype, male left valve, OS 8324, external lateral view, ×61; see also Pl. 8, fig. 7.

Figs 11, 12 *Clithrocytheridea*? *semiluna* sp. nov. Paratype, right valve, OS 8155; 11, external lateral view, ×136; 12, internal lateral view, ×138.

DESCRIPTION. Sexual dimorphism marked; presumed male almost rectangular, with dorsal and ventral margins parallel, female trapezoidal, being higher and wider behind the middle. Females are also comparatively wider throughout than males. Anterior margin in both sexes symmetrically rounded; posterior margin meets the ventral margin abruptly but is continuous with it and forms part of the posterodorsal curve. Posterior end incised in dorsal view. Left valve overlaps right. Internal features typical of genus; duplicature not well developed and marginal pore canals not easy to see.

DIMENSIONS (µm).	L	H	W
Holotype, male carapace OS 8163	745	320	280
Paratype, female carapace OS 8164	745	375	345

REMARKS. *K. burdigalia* looks very similar to *K. liebaui* but the two can be separated readily; the presumed females of *K. burdigalia* are higher behind mid-length, and the presumed males are not very slender, in both ways being different from *K. liebaui*.

Krithe liebaui sp. nov. Pl. 8, figs 4–7; Pl. 9, figs 8–10; Fig. 7a

NAME. In honour of Dr Alexander Liebau.

DIAGNOSIS. A species of *Krithe* with thirteen marginal pore canals along the anterior and three along the mid-ventral margin. There is marked sexual dimorphism.

HOLOTYPE. A female left valve, OS 8322. Four paratypes, OS 8161, 8323, 8324, 8326. Sample FCRM 1737, South Mtwero; Lower Miocene.

OTHER MATERIAL. Seventeen complete specimens and 15 broken ones, from the same sample. Also occurs in FCRM 1738, 1742.

DESCRIPTION. Shape of carapace depends on sex of specimen; right valves of presumed males slender and subtriangular with greatest height at the anterior cardinal angle. Right valves in females have the greatest height in the middle; female left valves have dorsal and ventral margins almost straight and parallel. Anterior margins rounded in both sexes; posterior margins acutely angled in lateral view and incised in dorsal view. Surface smooth. Internally, duplicature broad; line of concrescence and inner margin separated, forming a comparatively wide anterior vestibule. Inner margin U-shaped and slightly broader towards the front. Selvage runs peripherally except at the posterior margin, where it runs well inside the lateral outline, giving the posterior an indented appearance. Seen from inside, the posterior margin is divided into two compartments. Marginal pore canals, about thirteen anteriorly and three ventrally, are mostly simple and more or less straight; for descriptive purposes they are numbered. MPC 1′ is false and is the only one running in the dorsal half of the anterior margin. MPC 2 and 3 have a common origin and in some specimens do not separate until mid-length.

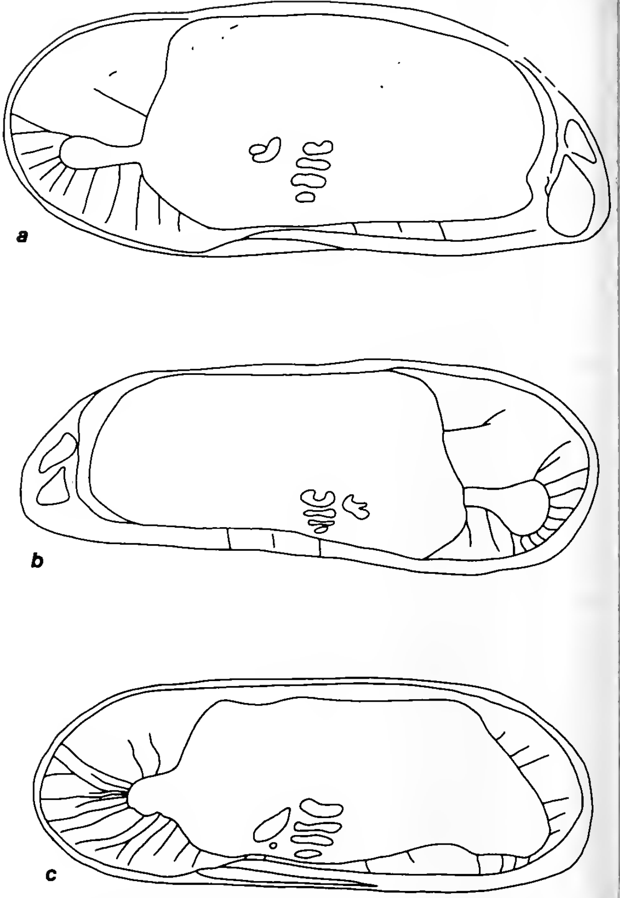


Fig. 7 Krithidae. Internal lateral views showing nature of marginal pore canals and muscle scar patterns. a, *Krithe liebaui* sp. nov. Paratype, ♀ right valve OS 8161. ×120. b, *Ommatokrithe prolata* Ahmad. Holotype, ♀ left valve OS 7768. ×100. c, *Parakrithe cicatricosa* sp. nov. Paratype, ♀ right valve OS 8169. ×150.

DIMENSIONS (µm).	L	H	W
Holotype, female left valve OS 8322	750	375	190
Paratype, male right valve OS 8323	760	320	150
Paratype, male left valve OS 8324	755	370	190
Paratype, male left valve OS 8326	745	380	195
Paratype, female right valve OS 8161	705	345	170

REMARKS. *K. cubensis* van den Bold 1946 has more numerous marginal pore canals in the dorsal half of the anterior margin and along the posterior margin. In general shape and marginal pore canal pattern, *K. dolichodeira* van den Bold 1946, from the Miocene of the Caribbean region, resembles *K. liebaui*, but *K. dolichodeira* has shorter marginal pore canals and is also smaller; it has a length of about 560 µm compared with over 700 µm for *K. liebaui*. *K. hiwanneensis* Howe &

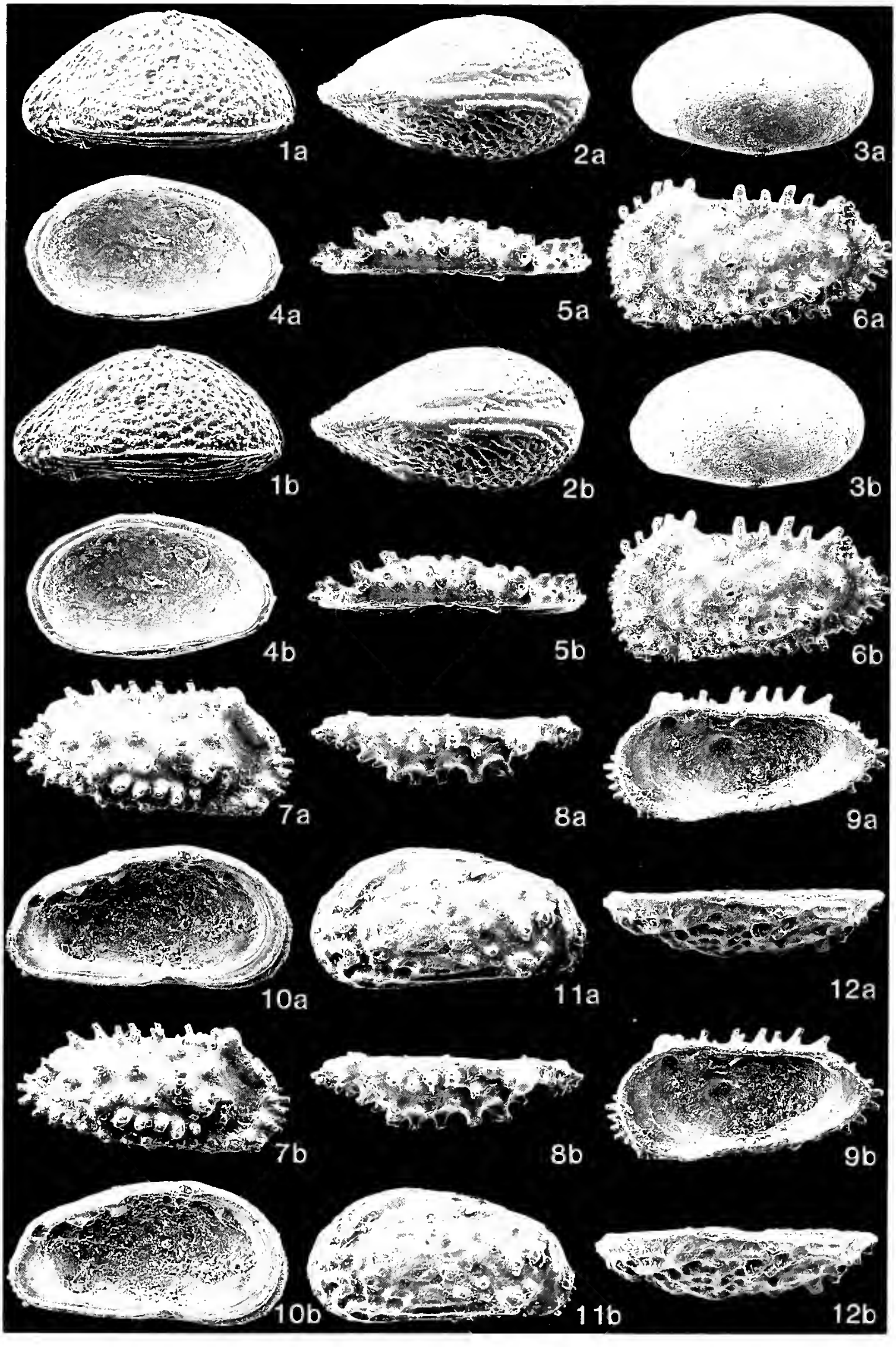
PLATE 10

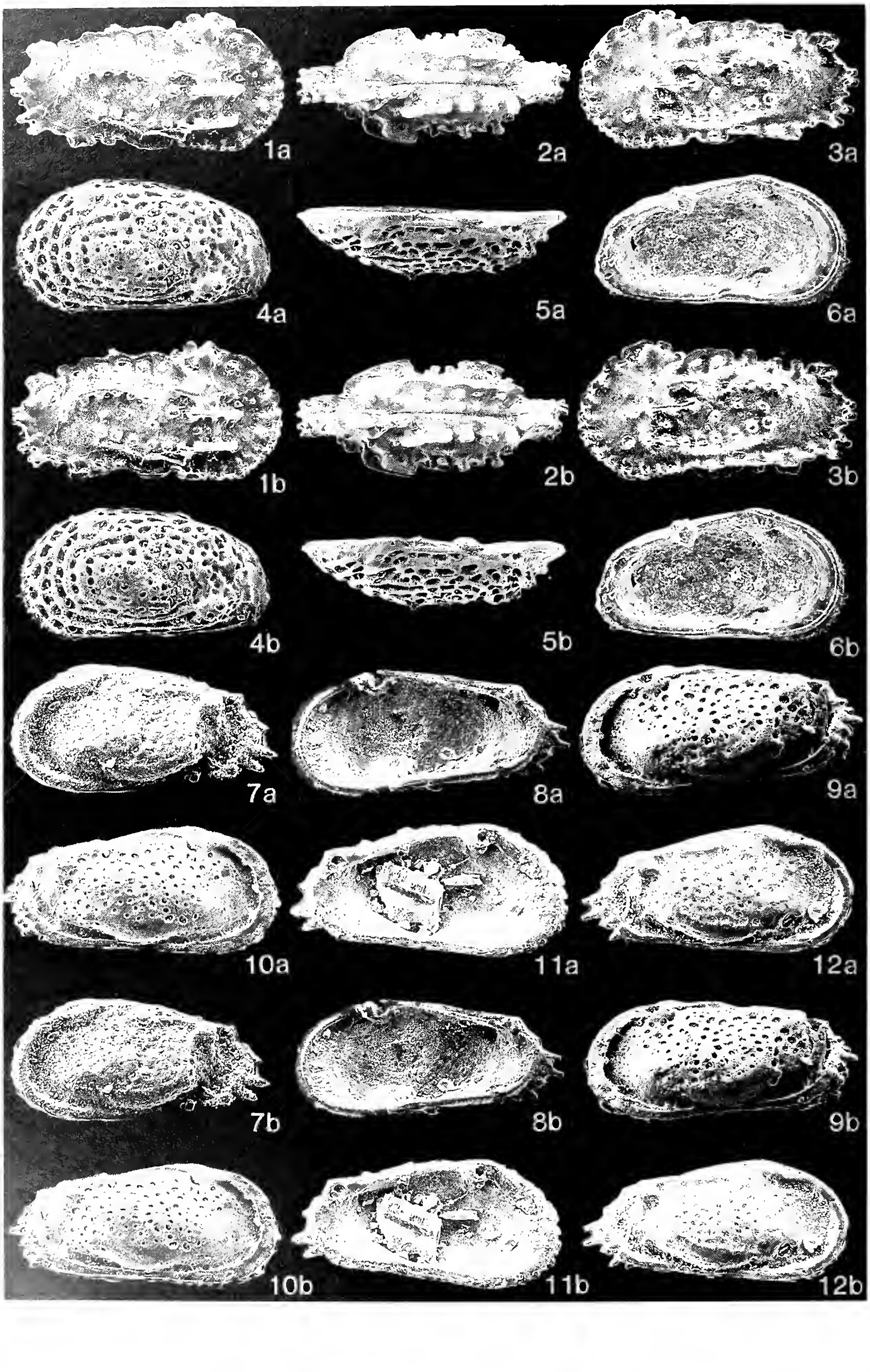
Figs 1, 2 *Clithrocytheridea*? *semiluna* sp. nov. **Holotype**, carapace, OS 8154; 1, lateral view from left, ×109; 2, dorsal view, ×109.

Figs 3, 4 *Rostrocytheridea*? sp. Right valve, OS 7915; 3, external lateral view, ×95; 4, internal lateral view, ×100.

Figs 5–9 *Trachyleberis duplex* sp. nov. Figs 5, 6, **holotype**, left valve, OS 7834; 5, dorsal view, ×56; 6, external lateral view, ×56. Figs 7–9, paratype, right valve, OS 7833; 7, external lateral view, ×48; 8, dorsal view, ×47; 9, internal lateral view, ×48.

Figs 10–12 *Gujaratella*? *tanzaniensis* sp. nov. **Holotype**, left valve, OS 7835; 10, internal lateral view, ×89; 11, external lateral view, ×86; 12, dorsal view, ×88.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

Lea (*in* Howe & Law 1936) has shorter marginal pore canals. *K. perattica* Alexander 1934 resembles *K. liebaui* in general shape and in having the ends of the marginal pore canals thickened; however, the latter has marginal pore canals concentrated along the anterior margin while the former has them distributed all along the ventral and posterior margins. *K. sawanensis* Hanai 1959, from the Upper Pliocene of Japan, is easily distinguished from the Tanzanian species by its larger size, greater number of false marginal pore canals interspersed between true ones, and less pronounced sexual dimorphism.

Krithe medioelata sp. nov. Pl. 8, figs 8–11

NAME. 'Highest in the middle'.

DIAGNOSIS. A species of *Krithe* with the greatest height in the middle or slightly in front of it. Dorsal margin strongly arched.

HOLOTYPE. A carapace, OS 8166. A carapace, OS 8167, is a paratype. Sample FCRM 2034, Lindi Creek, east shore; Upper Eocene.

OTHER MATERIAL. Three specimens from the same sample.

DESCRIPTION. Carapace subovate in lateral view with the greatest height slightly in front of the middle and greatest width almost at mid-length. Anterior margin rounded, dorsal strongly arched, ventral margin almost straight. Carapace lens-shaped in dorsal view, with a strongly incised posterior margin. No sexual dimorphism apparent. Left valve overlaps right. Lateral surface smooth, eye tubercle absent. Internal features typical of the genus; marginal pore canals not visible in the only single valve found intact.

DIMENSIONS (μm).	L	H	W
Holotype, carapace OS 8166	820	435	390
Paratype, carapace OS 8167	790	425	375

REMARKS. *K. echolsae* Esker 1968, from the Danian of Tunisia, has a curved posterodorsal margin compared with the sloping margin of *K. medioelata*. *K. whitecliffensis* Crane 1965, *K. rutoti* Keij 1957, *K. cubensis* van den Bold 1946, *K. contracta* Oertli 1961, *K. langhiana* Oertli 1961, *K. galei* Crouch 1949, and some other species with similar outlines can be distinguished from *K. medioelata* by the fact that their greatest height in lateral view is behind the middle rather than in front of it as in the Tanzanian species.

Genus ***OMMATOKRITHE*** Ahmad, 1977*d*

TYPE SPECIES. *Ommatokrithe prolata* Ahmad, 1977*d*.

Ommatokrithe prolata Ahmad, 1977*d* Pl. 9, figs 4–6; Fig. 7b

1977*d* *Ommatokrithe prolata* Ahmad: 131–134.

HOLOTYPE. A female left valve, OS 7768. Paratypes, three single valves, OS 7769–71. Sample FCRM 1737, South Mtwero; Lower Miocene.

OTHER MATERIAL. Four single valves from the same sample. Also occurs in FCRM 1738.

DESCRIPTION. Carapace elongate, subrectangular in lateral view, with dorsal and ventral margins straight and parallel; anterior margin rounded, posterior obliquely truncate. Posterior incised in dorsal view; posterior end divided into two compartments internally, behind the selvage. Lateral surface smooth except for a glassy round eye-tubercle just below anterior cardinal angle. Internally, duplicature wide. Inner margin and line of concrescence separated in the mid-anterior region, where there is a moderately wide vestibule. Inner margin extends anteriorly for a considerable distance; marginal pore canals are therefore short; for descriptive purposes they are numbered. MPC 1 occurs in the dorsal half and is long; MPC 2 and 3 bifurcate from a common canal; 4 to 12 are short, straight and parallel; 13 is elongate and curves towards the front; 14 runs along the inner margin; the ventral canals 15 to 17 occur along the midventral margin, MPC 16 being false. Normal pores large, sieve type and regularly distributed. Muscle scar pattern consists of four adductor scars decreasing in size from top to bottom, with a three-fold frontal scar and five to seven dorsal ones. Hinge adont, partly crenulate in the posterior quarter.

DIMENSIONS (μm).	L	H	W
Holotype, female left valve OS 7768	785	375	170
Paratype, male left valve OS 7769	780	365	175

REMARKS. So far, no other Krithidae species with an eye tubercle has been described.

Genus ***PARAKRITHE*** van den Bold, 1958*a*

TYPE SPECIES. *Cytheridea* (*Dolocytheridea*) *vermunti* van den Bold, 1946.

Parakrithe cicatricosa sp. nov. Pl. 9, fig. 7; Fig. 7c

NAME. 'Scarred', in reference to the large number of dorsal muscle scars.

DIAGNOSIS. A species of *Parakrithe* with a large number of dorsal muscle scars, and 16 anterior marginal pore canals, about half of which are false. Sexual dimorphism present.

HOLOTYPE. A female left valve, OS 8168. Paratype a female right valve, OS 8169. Sample FCRM 1737, South Mtwero; Lower Miocene.

OTHER MATERIAL. 48 specimens from samples FCRM 1737, 1738, 1742, 1989, 2014, 2016.

DESCRIPTION. Carapace small, elongate, and subrectangular to subovate in lateral view. Anterior margin symmetrically rounded, posterior subrounded, rather broadly curved in the

PLATE 11

Figs 1–3 *Carinocythereis* sp. Carapace, OS 7991; 1, lateral view from right, ×71; 2, dorsal view, ×70; 3, lateral view from left, ×71.

Figs 4–6 Genus B sp. Left valve, OS 8113; 4, external lateral view, ×74; 5, dorsal view, ×79; 6, internal lateral view, ×74.

Figs 7–12 *Occultocythereis africana* sp. nov. Figs 7, 11, paratype, female left valve, OS 7974; 7, external lateral view, ×89; 11, internal lateral view, ×92. Figs 8, 12, paratype, female right valve, OS 7972; 8, internal lateral view, ×91; 12, external lateral view, ×89. Figs 9, 10, **holotype**, female carapace, OS 7976; 9, lateral view from left, ×107; 10, lateral view from right, ×107.

upper half and narrowly curved in the lower. Sexual dimorphism occurs; dorsal and ventral margins diverge posteriorly in presumed females but are almost parallel in presumed males. Lateral surface smooth and without an eye tubercle. Internally, duplicature moderately wide, with a fairly wide anterior vestibule. About 30 straight marginal pore canals, 16 of them along the anterior margin, where true marginal pore canals are interspersed with false ones. Muscle scar pattern consists of four adductor scars arranged in a vertical row, with an elongate scar in front and seven to eight dorsal scars. Normal pores large, sieve type and widely scattered.

DIMENSIONS (μm).	L	H	W
Holotype, female left valve OS 8168	520	260	140

REMARKS. A large number of carapaces from places other than the type locality are almost identical in outline but it was not possible to see their marginal pore canals. These specimens are tentatively classified as *P. cicatricosa*.

Family **TRACHYLEBERIDIDAE** Syvester-Bradley, 1948
Subfamily **TRACHYLEBERIDINAE** Sylvester-Bradley, 1948
Tribe **TRACHYLEBERIDINI** Sylvester-Bradley, 1948

Genus ***TRACHYLEBERIS*** Brady, 1898

TYPE SPECIES. *Cythere scabrocuneata* Brady, 1880.

Trachyleberis duplex sp. nov. Pl. 10, figs 5–9

NAME. 'Double', with reference to anterior and ventral spines occurring in pairs.

DIAGNOSIS. A species of *Trachyleberis* with a double row of spines along the anterior margin and another along the ventral margin. Anterior cardinal angle well marked.

HOLOTYPE. A female left valve, OS 7834. Paratype a male right valve, OS 7833. Sample FCRM 2010, stream south-west of Mtwero; Lower Miocene. No other material.

DESCRIPTION. Carapace elongate in side view, greatest length at mid-height and greatest height at anterior cardinal angle. Anterior margin evenly rounded, a double row of spines following the curve; outer spines smaller and more numerous than inner ones, evenly spaced and well developed. Posterior margin triangular, with spines, mostly bifid. Dorsal margin straight, with a row of spines, also mostly bifid. Ventral margin straight or slightly curved, with a double row of spines. Surface spiny, especially medially, where there is a scattered row, usually arranged in a zigzag way. Eye tubercle with a strong spine just behind it. Inner margin and line of concrescence coincide; hinge holamphidont. Other internal features typical of genus.

DIMENSIONS (μm).	L	H	W
Holotype, female left valve OS 7834	815	465	240
Paratype, male right valve OS 7833	955	475	240

REMARKS. The pattern of ornament is similar to that of *T. pennyi* Neale 1975 from the Santonian of Western Australia, but in side view the Tanzanian species has a more triangular posterior end and strongly projecting anterodorsal margin. It is also larger than *T. pennyi*.

Genus ***GUJARATELLA*** Khosla, 1978

TYPE SPECIES. *Gujaratella boldi* Khosla, 1978.

Gujaratella*? *tanzaniensis sp. nov. Pl. 10, figs 10–12

NAME. 'From Tanzania'.

DIAGNOSIS. A tuberculate species with reduced anterior denticulation and no spines, but with a well developed anterior vestibule.

HOLOTYPE. A female left valve, OS 7835. Paratype a female left valve, OS 7837. Sample FCRM 2010, stream south-west of Mtwero; Lower Miocene. The only surviving specimens, but see 'Remarks' below.

DESCRIPTION. Carapace shape determined by sexual dimorphism; in side view presumed males are elongate, subrectangular, with a straight dorsal margin and a straight or slightly concave ventral margin, these two margins converging posteriorly. Female has dorsal margin slightly arched, subparallel to ventral margin. Anterior margin evenly rounded, posterior rather produced below, and the posterodorsal margin slightly concave. Greatest height at the anterior cardinal angle and greatest length along ventral side. External surface tuberculate. Eye tubercle elongate, running into the anterior marginal rim, which consists of a semicircular double line of tubercular spines joined to each other so as to form semicircular enclosures open towards the front. Subcentral tubercle an elongated swollen boss. Anteroventral complex consists of three or four tubercles joined together and merging into a thin ventral ridge with another thin ridge below. Other ubercles, of various sizes, have normal pore canals opening at their tips. Internally, duplicature moderately wide, inner margin and line of concrescence separate; there is a fairly wide vestibule. Selvage placed almost at the middle of the duplicature, well developed and following a sinuous course along the ventral margin. Muscle scars cannot be seen clearly. Hinge of right valve consists of an anterior tooth with distal part low and proximal part higher; median groove crenulate and posterior tooth slightly elongate and smooth. Immediately below and in front of the anterior hinge tooth there is a prominent ocular sinus. Hinge of left valve complementary to that of right.

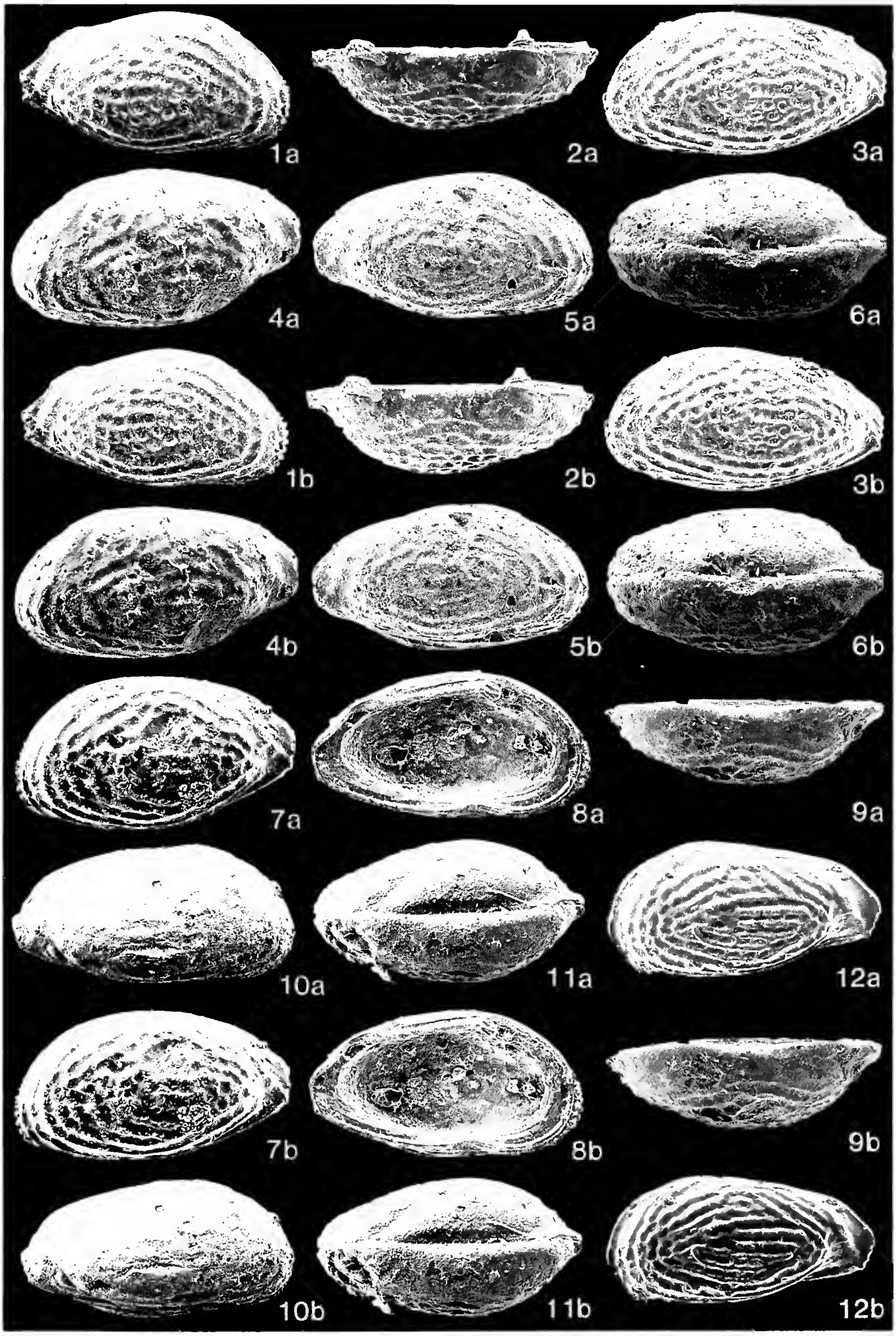
DIMENSIONS (μm).	L	H	W
Holotype, female left valve OS 7835	515	285	140

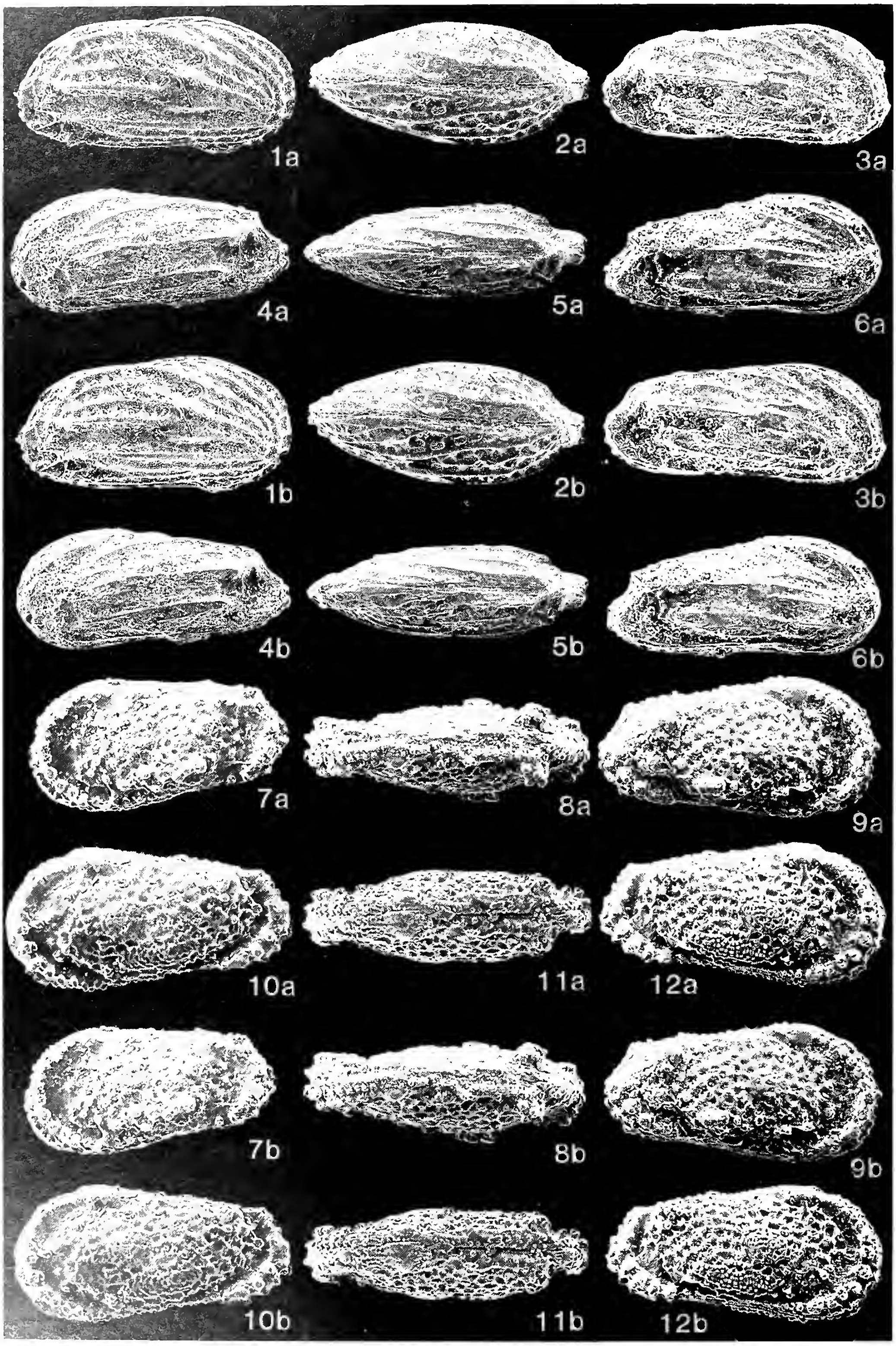
REMARKS. Unfortunately it has not been possible to figure the one male specimen of this species that was found, because of its fragility. The species is provisionally placed in the genus

---

PLATE 12

Figs 1–12 *Leguminocythereis dinglei* sp. nov. Figs 1, 2, paratype, male carapace, OS 8195; 1, lateral view from right, ×55; 2, dorsal view, ×57. Fig. 3, paratype, male carapace, OS 8196, lateral view from left, ×60. Figs 4–6, **holotype**, female carapace, OS 8194; 4, lateral view from left, ×57; 5, lateral view from right, ×54; 6, dorsal view, ×55. Figs 7–9, paratype, female left valve, OS 8198; 7, external lateral view, ×58; 8, internal lateral view, ×57; 9, dorsal view, ×58. Figs 10, 11, paratype, male carapace, OS 8199; 10, lateral view from right, ×48; 11, dorsal view, ×46. Fig. 12, paratype, juvenile? left valve, OS 8200, external lateral view, ×67.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

Gujaratella because of its external appearance, although it has a distinct anterior vestibule not found in that genus. The muscle scars and marginal pore canals were not clearly observed in this material.

Genus *HAUGHTONILEBERIS* Dingle, 1969*b*

TYPE SPECIES. *H. haughtoni* Dingle, 1969*b*.

Haughtonileberis radiata Dingle 1976 Pl. 13, figs 1–2

1976 *Haughtonileberis radiatus* (sic, recte *radiata*) Dingle: 46.

1976 *Leguminocythereis*? sp. 1 of Dingle: 44; fig. 6 (a, b); fig. 10 (23).

FIGURED SPECIMEN. A female carapace, OS 8174. Sample FCRM 1578, coastal cliff west of Ras Tapuri; Middle Oligocene.

OTHER MATERIAL. One right valve (OS 7810), also from FCRM 1578. Also occurs in FCRM 1576.

DIMENSIONS (μm).	L	H	W
Female carapace OS 8174	895	435	380

REMARKS. Originally described from the Upper Oligocene–Upper Eocene of borehole SOEKOR JC-1 off the coast of Natal, South Africa. The species described as *Leguminocythereis*? sp. 1 by Dingle in the same paper is, in the present authors' view, a female dimorph of *H. radiata*.

Haughtonileberis rastapuriensis sp. nov. Pl. 13, figs 3–6

NAME. After the type locality, Ras Tapuri.

DIAGNOSIS. A species of *Haughtonileberis* with a prominent dorsal ridge curving towards, but stopping short of, the median ridge, which bifurcates in the anterior half of the valve. There are two ventrolateral ridges joined at their posterior ends, and an ocular ridge along the anterodorsal margin.

HOLOTYPE. A male carapace, OS 7802. Two paratypes, OS 7803, OS 7804. Sample FCRM 1575, shore south-west of Ras Tapuri; Middle Oligocene.

OTHER MATERIAL. Six specimens in the BM(NH) from the same sample, including OS 7807. Another 20 specimens from FCRM 2010, Lower Miocene, are kept at the BP Research Centre, Sunbury-on-Thames. Also occurs in FCRM 1574, 1576 and 1578.

DESCRIPTION. Carapace medium-sized, elongate in side view, tapering posteriorly, with greatest height at anterior cardinal angle. Anterior margin rounded, dorsal margin straight and sloping towards posterior. Ventral margin straight to slightly concave; posteroventral margin convex and posterodorsal concave. Sexes distinct, presumed males being slightly more slender and elongated than presumed females. External ornament consists of a series of ridges. There is a dorsal ridge, slightly concave downward, in the anterior half; a median ridge, bifid in the anterior part and curved dorsally at the posterior end in some specimens; a pair of ventrolateral ridges joined at their posterior ends; and an ocular ridge running along the anterodorsal margin. Two short ridges lie between the dorsal and median ones, and another two lie ventral to the ventrolateral ridges; of these last, one is short and lies in the middle third, while the other, longer, lies in the anterior half of the length. Duplicature fairly wide; marginal pore canals fine, straight and simple; there are 10 or 11 anteriorly and 6 or 7 posteriorly, the latter tending to occur in pairs. There are four adductor muscle scars in a vertical row, decreasing in size from dorsal to ventral; the two uppermost join at their posterior ends; and there is a V-shaped frontal scar which opens upwards. Hinge typical of genus, consisting of an anterior tooth, a small postjacent socket, a crenulate groove in the median section and a round knob-like posterior tooth in the right valve.

DIMENSIONS (μm).	L	H	W
Holotype, male carapace OS 7802	735	305	240
Paratype, female carapace OS 7803	700	310	250

REMARKS. The Lower Miocene specimens (FCRM 2010) are comparatively large (L = 800 μm), and have slightly less ornamentation, but otherwise seem to be the same species as *H. rastapuriensis*; they and the Mid-Oligocene specimens are therefore included in that species. It was difficult to decide whether *H. rastapuriensis* should be a new species, a subspecies or a morphotype of *H. fissilis* Dingle 1969*b*. The two are extremely close in general shape, ornament and other features. However, the Tanzanian species is larger and has two ventrolateral ridges instead of the single ridge of the South African species. The two are also from very different horizons; the South African species is reported from the Upper Senonian (?Upper Cretaceous) of Pondoland, while the Tanzanian species comes from Mid-Oligocene and Lower Miocene samples. For all these reasons, the new species is regarded as distinct from *H. fissilis*. There are some specimens from samples JOZ 889 and JOZ 896, from the Pliocene of the coastal area between Pangani, Tanzania, and Mombasa, Kenya, which are more akin to *H. fissilis*; these are hard to reconcile with the distribution of the present species, which occurs both geologically and geographically between the JOZ specimens and those from South Africa.

Genus *ACANTHOCYTHEREIS* Howe, 1963

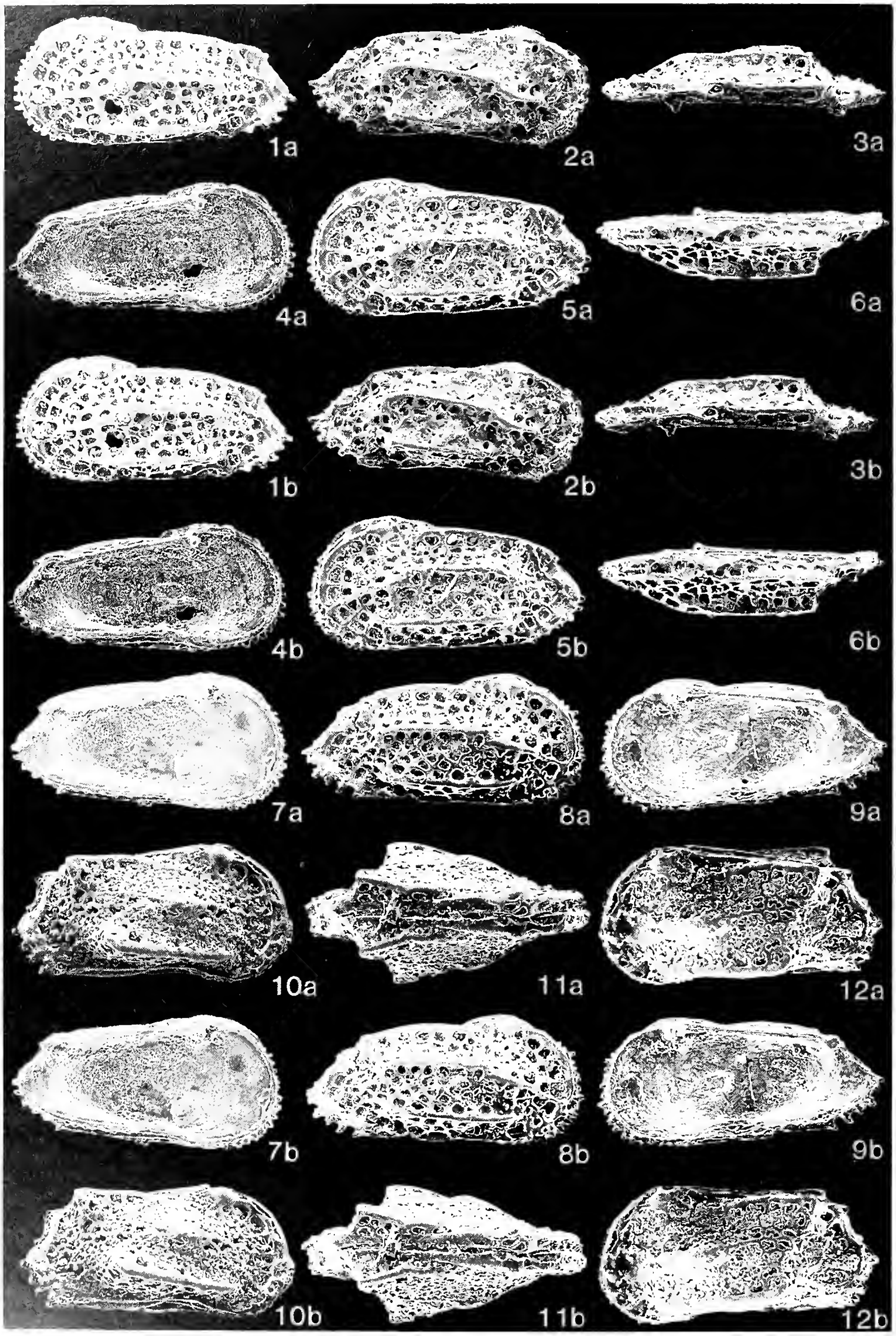
TYPE SPECIES. *Acanthocythereis araneosa* Howe, 1963.

PLATE 13

Figs 1, 2 *Haughtonileberis radiata* Dingle, 1976. Female carapace, OS 8174; 1, lateral view from right, ×51; 2, dorsal view, ×50.

Figs 3–6 *Haughtonileberis rastapuriensis* sp. nov. Figs 3, 5, **holotype**, male carapace, OS 7802; 3, lateral view from right, ×63; 5, dorsal view, ×61. Figs 4, 6, paratype, female carapace, OS 7803; 4, lateral view from left, ×64; 6, lateral view from right, ×64.

Figs 7–12 *Acanthocythereis postcornis* Siddiqui, 1971. Figs 7–9, female carapace, OS 8331; 7, lateral view from left, ×98; 8, dorsal view, ×107; 9, lateral view from right, ×106. Figs 10–12, male carapace, OS 8330; 10, lateral view from left, ×99; 11, dorsal view, ×99; 12, lateral view from right, ×98.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

Acanthocythereis postcornis Siddiqui, 1971 Pl. 13, figs 7–12

1971 *Trachyleberis* (*Acanthocythereis*) *postcornis* Siddiqui: 82; pl. 41, figs 9, 10; pl. 42, figs 1, 2, 7, 10.

FIGURED SPECIMENS. Two carapaces, a male OS 8330, and a female OS 8331. Sample FCRM 1578, coastal cliff west of Ras Tapuri; Middle Oligocene.

OTHER MATERIAL. Three carapaces (OS 8332–4) from sample FCRM 1575. Also occurs in FCRM 1578.

DIMENSIONS (µm).	L	H	W
Male carapace OS 8330	460	240	160
Female carapace OS 8331	420	230	160

REMARKS. The Tanzanian specimens differ slightly from the holotype of this species, showing characters reminiscent of *Acanthocythereis procapsus* (Siddiqui 1971); they could be placed in either species. However, because of their size and distinctive posterodorsal process, they appear closer to *A. postcornis* and are so classified here.

Genus *FALSOCYTHERE* Ruggieri, 1972

TYPE SPECIES. *Occultocythereis*? *maccagnoi* Ciampo, 1971.

Falsocythere maccagnoi (Ciampo, 1971) Pl. 17, figs 4–6

1971 *Occultocythereis*? *maccagnoi* Ciampo: 27; pl. 2, figs 7–9; pl. 3, fig. 1; pl. 7, fig. 1.
1972 *Falsocythere maccagnoi* (Ciampo) Ruggieri: 91.
1975 *Falsocythere maccagnoi* (Ciampo); Bonaduce, Ciampo & Masoli: 51; pl. 26, figs 6–7.

FIGURED SPECIMEN. A left valve, OS 7820. Sample FCRM 1566, Mongo Stream, Lindi; Lower Miocene. The only specimen.

DIMENSIONS (µm).	L	H	W
Left valve OS 7820	480	240	130

REMARKS. The Tanzanian specimen has a slightly more concave posterodorsal margin than Ciampo's species, but this is the only apparent difference.

Tribe COSTAINI Hartmann & Puri, 1974

Genus *CARINOCYTHEREIS* Ruggieri, 1956

TYPE SPECIES. *Cytherina carinata* Roemer, 1838.

Carinocythereis sp. Pl. 11, figs 1–3

FIGURED SPECIMEN. A carapace, OS 7991. Sample FCRM 1575, shore south-west of Ras Tapuri; Middle Oligocene.

OTHER MATERIAL. Two specimens from Sample FCRM 1578 (OS 8335–6). Also occurs in FCRM 1576, 1578.

DESCRIPTION. Carapace subrectangular with greatest height at anterior cardinal angle; valves very slightly tapering behind. Anterior margin symmetrically rounded, posterior truncate to somewhat rounded, both margins being denticulate. Dorsal and ventral margins modified by marginal ridges; these appear straight, subparallel, and slightly converging behind. Anterodorsal margin protrudes above prominent glassy eye tubercle. Surface ornamentation consists of an anterior peripheral rim joined to a ventral ridge which continues along the posterior margin. There are four other ridges, all with contiguous undercut clavae in the anterior third and with spines in the posterior two-thirds. Except for occasional spines and/or tubercles between the ridges, the lateral surface is smooth.

DIMENSIONS (µm).	L	H	W
Carapace OS 7991	645	350	300

REMARKS. The Tanzanian specimens have carapaces intermediate in shape between the European *Carinocythereis* and the Indo-Pacific *Ponticocythereis*. Unfortunately only three specimens were found, one of which was not well preserved, and no detailed work was possible.

Genus *COSTA* Neviani, 1928

TYPE SPECIES. *Cytherina edwardsi* Roemer, 1838 (subsequent designation, Howe 1955).

Costa*? *hullina sp. nov. Pl. 14, figs 10–12; Pl. 15, figs 1–3

NAME. After the University of Hull, Great Britain.

DIAGNOSIS. A species of *Costa*(?) with a weakly developed median ridge which curves dorsally and joins the better-developed dorsal ridge. Fossae mostly crimped and very variable in shape.

HOLOTYPE. A carapace, OS 7715. Another carapace, OS 7716, a juvenile, is a paratype. Sample FCRM 2033, Lindi Creek, east shore; Upper Eocene.

OTHER MATERIAL. Three specimens from samples FCRM 2033, 2034.

DESCRIPTION. Carapace subquadrate in lateral view, slightly tapering towards posterior margin; greatest height at the anterior angle and greatest width at about one-third of the length from posterior end. Anterior margin broadly rounded, posterior slightly concave above the middle and straight to slightly curved below. Dorsal margin straight, slightly modified by the dorsal ridge, and sloping towards the posterior. Ventral margin straight to slightly concave anteriorly. Right valve overlaps left. Surface ornament consists of three lateral ridges with pitted intercostal areas. Dorsal and ventral ridges strongly developed, former occurring only in posterior half

---

PLATE 14

Figs 1–9 *Costa trudis* Ahmad, 1977*c*. Figs 1, 4, 6, holotype, male left valve, OS 7692; 1, external lateral view, ×55; 4, internal lateral view, ×54; 6, dorsal view, ×55. Figs 2, 3, paratype, male right valve, OS 7693; 2, external lateral view, ×53; 3, dorsal view, ×53. Figs 5, 7, paratype, female left valve, OS 7694; 5, external lateral view, ×55; 7, internal lateral view, ×54. Figs 8, 9, paratype, female right valve, OS 7695; 8, external lateral view, ×54; 9, internal lateral view, ×55.

Figs 10–12 *Costa*? *hullina* sp. nov. **Holotype**, carapace, OS 7715; 10, lateral view from right, ×56; 11, dorsal view, ×58; 12, lateral view from left, ×57.

and latter mostly in anterior half; both these ridges curve upwards at the posterior end. Median ridge weakly developed and curves upward to join dorsal ridge at the back. Subcentral tubercle forms part of median ridge just in front of mid-length. Fossae in intercostal areas variable in shape and have crimped margins. Anteroventral and posteroventral margins denticulate, denticles along the posterior margin being fewer and stronger than the anterior ones. Eye tubercle well developed. As no single valves were found no interior details were seen.

DIMENSIONS (μm).	L	H	W
Holotype, carapace OS 7715	805	390	400
Paratype (juvenile), carapace OS 7716	650	325	260

REMARKS. Except for the weakly developed median ridge, *Costa*? *hullina* could be classified as a subspecies of *Hermanites paijenborchiana* Keij, 1957, from the Eocene of Belgium and France; no *Hermanites* species has a median ridge. The Tanzanian species also differs in having a shorter ventral ridge and a less developed subcentral tubercle. *C.*? *hullina* also differs from the typical *Costa* in that the median ridge is rather more weakly developed and bends upwards rather than downwards at the posterior end. *Hermanites haidingeri* (Reuss) subsp. *rectangularis* Ruggieri, 1962, resembles *C.*? *hullina* in outline and ornament, but has no median ridge and the ventral ridge is longer.

Costa trudis Ahmad, 1977*c* Pl. 14, figs 1–9

1977*c* *Costa trudis* Ahmad: 127–130.

HOLOTYPE. Male left valve, OS 7692. Seventeen paratypes, OS 7693–709. Sample FCRM 2010, stream south-west of Mtwero; Lower Miocene.

OTHER MATERIAL. Five single valves from samples FCRM 1745, 1989, 2010, 2015.

DESCRIPTION. Carapace elongate, slender, with greatest height at anterior cardinal angle, greatest width in posterior half, and greatest length along median line. Anterior margin symmetrically rounded, posterior pointed, with the point at mid-height; posterodorsal margin straight. Dorsal margin strongly modified in lateral view by dorsal ridge; ventral margin straight to slightly concave. Sexual dimorphism present; presumed females higher anteriorly than the more slender males. Surface ornament consists of three prominent ridges. Dorsal ridge runs from about one-third of the length from anterior end to just in front of posterior margin, where it curves downwards and disappears. Median ridge runs from just behind anterior margin, steps up a short distance further on, whence it runs parallel to dorsal ridge and curves down posteriorly. Ventral ridge subparallel to other two. Ocular ridge prominent, running from eye tubercle along anterior and ventral margins. Areas between ridges are strongly reticulate, the shapes of the fossae varying from triangular to subrectangular and subrounded. Internally, inner margin uniformly wide along free margin; marginal pore canals cannot be seen clearly. Muscle scars and hinge are typical of genus and eye tubercle is invisible from within. Right valve hinge consists of a slightly stepped but strongly produced anterior tooth, a socket, a crenulate bar and a posterior tooth which looks like a smooth knob in lateral view, but is elongate in dorsal view.

DIMENSIONS (μm).	L	H	W
Holotype, male left valve OS 7692	850	385	220
Paratype, male right valve OS 7693	860	370	150
Paratype, female left valve OS 7694	830	430	200
Paratype, female right valve OS 7695	845	390	190

REMARKS. *Costa trudis* can be distinguished from *Costa punctatissima punctatissima* Ruggieri 1961 by its more acuminate posterior and lack of a marginal rim. *Costa variabilicosta muhlemanni* van den Bold 1966 is also closely related, but the three-pronged ridge which runs vertically from the median to the ventral ridge in that species is missing in *C. trudis*; there are other differences in ornamental details.

Genus ***TRACHYLEBERIDEA*** Bowen, 1953

TYPE SPECIES. *Cythereis prestwichiana* Jones & Sherborn, 1889.

Trachyleberidea*? *cirrata sp. nov. Pl. 18, figs 6–10

NAME. 'Fringed', with reference to the muri having tufted spines projecting into the fossae.

DIAGNOSIS. A species of *Trachyleberidea* with a low subcentral tubercle, and an internal snap-knob at the mid-ventral margin of the right valve.

HOLOTYPE. A female carapace, OS 7988. Another female carapace, OS 8128, is a paratype. Sample FCRM 2010, stream south-west of Mtwero; Lower Miocene.

OTHER MATERIAL. Two specimens from samples FCRM 1575 (OS 7993) and 1628 (OS 8129).

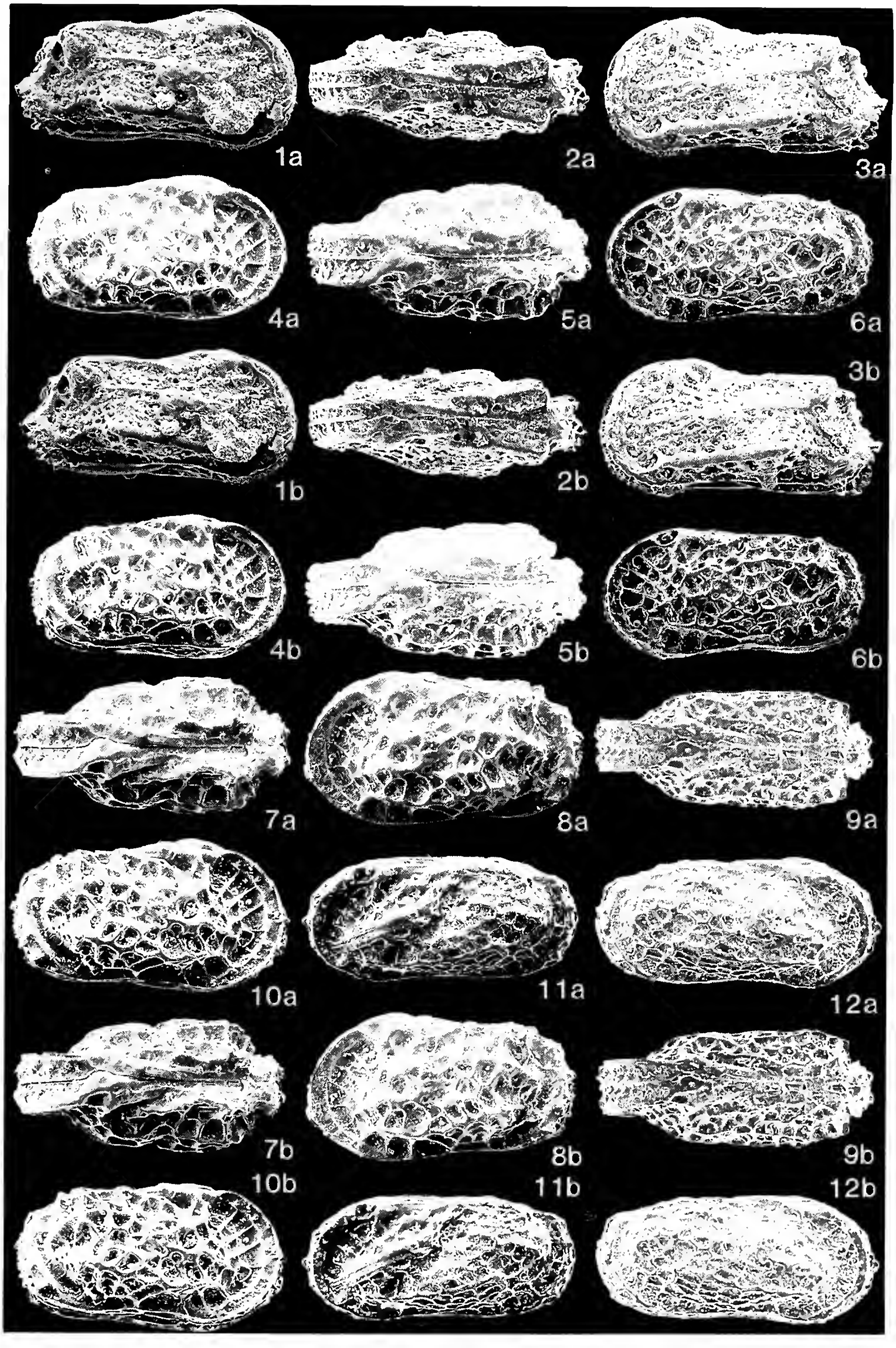
DESCRIPTION. Carapace subtriangular in side view, with greatest height at anterior cardinal angle. Anterior margin symmetrically rounded, posterior end triangular with posterodorsal margin straight to slightly concave. Dorsal margin straight, ventral slightly concave. Sexual dimorphism marked, presumed females being subtriangular compared with subrectangular presumed males; however, see remarks below. Lateral surface reticulate, fossae being concentrically arranged around subcentral tubercle. Muri have short spines which project into the fossae. A prominent thin median longitudinal ridge runs obliquely from subcentral tubercle towards postero-

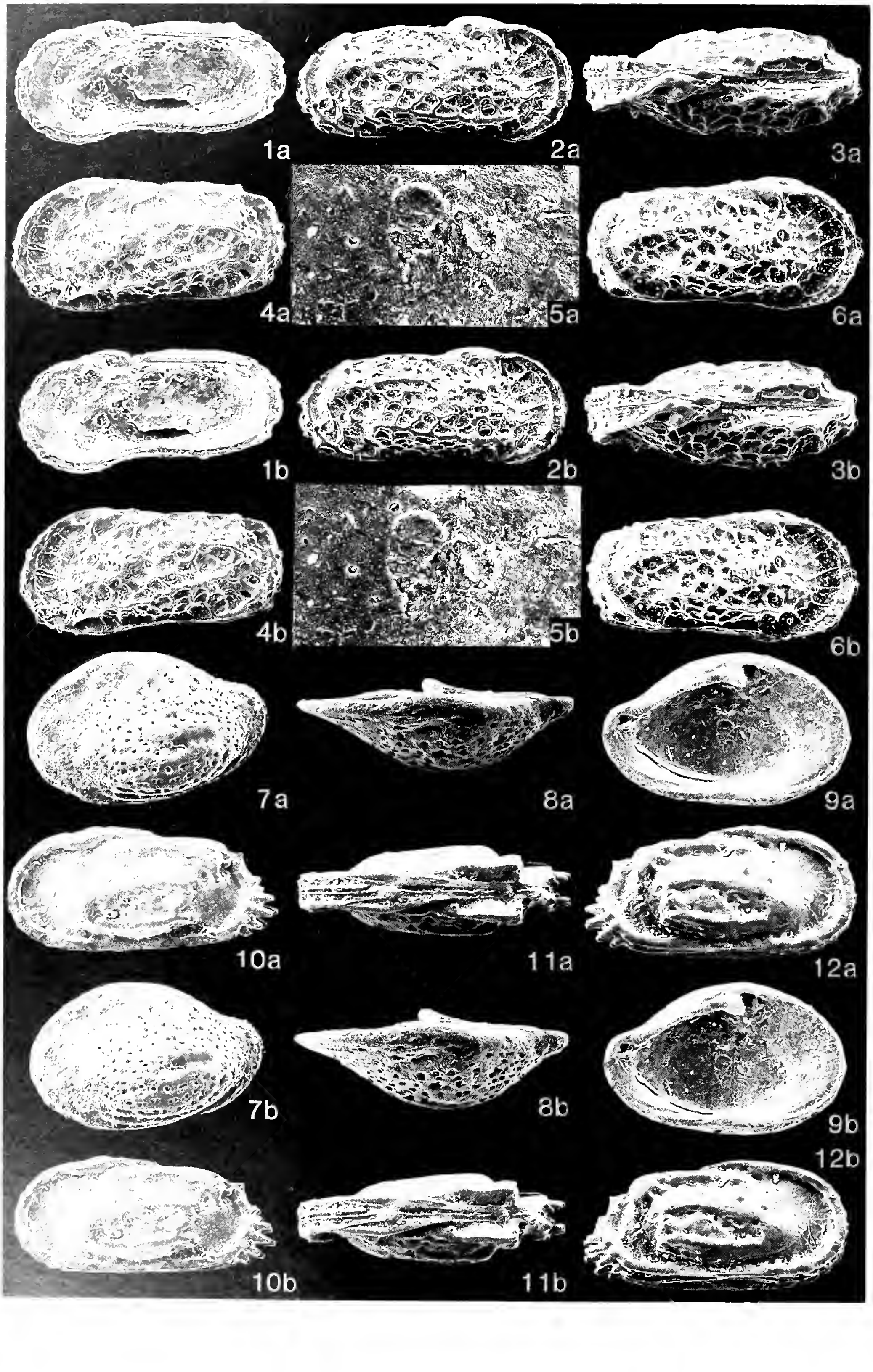
PLATE 15

Figs 1–3 *Costa*? *hullina* sp. nov. Paratype, juvenile carapace, OS 7716; 1, lateral view from right, ×71; 2, dorsal view, ×69; 3, lateral view from left, ×70.

Figs 4–10 *Stigmatocythere bornhardti* sp. nov. Figs 4, 5, **holotype**, female carapace, OS 8170; 4, lateral view from right, ×76; 5, dorsal view, ×84. Figs 6, 9, paratype, male carapace, OS 8172; 6, lateral view from left, ×70; 9, dorsal view, ×74. Figs 7, 8, 10, paratype, female carapace, OS 8173; 7, dorsal view, ×80; 8, lateral view from left, ×80; 10, lateral view from right, ×80.

Figs 11, 12 *Stigmatocythere intexta* sp. nov. **Holotype**, carapace, OS 8176; 11, lateral view from left, ×83; 12, lateral view from right, ×86.


1a
2a
3a
4a
5a
6a
3b
1b
2b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
12b
10b
11b

dorsal margin, curving down at its posterior end. Dorsal ridge not well marked; no ventral ridge. Few internal details visible. Hinge holamphidont, with a rounded knoblike anterior tooth in right valve, a round, slightly stepped tooth posteriorly and a median element consisting of an anterior socket and smooth postjacent groove. Right valve has a midventral snap-knob.

DIMENSIONS (μm).	L	H	W
Holotype, female carapace OS 7988	700	350	265
Paratype, female carapace OS 8128	700	355	290

REMARKS. The two different forms could possibly be regarded as separate species, but as they have the same basic pattern of ornament and occur together, they are taken to be male and female dimorphs of the same species. The generic assignment of this new species is difficult, but it agrees with *Trachyleberidea* in shape and visible internal details; however, none of the other *Trachyleberidea* species so far described has a snap-knob. The Tanzanian species also lacks the distinct ventral ridge of typical *Trachyleberidea*.

Genus *STIGMATOCYTHERE* Siddiqui, 1971

TYPE SPECIES. *Stigmatocythere obliqua* Siddiqui, 1971.

Stigmatocythere bornhardti sp. nov. Pl. 15, figs 4–10

NAME. After W. Bornhardt, the German geologist who first established the broad geological outlines of the Lindi area.

DIAGNOSIS. A species of *Stigmatocythere* with strong reticulation and well-marked sexual dimorphism.

HOLOTYPE. A female carapace, OS 8170. A female right valve OS 8171, a male carapace OS 8172, and a female carapace OS 8173, are paratypes. Sample FCRM 1745 (OS 8173 from 1746), Mbanja River; Lower Miocene.

OTHER MATERIAL. Four specimens from samples FCRM 1742 (Lower Miocene) and FCRM 1576, 1578 (Middle Oligocene). Additional specimens are in the collections of the BP Research Centre, Sunbury-on-Thames, from samples FCRM 1647, 1963 and 1964.

DESCRIPTION. Sexual dimorphism pronounced, affecting shape. Carapace of presumed male rectangular in side view; presumed female subquadrate. Anterior margin symmetrically rounded, posterior truncate. Dorsal margin modified by dorsal ridge, ventral margin slightly concave in the middle; these margins converge slightly towards posterior end. A strong ridge runs along dorsal, posterior and ventral margins. Entire surface reticulate, with the fossae arranged in no particular order. Some specimens are less strongly reticulate and in them three longitudinal ridges can be seen. Internal features typical of genus.

DIMENSIONS (μm).	L	H	W
Holotype, female carapace OS 8170	550	310	270
Paratype, male carapace OS 8172	610	310	260
Paratype, female carapace OS 8173	560	310	275

REMARKS. *Stigmatocythere bornhardti* is similar in shape to *S. obliqua* Siddiqui 1971, but there are a number of differences in detail; *S. obliqua* has a well developed eye tubercle and a ridge overhanging the ventral margin; *S. bornhardti* has a reduced eye tubercle and no overhanging ventral ridge. Siddiqui's species is smoother in the anterior third, while the Tanzanian species is equally reticulate all over. Sexual dimorphism also differs in the two; the presumed females of Siddiqui's species have strongly converging dorsal and ventral margins while the Tanzanian females are subquadrate. *S. bornhardti* also resembles *S. intexta* sp. nov. (below) but is more strongly reticulate.

Carbonnel's *Stigmatocythere* aff. *obliqua* Siddiqui (Carbonnel 1986: 110, figs 12–15) shows some resemblence to *S. bornhardti* but differs in its accentuated anterodorsal hinge 'ear'. The pattern of ornament, although somewhat similar, is less well developed, although this may be partly a matter of preservation.

Stigmatocythere intexta sp. nov.
Pl. 15, figs 11–12; Pl. 16, figs 1–4, 6

NAME. 'Interlaced', with reference to the ornament.

DIAGNOSIS. A species of *Stigmatocythere* which is almost uniformly reticulate. The ridges are subdued and the fossae shallow.

HOLOTYPE. A carapace, OS 8176. Six paratypes, OS 8177–82. Sample FCRM 2045, Lindi–Mingoyo Road; Upper Eocene.

OTHER MATERIAL. One specimen from the same sample. Also occurs in FCRM 1745, 1575 and 1628.

DESCRIPTION. Carapace medium sized, subrectangular in lateral view. Anterior margin symmetrically rounded, posterior truncate to rounded. Dorsal margin straight, ventral margin slightly concave in the middle. Eye tubercle glassy and well developed. Entire surface reticulate, the fossae being subrectangular, shallow and almost equal in size. The three ridges, dorsal, median and ventral, present but very much reduced; in some specimens ventral ridge almost non-existent. Internal features typical of genus.

DIMENSIONS (μm).	L	H	W
Holotype, carapace OS 8176	530	245	210
Paratype, right valve OS 8177	560	145	130
Paratype, carapace OS 8178	510	250	205

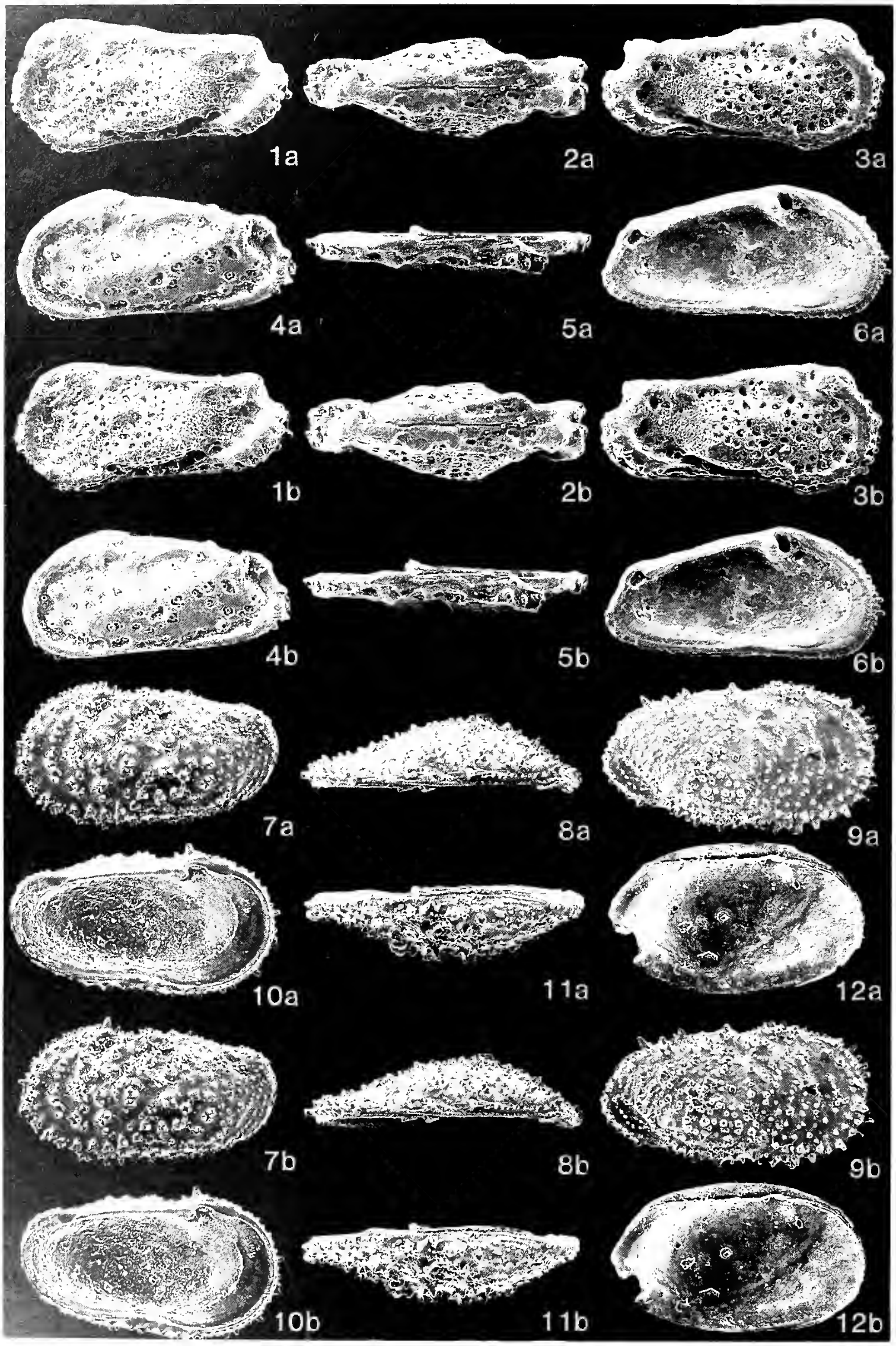
REMARKS. *S. intexta* only differs from *S. bornhardti* sp. nov., above, in having subdued ridges and therefore shallower

PLATE 16

Figs 1–4, 6 *Stigmatocythere intexta* sp. nov. Figs 1, 2, paratype, right valve, OS 8177; 1, internal lateral view, ×80; 2, external lateral view, ×81. Figs 3, 4, 6, paratype, carapace, OS 8178; 3, dorsal view, ×91; 4, lateral view from left, ×89; 6, lateral view from right, ×90.

Figs 5, 7–9 *Buntonia* sp. Left valve, OS 8183; 5, muscle scars, ×450; 7, external lateral view, ×87; 8, dorsal view, ×99; 9, internal lateral view, ×89.

Figs 10–12 *Ambocythere* sp. Carapace, OS 7975; 10, lateral view from left, ×95; 11, dorsal view, ×95; 12, lateral view from right, ×95.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

fossae. A number of specimens have intermediate ornamentation, and it is difficult to classify them with certainty in either species.

Tribe **PTERYGOCYTHEREIDINI** Puri, 1957*a*

Genus ***INCONGRUELLINA*** Ruggieri, 1958

TYPE SPECIES. *Incongruellina semispinescens* Ruggieri, 1958.

Incongruellina tonsa sp. nov. Pl. 17, fig. 12; Pl. 18, figs 1–5

NAME. 'Oar', referring to the ventrolateral alae.

DIAGNOSIS. A species of *Incongruellina* with prominent alae which make the valves wider than high. Posteriorly the alae end in spines.

HOLOTYPE. A carapace, OS 7908. Two carapaces, OS 7909, 7910, are paratypes. Sample FCRM 2010, stream south-west of Mtwero; Lower Miocene.

OTHER MATERIAL. Seven specimens, including OS 7992 from FCRM 1746. Also occurs in FCRM 1745.

DESCRIPTION. Carapace strongly calcified, medium-sized to large; greatest height at anterior cardinal angle, tapering posteriorly. Anterior margin symmetrically rounded, with 10 to 12 marginal denticles. Posterior bluntly produced at the bottom, with posterodorsal margin almost straight. Dorsal margin in left valve gently arched, almost straight in right. Left valve larger than right, overlap being conspicuous along mid-dorsal margin. Externally, ventrolateral marginal keel well developed and almost parallel to ventral margin, ending posteriorly in a spine. Ventral to the keel, two thin ridges run parallel to margin. Except for the glossy eyespot, lateral surface smooth. Internally duplicature moderately wide; line of concrescence and inner margin separated by a narrow vestibule. No marginal pore canals were seen, and a V-shaped frontal scar alone was visible in the muscle scar field.

DIMENSIONS (μm).	L	H	W
Holotype, carapace OS 7908	780	590	510
Paratype, carapace OS 7910	810	485	495
Paratype, carapace OS 7909	800	450	510

REMARK. *Incongruellina tonsa* is very like *I. semispinescens* Ruggieri 1958, but lacks a long posterior spine in the left valve.

Tribe **ECHINOCYTHEREIDINI** Hazel, 1967

Genus ***HENRYHOWELLA*** Puri, 1957*b*

TYPE SPECIES. *Cythere evax* Ulrich & Bassler, 1904.

Henryhowella sentosa sp. nov. Pl. 17, figs 7–11

NAME. 'Thorny'; with reference to the surface ornamentation.

DIAGNOSIS. A species of *Henryhowella* with spines typically trifid and arranged somewhat concentrically.

HOLOTYPE. A left valve, OS 7985. A juvenile right valve, OS 7986, is a paratype. Sample FCRM 2010, stream south-west of Mtwero; Lower Miocene.

OTHER MATERIAL. Two specimens from Samples FCRM 2010 and 2016.

DESCRIPTION. Carapace shape typical of genus. In side view, anterior margin evenly rounded; posterior obliquely curved below; posteroventral margin almost straight. Dorsal and ventral margins almost straight and parallel. Eye tubercle indistinct; anterior cardinal angle with a well-developed spine. Surface covered with spines, mostly trifid but sometimes bifid or quadrifid, concentrically arranged in anterior half and posterior third of carapace. Spines very small in posterior and posterodorsal regions, larger in ventral region. Internal features typical of genus except that median element of hinge is not crenulate; frontal scar not visible.

DIMENSIONS (μm).	L	H	W
Holotype, left valve OS 7985	660	410	200
Paratype, juvenile right valve OS 7986	590	350	180

REMARKS. *Henryhowella sentosa* resembles the *Echinocythereis*? sp. of Swain 1971, an immature valve from the Pleistocene of the south-eastern Pacific Ocean, but this does not have the characteristic trifid spines. The ornamentation and shape of the Tanzanian species are very similar to those of *Cythere acanthoderma* Brady from the Gulf of Mexico, but the latter has stronger marginal spines and a more broadly rounded posterior margin. The indistinct eye tubercle and concentrically arranged spines of the Tanzanian species resemble those of *Hystricocythere* Bate 1972, but the hinge is different.

Subfamily **BUNTONIINAE** Apostolescu, 1961

Genus ***BUNTONIA*** Howe & Chambers, 1935

TYPE SPECIES. *Buntonia shubutaenis* Howe & Chambers 1935 (= young of ?*Cythereis israelski* Howe & Chambers, 1935).

Buntonia sp. Pl. 16, figs 5, 7–9

FIGURED SPECIMEN. A left valve, OS 8183. Sample FCRM 1628, Kitunda Jetty road; Middle Oligocene.

OTHER MATERIAL. Three specimens in the collection of the BP Research Centre, Sunbury-on-Thames, from samples FCRM 1645, 1742, and 1745.

DESCRIPTION. Carapace pear-shaped in lateral view, with

PLATE 17

Figs 1–3 *Idiocythere* sp. A. Carapace, OS 8186; 1, lateral view from left, ×85; 2, dorsal view, ×85; 3, lateral view from right, ×85.

Figs 4–6 *Falsocythere maccagnoi* (Ciampo, 1971). Left valve, OS 7820; 4, external lateral view, ×94; 5, dorsal view, ×96; 6, internal lateral view, ×97.

Figs 7–11 *Henryhowella sentosa* sp. nov. Figs 7, 10, 11, **holotype**, left valve, OS 7985; 7, external lateral view, ×65; 10, internal lateral view, ×66; 11, dorsal view, ×69. Figs 8, 9, paratype, juvenile right valve, OS 7986; 8, dorsal view, ×78; 9, external lateral view, ×75.

Fig. 12 *Incongruellina tonsa* sp. nov. **Holotype**, carapace, OS 7908, lateral slightly oblique view from right, ×53. See also Pl. 18, fig. 3.

greatest height at two-fifths of the length, and greatest width about three-fifths of the length from anterior margin. Anterior margin elliptical and narrowly rounded; posterior margin upturned and rounded towards the dorsal. Dorsal margin merges imperceptibly into anterior margin, has an almost straight middle section, and slopes posteriorly, forming a distinct posterior cardinal angle. Ventral margin slightly convex upwards. External surface smooth along anterior margin (possibly a preservation phenomenon), but the rest is covered with small pits. Ventral half has six ridges running almost parallel to ventral margin. Dorsal half, separated from ventral by a longitudinal groove, has two small ridges at an angle to the dorsal margin. Marginal area and pore canals could not be seen because of poor preservation; the specimens in the BP Research Centre collection are better preserved and had 11 anterior marginal pore canals. There are four adductor scars with a V-shaped frontal scar. Hinge holamphidont; in left valve, an anterior socket is followed by a strong knob, a crenulate bar and a posterior socket.

DIMENSIONS (μm).	L	H	W
Left valve OS 8183	460	315	170

Genus *AMBOCYTHERE* van den Bold, 1958*b*

TYPE SPECIES. *Ambocythere keiji* van den Bold, 1958*b*.

Ambocythere sp. Pl. 16, figs 10–12

FIGURED SPECIMEN. A carapace, OS 7975. Sample FCRM 1566, Mongo Stream, Lindi; Lower Miocene. The only specimen.

DESCRIPTION. Carapace small, highest at one-third length from anterior end. Anterior margin symmetrically rounded; posterior end somewhat bluntly produced with posterodorsal part straight to slightly concave and posteroventral part rounded, with six denticles, three strong and three reduced. Dorsal margin strongly modified posteriorly by dorsal ridge; ventral margin almost straight. Dorsal and ventral margins converge posteriorly. Surface ornament consists of a carina-like rim extending from mid-dorsal ridge along anterior margin and continuing along ventral and posterior margins. Three short longitudinal ridges run from mid-length towards the back. The dorsal ridge thickens posteriorly where it curves downwards; the shorter median ridge bifurcates at its posterior end and meets dorsal and ventral ridges; ventral ridge straight, also bifurcating at posterior end. Small rounded pits occur in the central part of the carapace. As there is only a carapace internal details are unknown.

DIMENSIONS (μm).	L	H	W
Carapace OS 7975	495	230	175

REMARKS. This Tanzanian *Ambocythere* is more rectangular and has shorter ridges than any other species so far described.

Genus *OCCULTOCYTHEREIS* Howe, 1951

TYPE SPECIES. *Occultocythereis delumbata* Howe, 1951.

Occultocythereis africana sp. nov. Pl. 11, figs 7–12

NAME. 'From Africa'.

DIAGNOSIS. A species of *Occultocythereis* with a prominent anterior marginal ridge; dorsal ridge in the posterior half curving sharply down at the posterior end. A ventrolateral swelling. Surface ornamented with round pits.

HOLOTYPE. A female carapace, OS 7976. Two specimens, OS 7972, 7974, are paratypes. Sample FCRM 1989, Likonga bridge; Lower Miocene.

OTHER MATERIAL. One specimen (OS 7978) from sample FCRM 2010.

DESCRIPTION. Carapace small, greatest height at anterior cardinal angle. Anterior end rounded, posterior subrounded below, concave to straight posterodorsally; dorsal and ventral margins almost straight, converging behind. Sexual dimorphism present; presumed males elongate compared with presumed females. Externally, a strong rim runs along free margins. A short dorsal ridge runs in posterior half, curving sharply at posterior end; another rather indistinct ridge, appearing as a ventrolateral swelling, ends in a short spine posteriorly. Five or six elongate marginal spines occur along posteroventral margin and there are a few very short ones at anterior end. Eye tubercle present as an opaque spot. Surface ornamented with round pits except in the anteroventral area, which is almost smooth. Inside, duplicature moderately wide; line of concrescence and inner margin coincide and there is no vestibule. Selvage runs at a short distance from outer margin. Marginal pore canals not clearly visible. Muscle scar pattern consists of four adductor scars in a vertical row with a V-shaped frontal scar. Hinge holamphidont, with a conical anterior tooth and an adjacent socket joined to a posterior tooth in right valve; corresponding elements occur in left.

DIMENSIONS (μm).	L	H	W
Holotype, female carapace OS 7976	435	215	170
Paratype, female left valve OS 7974	500	260	115
Paratype, female right valve OS 7972	500	255	115

REMARKS. *O. africana* is probably the same as the Gen. Indet. 5 sp. 1 of Dingle, 1976. *Occultocythereis hatraensis* Al-Sheikhly, 1982, shows some resemblance to this species but

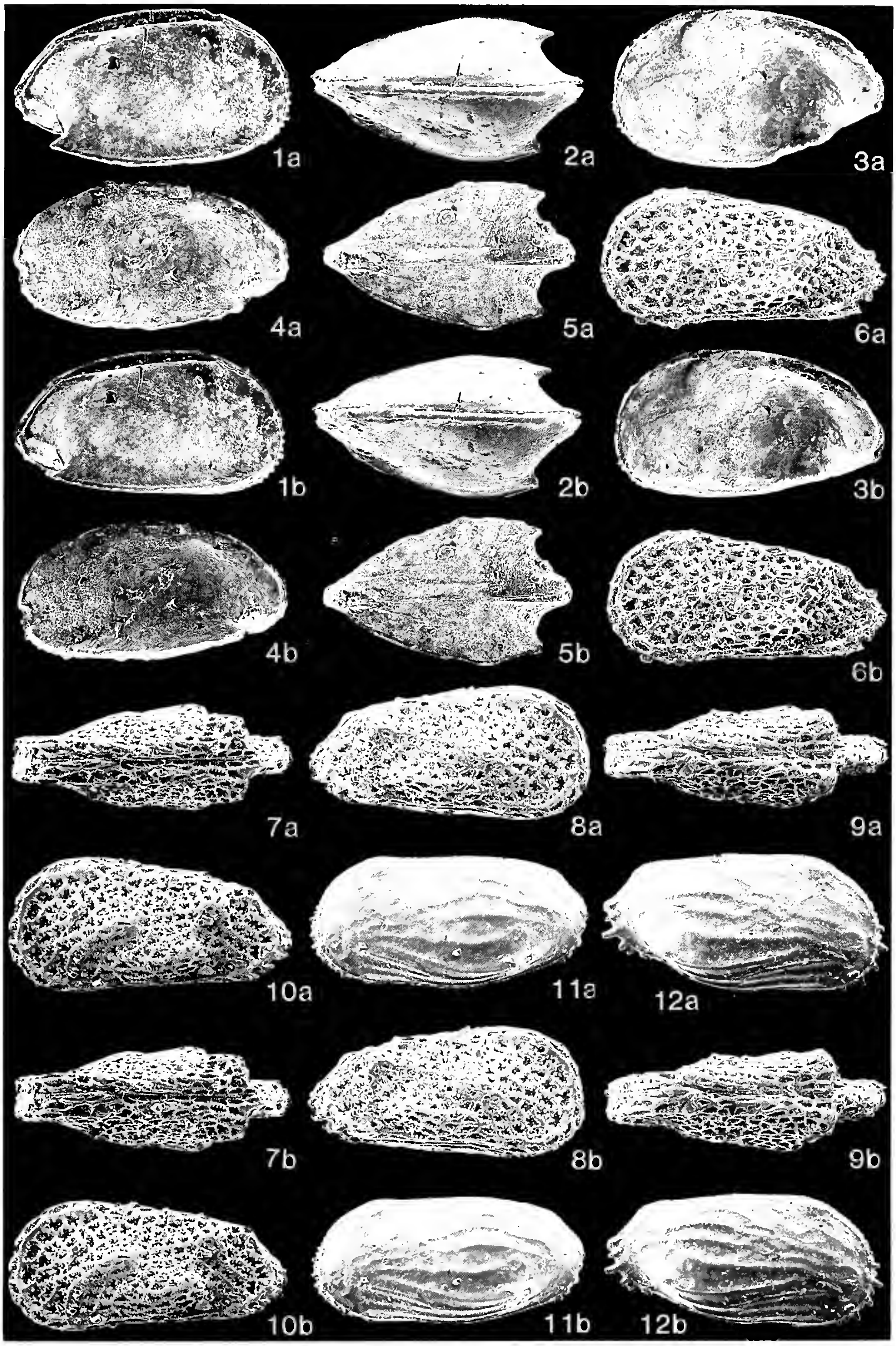
---

PLATE 18

Figs 1–5 *Incongruellina tonsa* sp. nov. Figs 1, 2, paratype, carapace, OS 7910; 1, lateral view from right, ×56; 2, dorsal view, ×54. Fig. 3, **holotype**, carapace, OS 7908, lateral view from left, ×56; see also Pl. 17, fig. 12. Figs 4, 5, paratype, carapace, OS 7909; 4, lateral view from left, ×56; 5, ventral view, ×51.

Figs 6–10 *Trachyleberidea? cirrata* sp. nov. Figs 6, 9, **holotype**, female carapace, OS 7988; 6, lateral view from left, ×66; 9, dorsal view, ×66. Figs 7, 8, 10, paratype, female carapace, OS 8128; 7, dorsal view, ×65; 8, lateral view from right, ×65; 10, lateral view from left, ×65.

Figs 11, 12 *Ruggieria* (*Ruggieria*) *furcilla* sp. nov. Fig. 11, **holotype**, left valve, OS 8201, external lateral view, ×39; see also Pl. 19, fig. 4. Fig. 12, paratype, carapace, OS 8202, lateral view from right, ×42; see also Pl. 19, fig. 3.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

differs from it in having a median ridge, a better-developed dorsal ridge and a punctate rather than a pitted surface.

Genus *IDIOCYTHERE* Triebel, 1958

TYPE SPECIES. *I. lutetiana* Triebel, 1958.

Idiocythere sp. A Pl. 17, figs 1–3

FIGURED SPECIMEN. A carapace, OS 8186. Sample FCRM 1746, Mbanja River; Lower Miocene. The only specimen.

DESCRIPTION. Carapace subrectangular in side view, with almost straight dorsal and ventral margins. Anterior margin rounded, posterior concave posterodorsally; both ends denticulate. Anterior marginal rim and dorsal and ventral ridges all well developed. Subcentral tubercle prominent; the rest of the surface pitted in the middle and smooth along the margins. No internal features were seen.

DIMENSIONS (μm).	L	H	W
Carapace, OS 8186	535	270	200

Subfamily **CAMPYLOCYTHERINAE** Puri, 1960
Tribe **LEGUMINOCYTHERINI** Howe, 1961

Genus *LEGUMINOCYTHEREIS* Howe (*in* Howe & Law, 1936)

TYPE SPECIES. *L. scarabaeus* Howe & Law (*in* Howe & Law, 1936).

Leguminocythereis dinglei sp. nov. Pl. 12, figs 1–12

NAME. In honour of Prof. R.V. Dingle, for his work on the South African ostracod fauna.

DIAGNOSIS. A species of *Leguminocythereis* with obliquely rounded anterior and produced truncated posterior margins. Lateral surface reticulate with coarse striae concentrically arranged at the margins but straight in the middle of the valve.

HOLOTYPE. A female carapace, OS 8194. Six specimens, OS 8195–200, are paratypes. Sample FCRM 1578 (OS 8196, FCRM 1575), coastal cliff west of Ras Tapuri; Middle Oligocene.

OTHER MATERIAL. 23 specimens from samples FCRM 1574 and 1576.

DESCRIPTION. Carapace medium to large, with greatest width in posterior half. Subtriangular to suboval in side view, tapering towards posterior end. Anterior margin cut away below, with spines along the ventral part; dorsal margin straight to gently arched, posterior end produced and truncate with a straight to concave posterodorsal margin. Ventral margin strongly modified by a swelling which appears convex in side view but is concave in the middle from below or internally. Carapace ovate in dorsal view. Sexual dimorphism present; in dorsal view presumed males less swollen anteriorly than are females. Six longitudinal ridges run along ventrolateral swelling, curving along anterior margin and following dorsal margin. Lateral surface reticulate; fossae rounded, more prominent centrally and almost non-existent along margins. Degree of development of the lateral ridges varies widely; a few specimens have reduced reticulation and may be almost smooth, though the original pattern of reticulation can usually be discerned. However, even when ornamentation is reduced, no other differences are visible, so this is regarded as intraspecific variation. Reduction in ornament may be directly proportional to size of carapace, but this is not an invariable rule. Duplicature fairly wide; line of concrescence and inner margin slightly separated anteriorly, forming a narrow vestibule. Selvage strongly developed along anteroventral and ventral margins. Marginal pore canals obscure due to strong calcification; in some specimens false marginal pore canals visible. Details of muscle scars difficult to see; in most specimens only two adductor scars are visible, with the middle two not apparent and frontal scars placed irregularly. In some specimens there are four adductor scars arranged in a row with two rounded scars in front. Hinge strongly holamphidont; in right valve a sharp anterior tooth projects from a platform the lower side of which has a socket joined to a crenulate groove, followed by a smooth elongate tooth which thickens posteriorly.

DIMENSIONS (μm).	L	H	W
Holotype, female carapace OS 8194	830	480	465
Paratype, male carapace OS 8195	800	456	290
Paratype, male carapace OS 8196	765	415	420
Paratype, female left valve OS 8198	790	450	270
Paratype, male carapace OS 8199	950	520	530
Paratype, juvenile(?) left valve OS 8200	665	355	195

REMARKS. The outline of the posterior margin, which is produced and truncate in *L. dinglei*, differentiates this from other species of *Leguminocythereis*; in fact this feature recalls the Mesozoic genera *Neocythere* and *Centrocythere*, which have a completely different hinge.

Genus *RUGGIERIA* Keij, 1957
Subgenus *RUGGIERIA* Keij, 1957

TYPE SPECIES. *Cythere micheliniana* Bosquet, 1852.

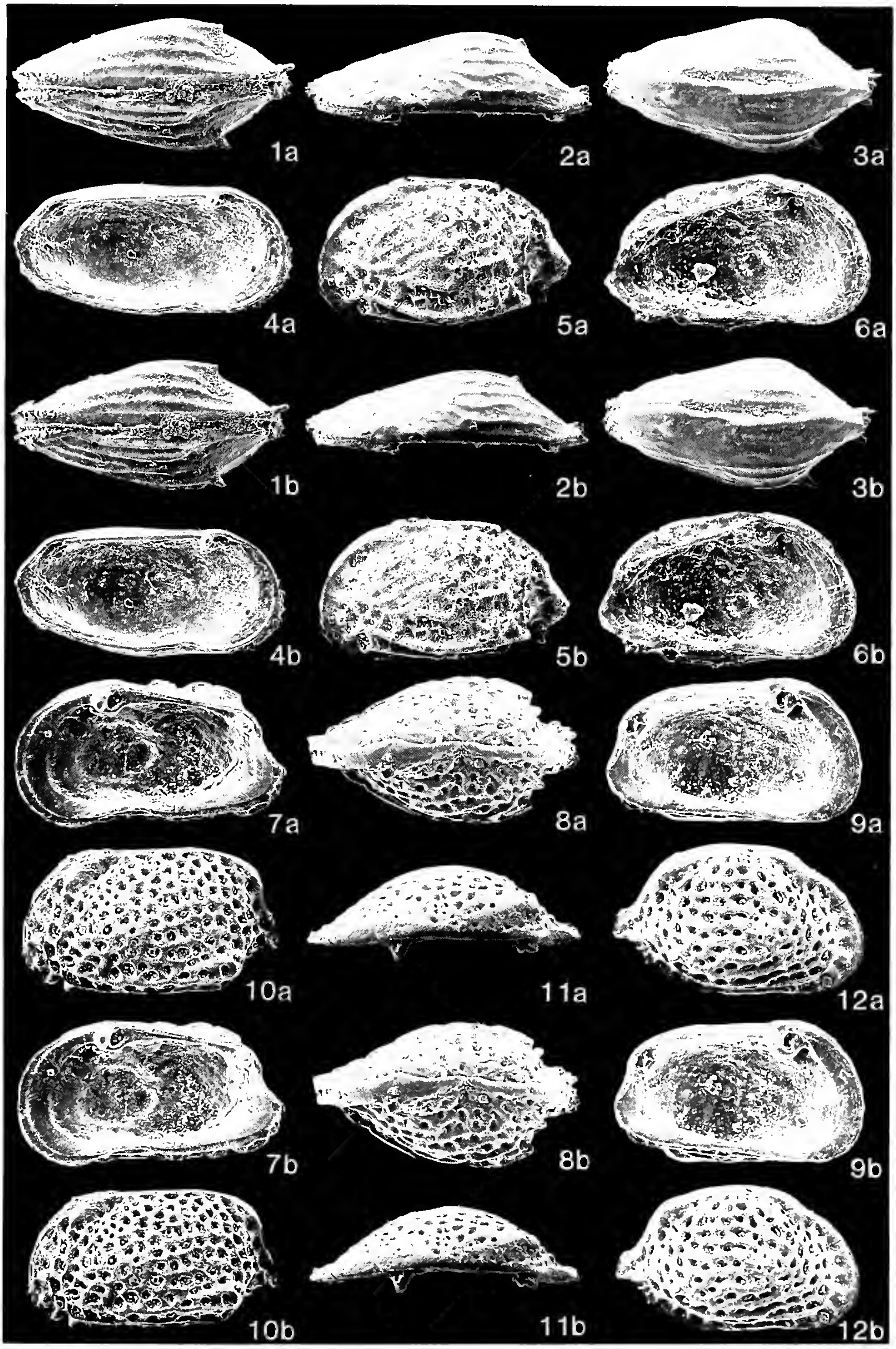
PLATE 19

Figs 1–4 *Ruggieria* (*Ruggieria*) *furcilla* sp. nov. Fig. 1, paratype, carapace, OS 8204, ventral view, ×39. Fig. 2, paratype, right valve, OS 8205, dorsal view, ×44. Fig. 3, paratype, carapace, OS 8202, dorsal view, ×43; see also Pl. 18, fig. 12. Fig. 4, **holotype**, left valve, OS 8201, internal view, ×39; see also Pl. 18, fig. 11.

Figs 5–8 *Procythereis aligera* sp. nov. Figs 5, 6, **holotype**, left valve, OS 8215; 5, external lateral view, ×69; 6, internal lateral view, ×65. Fig. 7, paratype, right valve, OS 8216, internal lateral view, ×73. Fig. 8, paratype, carapace, OS 8217, dorsal view, ×65.

Figs 9, 10 *Procythereis radiata* sp. nov. **Holotype**, left valve, OS 8219; 9, internal lateral view, ×75; 10, external lateral view, ×76.

Figs 11, 12 *Aurila concentrica* sp. nov. **Holotype**, female right valve, OS 8207; 11, dorsal view, ×78; 12, external lateral view, ×70.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

Ruggieria (Ruggieria) ***furcilla*** sp. nov.

Pl. 18, figs 11–12; Pl. 19, figs 1–4

NAME. 'Little fork', with reference to lateral ridges which form a fork-like pattern.

DIAGNOSIS. A species of *Ruggieria* with ridges which are convex upward in the dorsal part, almost straight in the middle, and concave upward in the ventral part of the lateral surface.

HOLOTYPE. A left valve, OS 8201. Five specimens, OS 8202–6, are paratypes. Sample FCRM 2014, stream south-west of Mtwero; Lower Miocene.

OTHER MATERIAL. 33 specimens from samples FCRM 2014, 2015. Additional specimens are in the collection of the BP Research Centre, Sunbury-on-Thames, from samples FCRM 1745, 1746.

DESCRIPTION. Carapace elongate, oval-shaped in lateral view. Dorsal margin straight; ventral margin strongly modified by ventrolateral swelling, appearing convex in lateral view but from inside concave anteriorly and convex posteriorly. Anterior margin symmetrically rounded; posterior upturned, straight in upper half and gently rounded below. Greatest height behind anterior margin, and greatest width in ventral half, behind mid-length. Eye tubercle prominent. Ornament consists of longitudinal ridges which are curved up in the dorsal half of the carapace, almost straight in the middle of it, and curved down in the ventral half. Intercostal areas smooth. Marginal zone moderately wide except at ventral margin, where it is narrow; inner margin and zone of concrescence coincide except along anteroventral margin, where there is a narrow vestibule. Normal pore canals widely spaced; marginal pore canals straight and wide apart. Muscle scar pattern with four adductor scars with their axis concave towards anterior end; second scar from the top relatively long. Two dorsal scars just above and a V-shaped frontal scar just in front of the adductor scars. Hinge typical of genus; in right valve it consists of a conical anterior tooth, a post-jacent socket which merges into a serrated straight groove, and a smooth ovate posterior tooth. Left valve has corresponding sockets, a conical anterior tooth, and a median crenulate bar.

DIMENSIONS (µm).	L	H	W
Holotype, left valve OS 8201	1140	530	320
Paratype, right valve OS 8205	1050	515	285
Paratype, carapace OS 8204	1175	540	560
Paratype, carapace OS 8202	1035	500	510

REMARKS. *R.* (*R.*) *furcilla* has some affinity with the genus *Keijella* Ruggieri 1967 because of its anteroventral vestibule, but it is placed in *Ruggieria* s. str. because, though a vestibule is present, it is confined to the anteroventral margin; in species of *Keijella* it extends along the entire anterior margin. Also, the hinge is more like that of *Ruggieria* s. str., and the outline of the carapace resembles that of some described species. *R. furcilla* probably represents an intermediate stage in the evolutionary development of *Ruggieria* s. str. into *Keijella*.

Keen (1974) described some *Ruggieria*-like ostracods from the Tertiary and Recent of West Africa. Only his *Ruggieria* sp. from Recent deposits of Sierra Leone shows any resemblence to *R. furcilla*, but differs in shape posteroventrally and in details of ornament, particularly in the ventrolateral region of the shell.

Ruggieria furcilla is closest to *R. triangulata* Omatsola 1972, a Recent species from the western Niger Delta, as figured by Babinot 1981 from the Oligocene of the Cote d'Ivoire, and *R.* aff. *triangulata* Carbonnel 1986 from the Eocene of Senegal. Carbonnel gives good line diagrams of the ornamentation pattern of these forms and the Tanzanian species differs in the detailed rib pattern, especially the four lower costae which swing upwards in the anterior half of their course. Although distinct, the present species is closely allied to the Senegal, Cote d'Ivoire and Niger forms and should be included in the *R. triangulata* species group.

Family **HEMICYTHERIDAE** Puri, 1953
Subfamily **HEMICYTHERINAE** Puri, 1953
Tribe **AURILINI** Puri, 1974

Genus ***AURILA*** Pokorný, 1955

TYPE SPECIES. *Cythere convexa* Baird, 1850.

Aurila concentrica sp. nov.

Pl. 19, figs 11–12, Pl. 20, figs 1–6

NAME. In reference to the concentric arrangement of fossae.

DIAGNOSIS. A medium-sized species of *Aurila*, subovate in lateral view, highest just behind the middle. Anterior and posterior margins together form an arc; posterior produced into a caudal process. Surface strongly reticulate with fossae arranged concentrically.

HOLOTYPE. A female right valve, OS 8207. Five specimens, OS 8208–12, are paratypes. Sample FCRM 1566, Mongo Stream, Lindi; Lower Miocene.

OTHER MATERIAL. 106 specimens from samples FCRM 1566 1989, 2010. Additional specimens are in the collection of the BP Research Centre, Sunbury-on-Thames, from samples FCRM 1575, 1576, 1578, 1689, 1692. Also occurs in FCRM 1574, 1737, 1745, 1746 and 2015.

DESCRIPTION. Carapace subovate, almond shaped, with

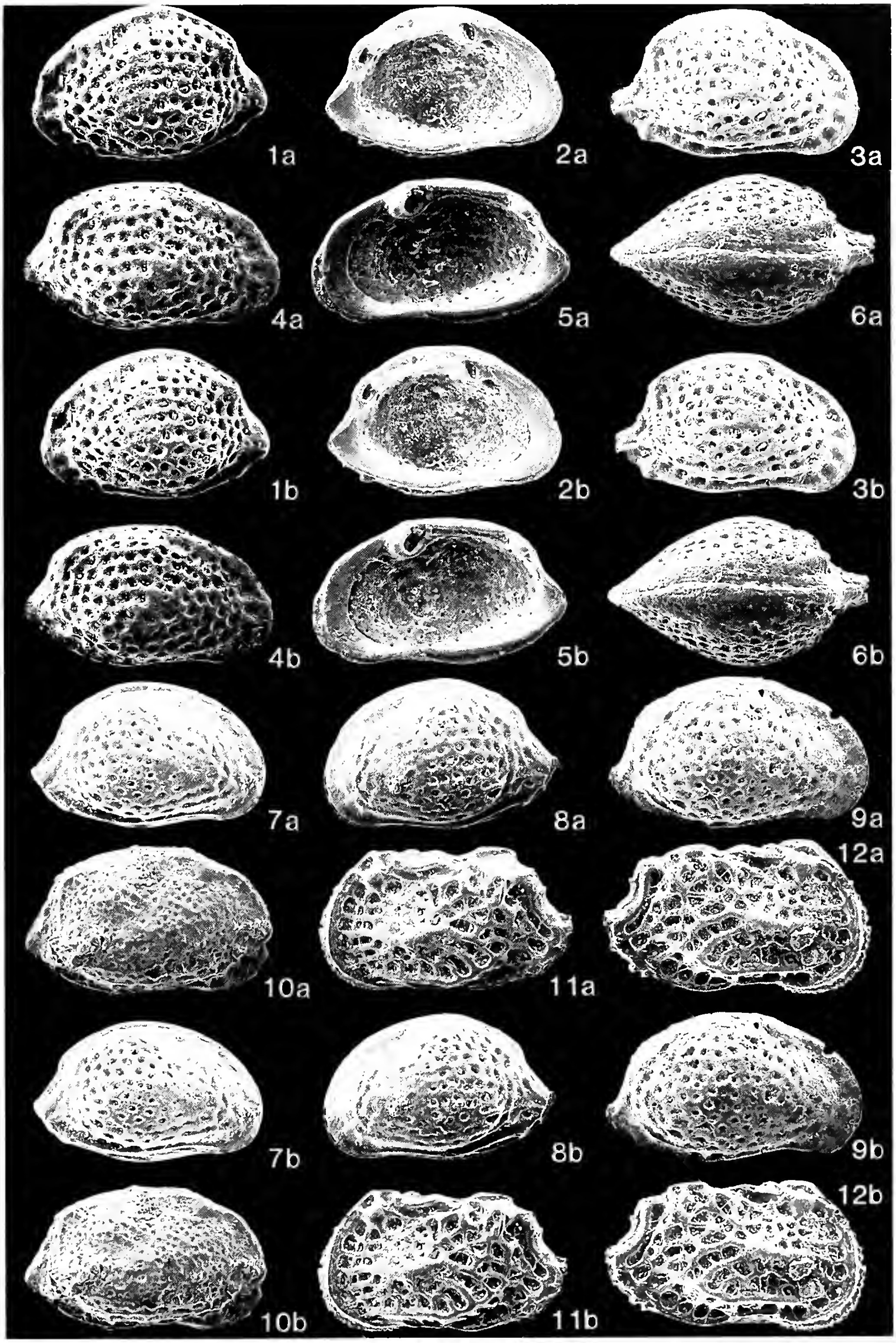
PLATE 20

Figs 1–6 *Aurila concentrica* sp. nov. Fig. 1, paratype, female left valve, OS 8208, external lateral view, ×69. Fig. 2, paratype, female left valve, OS 8210, internal lateral view, ×70. Fig. 3, paratype, female right valve, OS 8209, external lateral view, ×73. Figs 4, 5, paratype, male right valve, OS 8211; 4, external lateral view, ×74; 5, internal lateral view, ×76. Fig. 6, paratype, female carapace, OS 8212, dorsal view, ×62.

Figs 7–9 *Aurila concentrica* sp. nov., Morphotype A. Figs 7, 8, female carapace, OS 8213; 7, lateral view from right, ×58; 8, lateral view from left, ×58. Fig. 9, male right valve, OS 8214, external lateral view, ×62.

Fig. 10 *Aurila concentrica* sp. nov., Morphotype B. Male right valve, OS 8222, external lateral view, ×67.

Figs 11, 12 *Hermanites carchesium* sp. nov. Paratype, male carapace, OS 8224; 11, lateral view from left, ×54; 12, lateral view from right, ×57.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
12a
10a
11a
7b
8b
9b
12b
10b
11b

greatest height just behind the middle and greatest width in posterior half. Anterior and dorsal margins almost continuous, forming an arc; posterior margin produced into a caudal process almost at right angles to dorsal margin, joining ventral margin obliquely. Ventral margin slightly concave anteriorly and convex posteriorly. Sexual dimorphism pronounced, presumed females being slightly wider and higher but less elongate than presumed males. Left valve larger than right with a pronounced overlap along dorsal margin. Eye tubercle glassy, elongate. Surface coarsely reticulate, the fossae being subrectangular and arranged concentrically in six rows. Duplicature moderately wide; line of concrescence and inner margin slightly separated anteriorly to give a narrow vestibule. Selvage well developed, running parallel to outer margin. Marginal pore canals straight, mostly simple, including a few false ones. There are 35–40 at the anterior end and 6–8 at the posterior. Muscle scar pattern consisting of four adductor scars, the top three being divided into two, and three frontal scars. Hinge holamphidont; anterior tooth in right valve moderately high and sharp, followed by a socket joined to the elongate incised posterior tooth by a groove. Left valve with complementary hinge elements.

DIMENSIONS (μm).	L	H	W
Holotype, female right valve OS 8207	555	345	210
Paratype, female left valve OS 8208	560	380	240
Paratype, female right valve OS 8209	550	340	175
Paratype, female left valve OS 8210	555	365	185
Paratype, female carapace OS 8212	695	450	405

REMARKS. The Tanzanian species is difficult to place firmly in either *Aurila* or *Pokornyella*. While the hinge is more like that of *Aurila*, the number of anterior marginal pore canals is closer to the 20–25 of *Pokornyella* than to the 80 of *Aurila*. This probably represents an intermediate evolutionary stage between the earlier genus *Pokornyella* (Eocene–Oligocene) and the later *Aurila* (Oligocene–Recent).

Two morphotypes are distinguished: see below.

Morphotype A Pl. 20, figs 7–9

FIGURED SPECIMENS. A female carapace, OS 8213 (sample FCRM 1566), and a male right valve, OS 8214 (sample FCRM 1746); Mongo stream and Mbanja river, respectively; Lower Miocene.

DIMENSIONS (μm).	L	H	W
Female carapace OS 8213	660	430	375
Male right valve OS 8214	680	410	220

REMARKS. In this morphotype the anterior and dorsal margins together form an arc. The ornamentation is flatter than in the type.

Morphotype B Pl. 20, fig. 10

FIGURED SPECIMEN. A right valve, OS 8222. Sample FCRM 1578, coastal cliff west of Ras Tapuri; Middle Oligocene. Also occurs in FCRM 1576.

DIMENSIONS (μm).	L	H	W
Right valve OS 8222	595	370	190

REMARKS. The fossae are numerous but smaller and shallower than in typical *Aurila concentrica*. The ridges are almost non-existent, but the eye tubercle is better developed than in the type.

Genus *PROCYTHEREIS* Skogsberg, 1928

TYPE SPECIES. *Cythereis* (*Procythereis*) *torquata* Skogsberg, 1928.

Procythereis aligera sp. nov. Pl. 19, figs 5–8

NAME. 'Winged', with reference to the ala-like ventrolateral ridge.

DIAGNOSIS. A species of *Procythereis* with an ala-like ridge running along the ventrolateral swelling. Lateral surface reticulate but the fossae not prominent.

HOLOTYPE. A left valve, OS 8215. Three specimens, OS 8216–8, are paratypes. Sample FCRM 2010, stream south-west of Mtwero; Lower Miocene.

OTHER MATERIAL. Two specimens from the same locality and horizon (OS 8221).

DESCRIPTION. Carapace medium to large, heavily calcified. Subovate in lateral view with greatest height at anterior cardinal angle and greatest width behind mid-length. Anterior margin broadly and obliquely rounded towards venter, posterior produced in ventral half and concave in dorsal half. Dorsal margin almost straight, ventral slightly concave, strongly modified in lateral view by the ventral inflation. Surface irregularly reticulate with poorly developed fossae. Three median ridges run longitudinally from behind anterior margin, bending upwards in front of posterior end. Eye tubercle only moderately developed. The dorsal of the two ventrolateral ridges is ala-like and prominent. Duplicature narrow to moderately wide; line of concrescence and inner margin coincide. Selvage runs along outer margin except at mid-venter, where it stands out prominently. Muscle scar pattern consists of four adductor scars in a vertical row with two frontal scars in front of them. Hinge strongly holamphidont.

DIMENSIONS (μm).	L	H	W
Holotype, left valve OS 8215	660	400	205
Paratype, right valve OS 8216	605	335	225
Paratype, carapace OS 8217	675	415	380

REMARKS. *Procythereis aligera* is not a typical *Procythereis* in shape but is assigned to this genus because of its two frontal muscle scars; *Kingmania* and *Nephokirkos* both have only one, though they are more like *P. aligera* in shape. The new species can be distinguished from other *Procythereis* in being more ovate than rectangular and having a less prominent eye tubercle.

Procythereis radiata sp. nov. Pl. 19, figs 9–10

NAME. 'Rayed', with reference to the lateral ridges which radiate from the anteroventral region.

DIAGNOSIS. A subrectangular species of *Procythereis* with reticulate ornamentation, the longitudinal ridges radiating from the anteroventral region. Two parallel ridges originate from the eye tubercle and run along the anterior and ventral margins.

HOLOTYPE. A left valve, OS 8219. A left valve, OS 8220 (missing), is a paratype. Sample FCRM 1566, Mongo Stream, Lindi; Lower Miocene.

OTHER MATERIAL. One specimen from the same locality and horizon.

DESCRIPTION. Carapace subrectangular in lateral view, with ventral region strongly inflated, especially in posterior half. Anterior margin rounded, posterior bluntly produced in ventral half and concave posterodorsally. Dorsal margin straight, ventral hidden by the swelling in lateral view but straight and subparallel internally. Surface reticulate, the fossae being equal-sized and rounded; longitudinal ridges present, radiating from the anteroventral region. Eye tubercle prominent and elongate. Internally, duplicature moderately wide; line of concrescence and inner margin coincide; vestibule absent. Marginal pore canals straight, simple and fairly numerous. Muscle scar pattern consists of four adductor scars and three frontal; one or both of the median adductor scars probably divided but this is hard to see. Hinge strongly holamphidont. In left valve there is an anterior socket with a post-jacent knob-like tooth, followed by a smooth bar with an elongate socket behind.

DIMENSIONS (µm).	L	H	W
Holotype, left valve OS 8219	550	320	225

REMARKS. *Procythereis radiata* has a slightly different hinge from that of the type species, the median bar being smooth instead of crenulate as in *P. torquata* Skogsberg, 1928. So far, very few *Procythereis* species have been described; *P. radiata* can easily be distinguished from any of them by its rectangular shape, symmetrically rounded anterior margin, and the obliquely truncate and ventrally produced outline of the posterior margin.

Subfamily **THAEROCYTHERINAE** Hazel, 1967
Tribe **THAEROCYTHERINI** Hazel, 1967

Genus ***HERMANITES*** Puri, 1955

TYPE SPECIES. *Hermania reticulata* Puri, 1954.

Hermanites carchesium sp. nov.
Pl. 20, figs 11–12; Pl. 21, figs 1–6; Pl. 22, fig. 11

NAME. Latin *carchesium*, a Greek style of cup slightly contracted in the middle; with reference to the slight contraction in the middle of the carapace.

DIAGNOSIS. A strongly reticulate species of *Hermanites* with broadly rounded anterior margin, dorsal margin strongly modified in lateral view by a wavy marginal ridge, and the ventral margin modified by a straight ridge.

HOLOTYPE. A female carapace, OS 8223. Two male carapaces, OS 8224–5, are paratypes. Sample FCRM 2033, Lindi Creek, east shore; Upper Eocene.

OTHER MATERIAL. Eight specimens from the same locality and horizon, including OS 8321 (juvenile), pl. 22, fig. 11.

DESCRIPTION. Carapace subquadrate, with greatest height at anterior end and greatest width in posterior half at about two-thirds the length from anterior margin. Anterior margin symmetrically rounded, with 23 short denticles; posterior produced just below middle; five to seven strong denticles along posteroventral edge. Dorsal margin strongly modified by a wavy dorsal ridge. Posterodorsal margin concave, ventral margin straight to slightly concave in the middle and convex in posterior half. Sexual dimorphism present, presumed females being more quadrate and wider than males. Surface strongly reticulate. Strong anterior marginal ridge present; ventral ridge running from about a quarter to about three-fifths the length from the anterior margin, then curling upwards to form a loop. Subcentral tubercle elongate, not well developed; eye tubercle strongly developed. Fossae vary in shape, being quadrate and subrectangular in some parts and polygonal or triangular in others. Muscle scars and marginal pore canals not seen in the one poorly preserved adult single valve. Other internal features typical of genus.

DIMENSIONS (µm).	L	H	W
Holotype, female carapace OS 8223	750	440	370
Paratype, male carapace OS 8224	745	440	345
Paratype, male carapace OS 8225	750	460	400

REMARKS. It is very difficult to place *H. carchesium* in either *Hermanites* or *Quadracythere* solely on the basis of shape and ornamentation. There is a group of species closely allied with *H. carchesium* which could belong to either genus, these genera being distiguished only by the type of frontal scar, which could not be seen in the Tanzanian species. However, *H. carchesium* is most like *Hermanites* in dorsal view , and therefore is here placed in that genus. *H. carchesium* resembles *H. dameriacensis* Keij, 1958 in outline and ornament, differing only in having no pronounced loop connecting the dorsal and ventral ridges in the posterior half.

Hermanites mongoensis sp. nov. Pl. 22, figs 1–2

NAME. After Mongo Stream, the type locality.

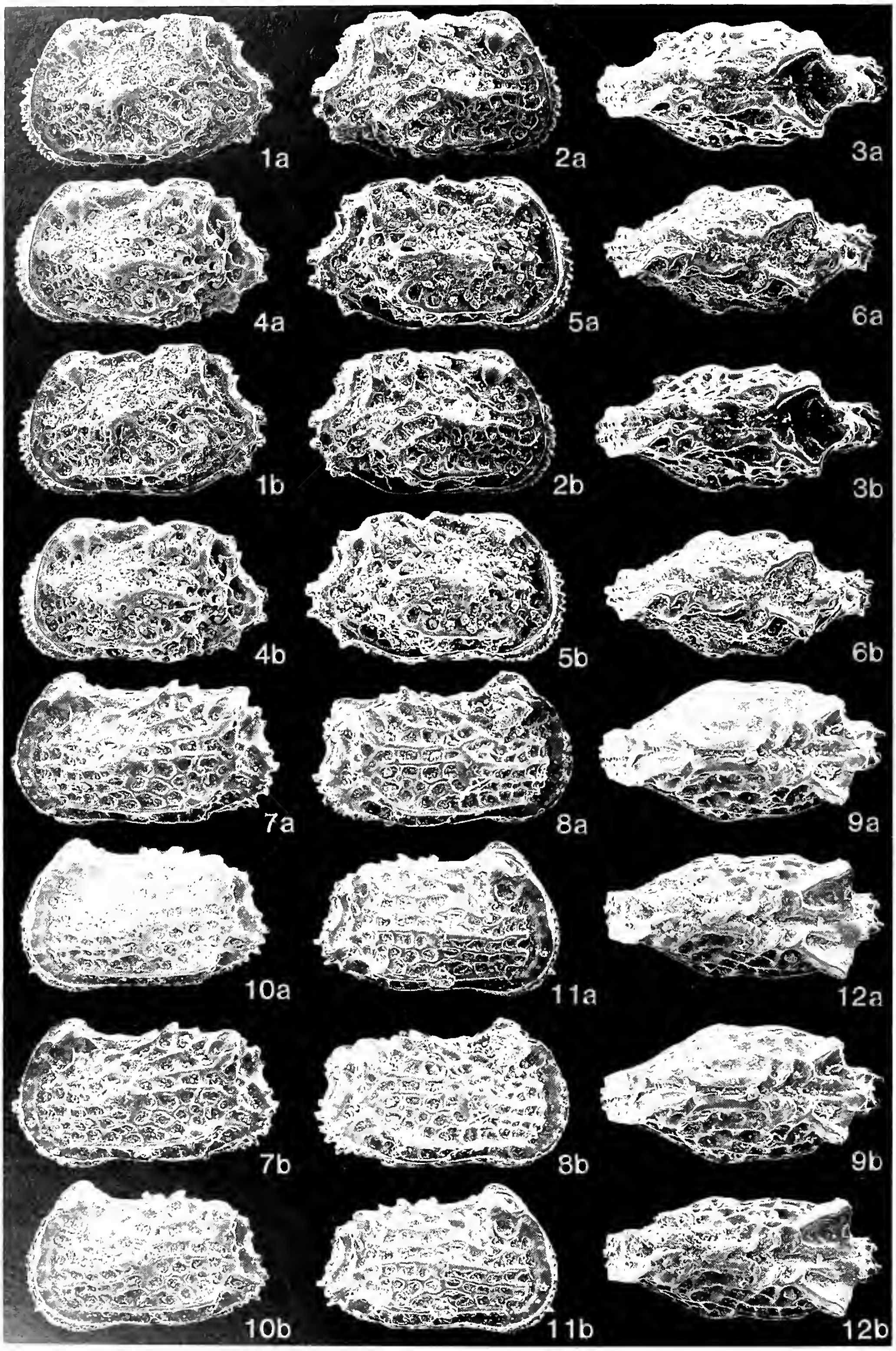
DIAGNOSIS. A species of *Hermanites* with dorsal ridge strongly modified in posterior half by the posterodorsal loop, which joins it to the median ridge; ventrolateral carina strongly developed.

HOLOTYPE. Right valve, OS 8232. Another valve, OS 8233 is a paratype. Sample FCRM 1566, Mongo Stream, Lindi; Lower Miocene.

OTHER MATERIAL. Five specimens from the same sample. Also occurs in FCRM 1745 and 2010.

DESCRIPTION. Carapace medium-sized, subquadrate to subrectangular, with greatest height at anterior end, tapering towards posterior. Anterior margin symmetrically rounded, posterior subacuminate and produced subventrally. Dorsal margin, with its marginal ridge, is almost straight and slopes posteriorly; it is strongly modified in posterior half by the posterodorsal loop which joins it to the median ridge. Ventral margin almost straight. Ventrolateral carina well developed, curving upwards near posterior end to join posterodorsal loop. Entire lateral surface reticulate, with broad fossae. Eye tubercle well developed. Duplicature moderately wide; inner margin regular, slightly separated from line of concrescence, leaving a narrow vestibule. Selvage a little distance from anterior margin, continuous along entire free edge. 20–25 marginal pore canals, mainly concentrated along the anteroventral margin, are mostly short, straight and simple. Four adductor muscle scars, located in the deep subcentral pit, are arranged in a vertical row and decrease in size from dorsal to ventral; one crescentic to U-shaped frontal scar. Hinge strongly holamphidont.

DIMENSIONS (µm).	L	H	W
Holotype, right valve OS 8232	680	380	240


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

REMARKS. Oligocene specimens vary somewhat from the holotype and are distinguished as Morphotypes A and B, below. *H. dameriacensis* Keij 1958 has a similar shape to *H. mongoensis* but differs in its less angular posterodorsal loop, its smooth rounded subcentral tubercle, and in the way the posterodorsal ridge joins the dorsal and ventral ridges; this junction is defined better than in *H. mongoensis*.

Morphotype A Pl. 22, figs 3–7

FIGURED SPECIMENS. Two female valves, OS 8238–9, and a male left valve, OS 8240. Sample FCRM 1578, coastal cliff west of Ras Tapuri; Middle Oligocene.

OTHER MATERIAL. Seven specimens.

DIMENSIONS (μm).	L	H	W
Female right valve OS 8238	810	450	270
Female left valve OS 8239	745	445	245
Male left valve OS 8240	840	455	280

REMARKS. Morphotype A differs from typical *H. mongoensis* in details of ornamentation; the posterodorsal loop is less sharp and the parts of the median ridge are differently arranged. Morphotype A clearly represents an earlier stage in the evolutionary development of *Hermanites mongoensis*, s. str.

Morphotype B Pl. 22, figs 8–10

FIGURED SPECIMEN. A male left valve, OS 8242. Sample FCRM 1578, coastal cliff west of Ras Tapuri; Middle Oligocene. The only specimen.

DIMENSIONS (μm).	L	H	W
Male left valve OS 8242	710	370	235

REMARKS. Morphotype B is rectangular. In lateral view the ventral margin is strongly modified by the overhanging ventral ridge, which gives it a distinctive shape.

Hermanites percultus sp. nov. Pl. 21, figs 7–12; Fig. 8

NAME. 'Highly ornamented', with reference to the strongly reticulated surface.

DIAGNOSIS. A species of *Hermanites* with a strongly reticulate lateral surface, a straight, pronounced ventral ridge and a raised posterodorsal tubercle, which gives it a characteristic appearance in dorsal view.

HOLOTYPE. A female carapace, OS 8226. Five carapaces, OS 8227–31, are paratypes. Sample FCRM 2033, Lindi Creek, east shore; Upper Eocene.

OTHER MATERIAL. Two specimens.

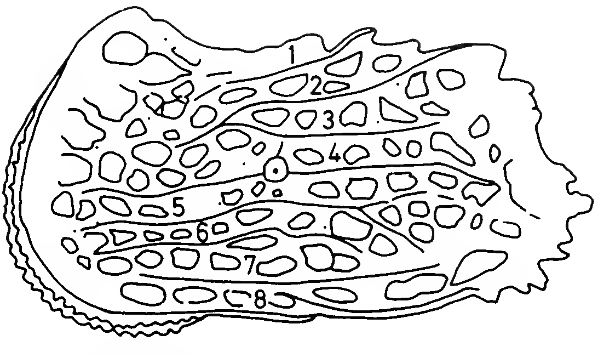


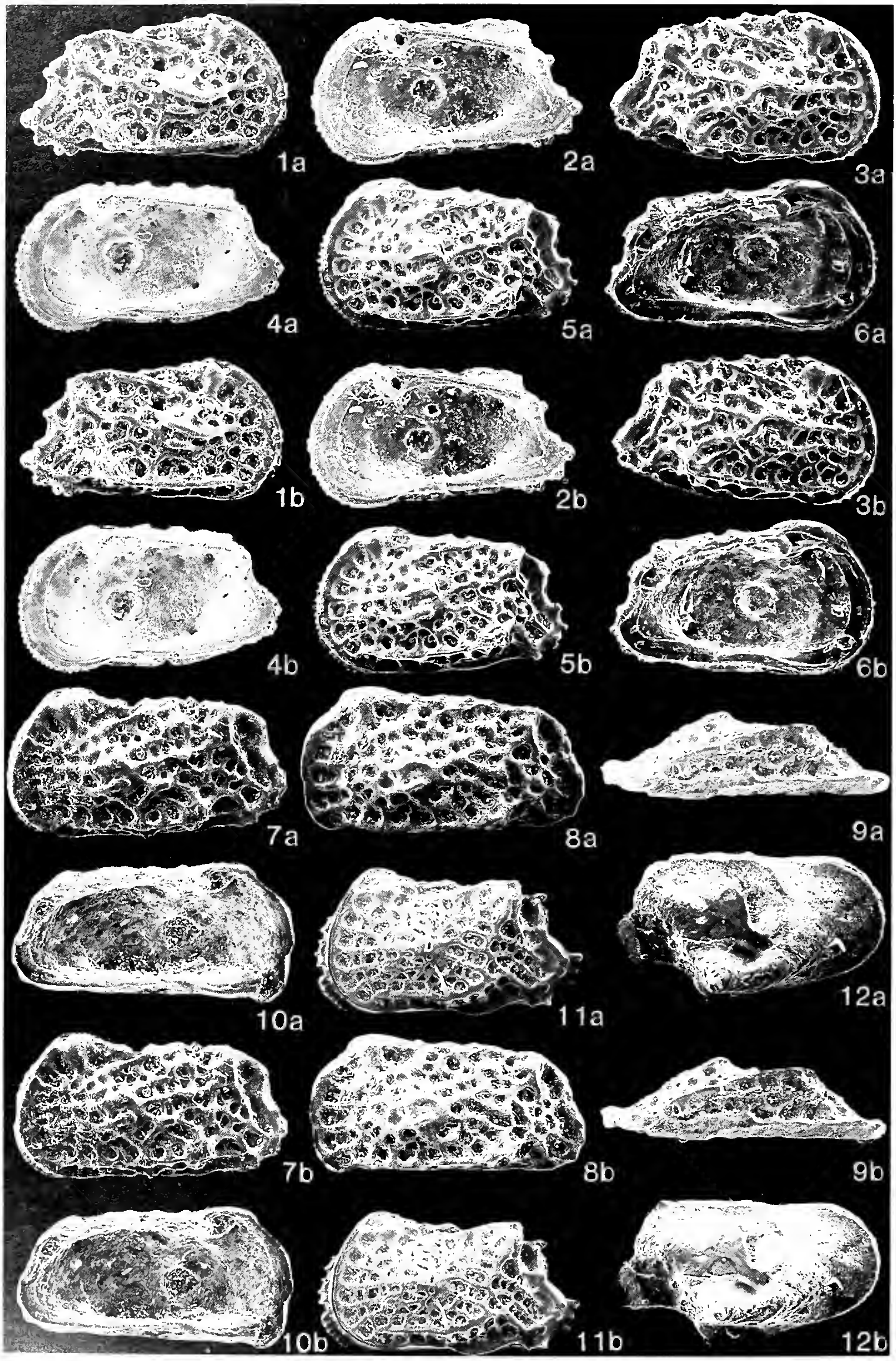
Fig. 8 *Hermanites percultus* sp. nov. Paratype OS 8227. Carapace from left, lateral surface showing the ornament. ×110. 1–8, the ridges described in the text.

DESCRIPTION. Carapace subrectangular in lateral view, with greatest height at anterior cardinal angle. Dorsal and ventral margins straight, converging slightly towards posterior. Anterior margin broadly rounded with a very distinct anterior cardinal angle; it has 18–20 marginal denticles. Posterior margin curving into ventral margin in lower half and concave posterodorsally; it has three to five large, strong marginal denticles. In dorsal view, greatest width in anterior third. Posterodorsal tubercles give carapace a winged appearance. Sexes distinct; while presumed females are more rectangular, with dorsal and ventral margins subparallel, presumed males taper posteriorly. Surface strongly reticulate, fossae being subrectangular. There are eight longitudinal ridges, here numbered from top to bottom for convenience in description. Ridge 1–3 are well developed posteriorly and subparallel forward to mid-length, losing their identities further forward; ridge 4 runs from anterior to posterior and includes the rather small subcentral tubercle; 5 and 6 are subparallel to 4 anteriorly but lose their identities further back; ridge 7 is straight and strong, running parallel to the ventral margin; ridge 8 is a continuation of the anterior marginal rim and runs as far as mid-venter, where it is replaced by another short ridge running parallel to the ventral margin. Duplicature fairly wide, narrowing slightly towards anterodorsal margin. Selvage very well developed, running almost in the middle of marginal zone but curving in mid-ventral region, where it is raised and is concave to outer margin. Normal pore canals few and widely spaced. Marginal pore canals fairly numerous, straight and simple, mostly concentrated along the anterodorsal margin. Muscle scars cannot be seen in any adult specimens, but in the less calcified juveniles the frontal scar is crescentic. Hinge strongly developed, consisting of a strong anterior knob-like tooth, post-jacent socket, a crenulate bar and a very backwardly placed, elongate posterior tooth.

PLATE 21

Figs 1–6 *Hermanites carchesium* sp. nov. Figs 1, 2, paratype, male carapace, OS 8225; 1, lateral view from left, ×55; 2, lateral view from right, ×54. Fig. 3, paratype, male carapace, OS 8224, dorsal view, ×63. Figs 4–6, **holotype**, female carapace, OS 8223; 4, lateral view from left, ×55; 5, lateral view from right, ×57; 6, dorsal view, ×59.

Figs 7–12 *Hermanites percultus* sp. nov. Figs 7–9, paratype, male carapace, OS 8227; 7, lateral view from left, ×57; 8, lateral view from right, ×56; 9, dorsal view, ×61. Figs 10–12, **holotype**, female carapace, OS 8226; 10, lateral view from left, ×59; 11, lateral view from right, ×58; 12, dorsal view, ×65.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

DIMENSIONS (μm).	L	H	W
Holotype, female carapace OS 8226	695	440	340
Paratype, male carapace OS 8227	760	445	350

REMARKS. *H. percultus* is quite distinct from all the other *Hermanites* species described so far, but is tentatively placed in that genus because of some internal details and the pattern of exterior ridges. In general shape it also resembles a number of species described under *Bradleya* Hornibrook 1952, and *Agrenocythere* Benson 1972. *H. percultus* differs from typical *Hermanites* in the following respects:

(i) There is a vestibule, and the line of concrescence and the inner margin do not coincide as in other *Hermanites*.

(ii) The posterior tooth is very backwardly placed in the new species.

(iii) The marginal pores are simple, not thickened in the middle as in most species of *Hermanites*.

(iv) *H. percultus* is rectangular, compared with the usual tapering shape of *Hermanites* species.

(v) The subcentral tubercle is unlike that of typical *Hermanites*, being more like what Benson (1972) called a bridte.

Tribe **BRADLEYINI** Benson, 1972

Genus ***BRADLEYA*** Hornibrook, 1952

TYPE SPECIES. *Cythere arata* Brady, 1880.

Bradleya? sp. A — Pl. 23, figs 1–3

FIGURED SPECIMEN. A right valve, OS 8187. Sample FCRM 1566, Mongo Stream, Lindi; Lower Miocene. The only specimen.

DESCRIPTION. A species of *Bradleya*? with strong ventrolateral carina, posterodorsal loop and subcentral tubercle. Surface smooth with underlying reticular 'ghost' pattern. Carapace subrectangular to suboval in lateral view, with greatest height at anterior cardinal angle; tapering posteriorly. Anterior margin symmetrically rounded, posterior bluntly produced and truncate. Dorsal margin modified by dorsal ridge but otherwise straight; ventral margin straight to slightly concave in the anterior half. Ornament consists of a posterodorsal loop, a ventrolateral carina and a subcentral tubercle. Lateral surface smooth, but with the sort of underlying reticulation termed 'reticular ghosts' by Benson (1972). Duplicature moderately wide; selvage well developed, running almost halfway between inner margin and flange. Flange groove prominent. Marginal pore canals, about 17 anteriorly and 8 posteriorly, mostly simple, short and equally spaced. There are four adductor muscle scars, the second from the top being longest, all arranged in a row behind a divided frontal scar. Hinge strongly holamphidont.

DIMENSIONS (μm).	L	H	W
Right valve OS 8187	820	450	310

REMARKS. *Bradleya lactea pakaurangia* Hornibrook 1952 resembles *Bradleya*? sp. A in general shape but has a strong posterodorsal loop with the median ridge well developed in the posterior half, whereas *Bradleya*? sp. A has no median ridge. The conspicuous normal pores of Hornibrook's species are not present in our African one. *B. semiarata* Hornibrook is also closely allied to *Bradleya*? sp. A but has an almost straight posterior marginal outline compared with the bluntly produced posterior of the latter. The generic placement of *Bradleya*? sp. A is tentative; though it probably belongs to the same genus as *B. lactea pakaurangia*, it is doubtful whether the latter is congeneric with the type species *B. arata* (Brady).

Bradleya? sp. B — Pl. 23, figs 4–5

FIGURED SPECIMEN. A carapace, OS 8328. Sample FCRM 1578, coastal cliff west of Ras Tapuri; Middle Oligocene.

OTHER MATERIAL. Four carapaces, including OS 8329, from FCRM 1578.

DESCRIPTION. Carapace subrectangular in side view, with greatest height at anterior cardinal angle, valves tapering posteriorly. Anterior margin denticulate, broadly rounded; posterior margin strongly concave in the posterodorsal half and convex posteroventrally. Dorsal margin strongly modified by dorsal ridges; ventral margin slightly concave in anterior half, to almost straight behind. Ornament consists of a marginal ridge running from well-developed eye tubercle along anterior, ventral and posterior margins and parallel to them. Posterodorsal loop-like ridge prominent; subcentral tubercle well developed. Surface smooth except for small compartments enclosed by low ridges along posterodorsal, anterior and ventral margins. No single valves were found so no internal details were seen.

DIMENSIONS (μm).	L	H	W
Carapace OS 8328	570	315	280

REMARKS. This species is less subrectangular than *Bradleya*? sp. A, and the dorsal ridge is loop-like rather than straight and mostly parallel to the dorsal margin; also, the ghostly ornamentation is absent. The present species resembles *B. lactea pakaurangia* Hornibrook, but the outline of the posterior margin is different and the maximum height is

PLATE 22

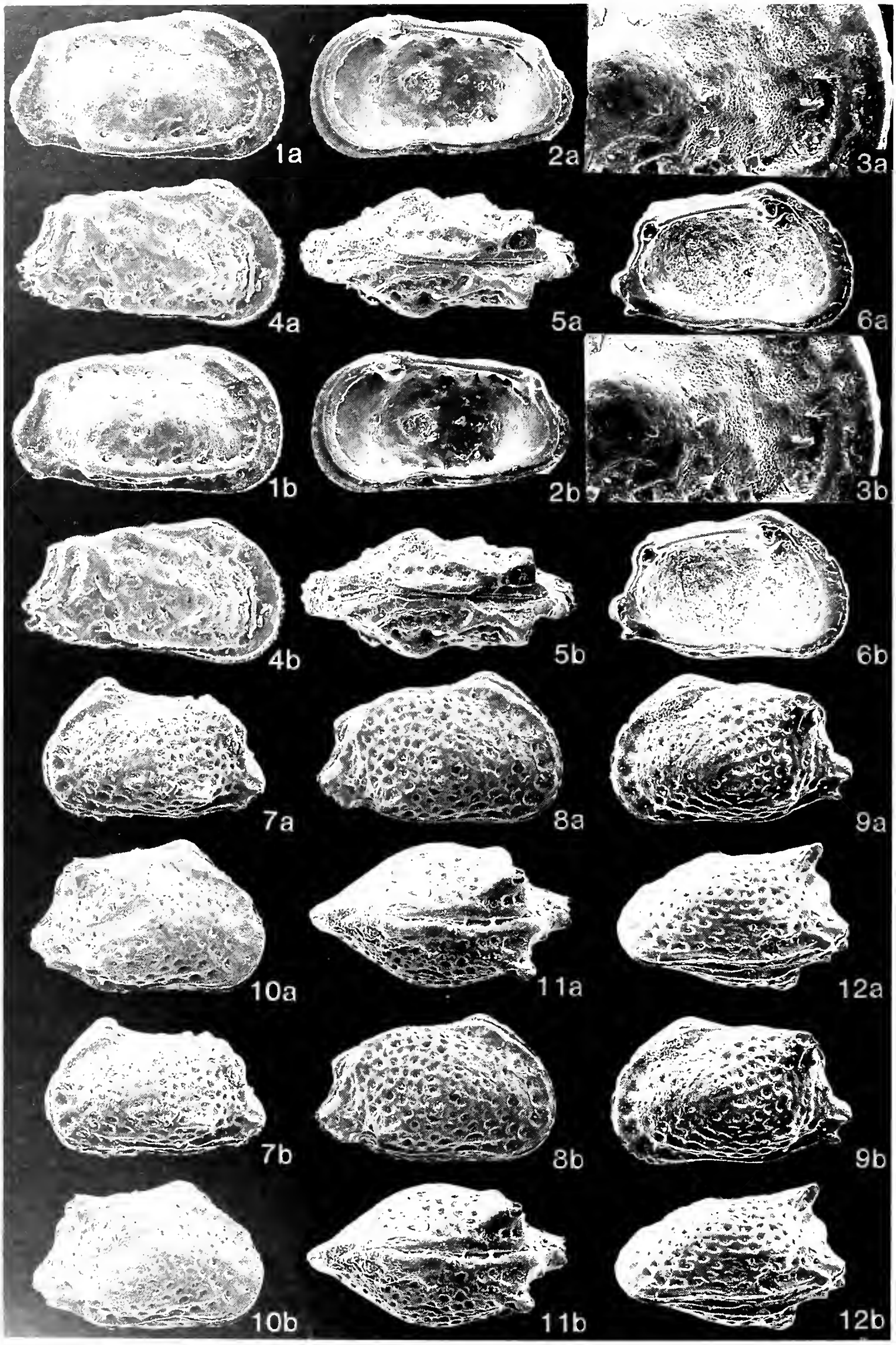
Figs 1, 2 *Hermanites mongoensis* sp. nov. **Holotype**, right valve, OS 8232; 1, external lateral view, ×63; 2, internal lateral view, ×64.

Figs 3–7 *Hermanites mongoensis* sp. nov., Morphotype A. Figs 3, 4, female right valve, OS 8238; 3, external lateral view, ×54; 4, internal lateral view, ×54. Figs 5, 6, female left valve, OS 8239; 5, external lateral view, ×56; 6, internal lateral view, ×59. Fig. 7, male left valve, OS 8240, external lateral view, ×54.

Figs 8–10 *Hermanites mongoensis* sp. nov., Morphotype B. Female left valve, OS 8242; 8, external lateral view, ×65; 9, ventral view, ×65; 10, internal lateral view, ×64.

Fig. 11 *Hermanites carchesium* sp. nov. Juvenile left valve, OS 8321, external lateral view, ×72.

Fig. 12 *Bythoceratina* sp. A. Right valve, OS 8317, external lateral view, ×75.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

subventral rather than at mid-height as in Hornibrook's species.

Genus *QUADRACYTHERE* Hornibrook, 1952

TYPE SPECIES. *Cythere truncula* Brady, 1898.

Quadracythere arcana (Lubimova & Guha, 1960)

1960 *Cythereis arcanus* (sic, recte *C. arcana*) Lubimova & Guha (in Lubimova *et al.*): 33; pl. 34, figs 3–5.

1971 *Quadracythere* (*Hornibrookella*) *arcana* (Lubimova & Guha) Siddiqui: 67; pl. 34, figs 3–5.

Quadracythere arcana cornigera subsp. nov.

Pl. 25, figs 4–8

NAME. 'Horned', with reference to the strong posterodorsal alae.

HOLOTYPE. A female carapace, OS 7844. Two specimens, OS 7845, 8258, are paratypes. Sample FCRM 2033, Lindi Creek, east shore; Upper Eocene.

OTHER MATERIAL. 74 specimens, including juveniles, from samples FCRM 1575, 1578, 2033. See Remarks below for specimens from FCRM 1566 (Lower Miocene), e.g. OS 8257.

DIMENSIONS (µm).	L	H	W
Holotype, female carapace OS 7844	570	350	330
Paratype, male carapace OS 7845	620	355	350
Juvenile left valve (? this species) OS 8257	485	300	150

REMARKS. The new subspecies differs from *Q. arcana* s. str., from the Middle Eocene of Kutch, India, in having stronger posterodorsal alae, which give it a different shape in dorsal view. It also shows distinct sexual dimorphism, the presumed males being subrectangular compared with the more quadrate females. Only provisionally classified here are a large number of juvenile single valves from Lower Miocene samples (e.g. FCRM 1566; Pl. 25, fig. 8) which may not belong here, but this is the only species which they resemble in shape.

Quadracythere? *acuta* sp. nov.

Pl. 24, figs 4–7

NAME. 'Pointed', with reference to the posterior extremity.

DIAGNOSIS. A species of *Quadracythere*(?) with coarsely reticulate ornament, the ridges being blade-like.

HOLOTYPE. A female carapace, OS 8245. A male carapace, OS 8247, is a paratype. Sample FCRM 2033, Lindi Creek, east shore; Upper Eocene.

OTHER MATERIAL. Two carapaces. Also occurs in FCRM 1578.

DESCRIPTION. Carapace medium-sized to large, with greatest height at anterior cardinal angle and greatest length in ventral half. Anterior margin rounded; posterior end acuminate in lateral view, making a pronounced posterior cardinal angle; both margins denticulate. Dorsal margin almost straight, ventral concave in the middle and convex on either side; posterodorsal margin concave. Sexes distinct, presumed males being shorter and more slender than females. Surface coarsely reticulate with sharp muri running predominantly longitudinally. Eye tubercle strongly developed. No internal details seen.

DIMENSIONS (µm).	L	H	W
Holotype, female carapace OS 8245	810	500	390
Paratype, male carapace OS 8247	820	485	385

REMARKS. The produced and upturned posterior margin, sharp muri and shape intermediate between *Quadracythere* and *Agrenocythere* suggest that this species could be placed in either genus. However, *Agrenocythere* has no eye tubercle, so the species is tentatively assigned to *Quadracythere*.

Quadracythere distenta sp. nov.

Pl. 24, fig. 12; Pl. 25, figs 1–3

NAME. 'Swollen', with reference to the carapace.

DIAGNOSIS. A species of *Quadracythere* almost quadrate in lateral view, with length to height ratio of 3:2. Ridges on the surface slope longitudinally from the posterodorsal to the anteroventral region.

HOLOTYPE. A carapace, OS 8250. Another carapace, OS 8251, is a paratype. Sample FCRM 1989, Likonga bridge; Lower Miocene.

OTHER MATERIAL. Four specimens from samples FCRM 1566 (e.g. OS 8252), 1989.

DESCRIPTION. Carapace tumid, subquadrate, with greatest height at anterior cardinal angle and greatest width about two-thirds of the length from the front. Anterior margin broadly rounded, posterior margin produced subventrally and obliquely truncated. Posterodorsal margin concave; dorsal and ventral margins modified in lateral view by marginal keels, dorsal margin being otherwise straight and ventral margin concave in the middle. Lateral surface reticulate, predominant lateral ridges sloping from posterodorsally to anteroventrally. Ridges are subparallel to margins along anterior and posterior ends. Duplicature moderately wide. Normal pores fairly numerous and widely scattered. Muscle scars could not

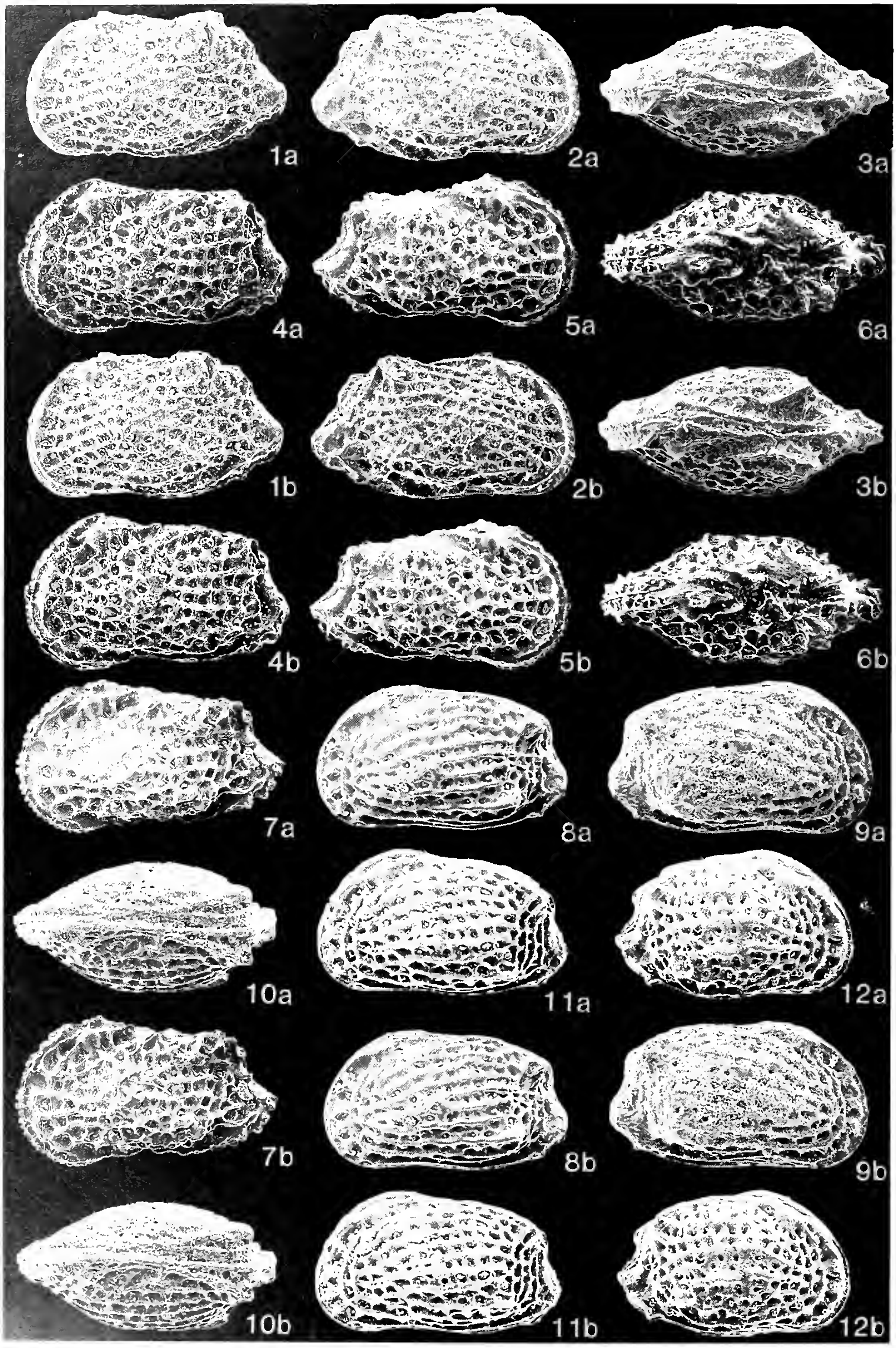
---

PLATE 23

Figs 1–3 *Bradleya*? sp. A. Right valve, OS 8187; 1, external lateral view, ×55; 2, internal lateral view, ×52; 3, 'ghost' reticulation on external lateral surface, ×123.

Figs 4, 5 *Bradleya*? sp. B. Carapace, OS 8328; 4, lateral view from right, ×76; 5, dorsal view, ×79.

Figs 6–12 *Quadracythere vanga* sp. nov. Figs 6, 9, paratype, female left valve, OS 8255; 6, internal lateral view, ×63; 9, external lateral view, ×63. Fig. 7, paratype, male carapace, OS 8254, lateral view from left, ×68. Fig. 8, **holotype**, male carapace, OS 8253, lateral view from right, ×68. Figs 10–12, paratype, female carapace, OS 8256; 10, lateral view from right, ×62; 11, dorsal view, ×70; 12, ventrolateral view from left, ×62.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

be seen; hinge and other internal features typical of the genus.

DIMENSIONS (µm).	L	H	W
Holotype, carapace OS 8250	675	435	410
Left valve OS 8252	640	415	250

REMARKS. *Q. hornibrooki* Holden 1967 differs from *Q. distenta* in having the greatest height just behind the anterior margin. *Q. kenti* sp. nov. (below) is very similar to *Q. distenta*, but as they have slightly different patterns of ornamentation and *Q. distenta* is larger, the two are here considered to be distinct species.

Quadracythere kenti sp. nov. Pl. 24, figs 8–11

NAME. In honour of the late Sir Peter Kent, F.R.S., in recognition of his contribution to Tanzanian geology.

DIAGNOSIS. A subrectangular species of *Quadracythere* with reticulate surface, about ten ridges running from the posterior towards the anteroventral area. The three ventral ridges curve along, and run parallel to, the anterior and posterior margins.

HOLOTYPE. A male carapace, OS 8248. A female carapace, OS 8249, is a paratype. Sample FCRM 1989, Likonga bridge; Lower Miocene.

OTHER MATERIAL. Two carapaces from the type locality and horizon.

DESCRIPTION. Carapace medium-sized, subrectangular in lateral view, with greatest height at anterior cardinal angle and greatest width at mid-length. Anterior margin asymmetrically rounded, posterior produced subventrally. Dorsal margin almost straight; ventral margin straight to slightly concave in the middle. Sexual dimorphism present, presumed females being subquadrate compared with males, which taper posteriorly. In dorsal view, carapace lens-shaped. Surface reticulate. About ten ridges run posterodorsally to anteroventrally. The three ventral ridges continue along, and run parallel to, the anterior and posterior margins. Ridges alate posterodorsally and posteroventrally.

DIMENSIONS (µm).	L	H	W
Holotype, male carapace OS 8248	640	380	330
Paratype, female carapace OS 8249	595	360	325

REMARKS. *Q.? sulcatopunctata* (Reuss) subsp. *mediterranea* Ruggieri, 1962 is the only species of *Quadracythere* with some resemblance to *Q. kenti*, but besides some other minor differences of ornamentation, Ruggieri's subspecies does not have ridges running parallel to the posterior margin. For comparison with *Q. distenta* see remarks under that species.

Quadracythere subquadra Siddiqui, 1971 Pl. 24, figs 1–3

1971 *Q.* (*Hornibrookella*) *subquadra* Siddiqui: 68; pl. 34, figs 6–11.

FIGURED SPECIMEN. A carapace, OS 8243. Sample FCRM 1575, shore south-west of Ras Tapuri; Middle Oligocene.

OTHER MATERIAL. 29 specimens from samples FCRM 1574–8.

DIMENSIONS (µm).	L	H	W
Carapace OS 8243	670	380	320

REMARKS. Siddiqui (1971) described this species from the Upper Chocolate Clays (Upper Eocene) of the Zao River, Pakistan. The Tanzanian specimens differ slightly from these in being more produced posteriorly; they also lack the distinct subcentral tubercle which is characteristic of Pakistani ones.

Quadracythere trijugis Holden, 1976 Pl. 25, fig. 9

1976 *Quadracythere trijugis* Holden: 23, figs 14–15; pl. 5, fig. 24.

FIGURED SPECIMEN. A right valve, OS 7843. Sample FCRM 2010, stream south-west of Mtwero; Lower Miocene.

OTHER MATERIAL. 11 specimens from samples FCRM 1575, 1578, 2010.

REMARKS. This species was originally described from the Upper Miocene of the Sand Island hole and the Lower Miocene of the Reef hole, Midway area, Hawaiian Islands. The Tanzanian specimens are identical with Holden's paratype USNM 184435 (1976: pl. 5, fig. 24) which has been described as 'young'. The internal details of the Tanzanian specimens suggest that these are juveniles as well.

DIMENSIONS (µm).	L	H	W
Right valve, juvenile? OS 7843	595	330	160

Quadracythere vanga sp. nov. Pl. 23, figs 6–12

NAME. 'A spade' (late Latin), with reference to the shape in lateral view.

DIAGNOSIS. A species of *Quadracythere* with a strongly protruding anterior cardinal angle, particularly in left valve.

HOLOTYPE. A male carapace, OS 8253. Three specimens, OS 8254–6, are paratypes. Sample FCRM 1578, coastal cliff west of Ras Tapuri; Middle Oligocene.

OTHER MATERIAL. Two specimens.

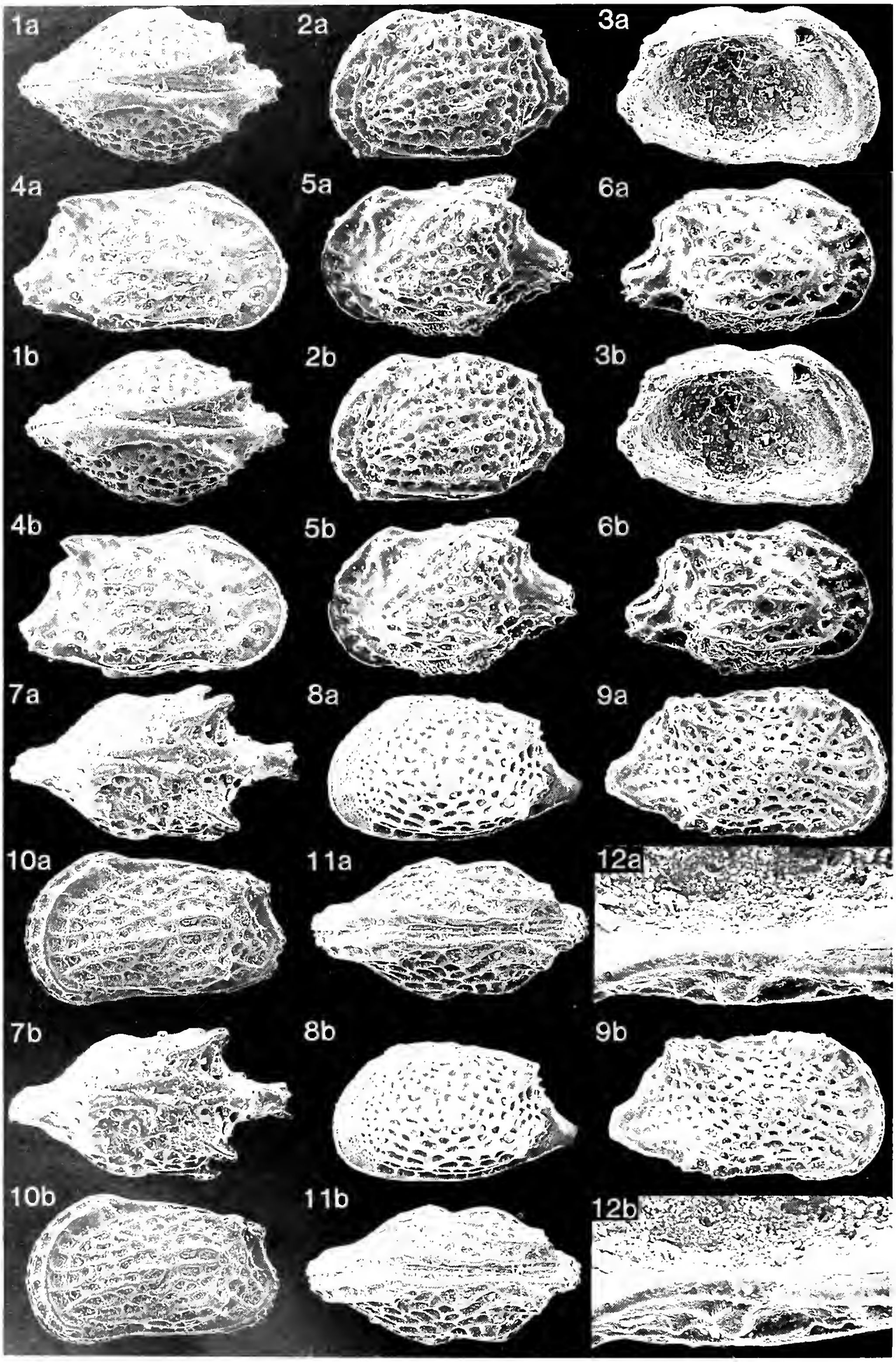
PLATE 24

Figs 1–3 *Quadracythere subquadra* Siddiqui, 1971. Carapace, OS 8243; 1, lateral view from left, ×64; 2, lateral view from right, ×64; 3, dorsal view, ×69.

Figs 4–7 *Quadracythere*? *acuta* sp. nov. Fig. 4, **holotype**, female carapace, OS 8245, lateral view from left, ×54. Figs 5–7, paratype, male carapace, OS 8247; 5, lateral view from right, ×51; 6, dorsal view, ×56; 7, lateral view from left, ×53.

Figs 8–11 *Quadracythere kenti* sp. nov. Figs 8–10, **holotype**, male carapace, OS 8248; 8, lateral view from left, ×63; 9, lateral view from right, ×67; 10, dorsal view, ×67. Fig. 11, paratype, female carapace, OS 8249, lateral view from left, ×69.

Fig. 12 *Quadracythere distenta* sp. nov. **Holotype**, carapace, OS 8250, lateral view from right, ×58. See also Pl. 25, fig. 1.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

DESCRIPTION. Carapace medium-sized, with greatest height at anterior cardinal angle and greatest length subventral. Anterior margin broadly and obliquely rounded towards venter; posterior end with subventral caudal process. Anterior cardinal angle strongly protruding particularly in left valve; dorsal margin almost straight. Lateral surface reticulate. Carapace alate both dorsally and ventrally in the posterior half, ventral alae being sharper and more triangular than dorsal ones. Posterior margin has two or three marginal spines. Sexual dimorphism present, presumed males being narrower posteriorly than females. Duplicature moderately broad and very regular, selvage well developed mid-ventrally. Marginal pore canals obscure but seven or eight false ones visible. Muscle scars also obscure; only a V-shaped frontal scar and two adductor scars are visible. Hinge strongly holamphidont.

DIMENSIONS (μm).	L	H	W
Holotype, male carapace, OS 8253	585	370	320
Paratype, female left valve, OS 8255	630	405	220
Paratype, male carapace, OS 8254	540	345	285
Paratype, female carapace, OS 8256	610	410	350

REMARKS. *Q. vanga* is distinguished from the other Tanzanian species and from *Q. brachypygaia* van den Bold, 1965, from the Oligo-Miocene of Puerto Rico, by its strongly protruding anterior cardinal angle. In this respect it resembles *Q. orbignyana* (Bosquet) *emend.* Keij, 1957, but the latter has stronger reticulation.

Quadracythere sp. A Pl. 25, figs 10–11

FIGURED SPECIMEN. A carapace, OS 8244. Sample FCRM 2033, Lindi Creek, east shore; Upper Eocene. The only specimen.

DESCRIPTION. Carapace subrectangular in lateral view, with greatest height at anterior cardinal angle and greatest width just behind mid-length. Anterior margin broadly rounded; posterodorsal margin concave, posteroventral bluntly produced. Dorsal margin almost straight, making a pronounced cardinal angle with posterior margin. Ventral margin straight to slightly concave in the middle. Lateral surface strongly reticulate, with foveolate muri and the ridges mostly longitudinal. Ocular ridge strongly developed, running parallel to anterior and ventrolateral margins. No internal details visible.

DIMENSIONS (μm).	L	H	W
Carapace OS 8244	780	490	415

REMARKS. *Quadracythere* (*Hornibrookella*) sp. A of Siddiqui, 1971, from the Middle–Upper Eocene Upper Chocolate Clays of the Zao River section, Sulaiman Range, Pakistan, is very similar to *Quadracythere* sp. A from Tanzania. But while the Tanzanian species is wider behind the middle, Siddiqui's species is wider in the anterior half. In addition, the fossae in the Tanzanian species are arranged longitudinally, while in the Pakistani species they are somewhat concentrically arranged around the subcentral tubercle.

Genus ***CRENALEYA*** nov.

NAME. From botanical Latin *crena*, a rounded projection; with reference to the round projecting snap-knob in the right valve of the type species.

DIAGNOSIS. Carapace elongate in side view, subrectangular, with dorsal and ventral margins straight and slightly converging posteriorly. Valves inflated ventrally, with greatest width about a third of the length from posterior end. Sexual dimorphism marked. Lateral surface reticulate, with deep fossae and crimped muri; eye tubercle present. Muscle scars not clearly visible in adults, but in less calcified juveniles the pattern consists of four adductor scars arranged in a row, with a V-shaped frontal scar. Hinge strongly holamphidont, closure further strengthened by a ventral snap-knob in right valve. There is no socket in left valve; instead the knob rests against the external surface of the mid-ventral margin.

TYPE SPECIES. *Crenaleya tuberis* sp. nov.

REMARKS. The new genus appears to be related to *Oertliella* Pokorný, 1964*a*, *Bradleya* Hornibrook, 1952, *Urocythereis* Ruggieri, 1950, *Agrenocythere* Benson, 1972, *Phalcocythere* Siddiqui, 1971, and some species of *Hermanites* Puri, 1955. It can be distinguished from *Oertliella* by the absence of a strong ventrolateral ridge, a dorsal ridge often reduced to spines, and a hemiholamphidont hinge, all of which are characteristic of *Oertliella*. *Crenaleya* differs from *Bradleya* in lacking dorsal and ventral ridges, which are found in that genus. In side view, *Crenaleya* resembles *Urocythereis*, but in dorsal view the latter is lens-shaped, while the former is trapezoid, being very wide posteriorly; also, *Urocythereis* has the frontal muscle scar divided. *Phalcocythere* has a ventral ridge, distinguishing it from the new genus. Some species of *Agrenocythere* (e.g. *A. pliocenica* (Segueza)) and *Hermanites* (e.g. *H. volans* Neale, 1975) resemble the new genus, but they all have dorsal and/or ventral ridges; *Agrenocythere* also lacks eye tubercles. The new genus is further distinguished by the ventral snap-knob in the right valve and by the posteroventral inflation.

It is not known whether *Bradleya? cornuelina* (Bosquet) *emend.* Keij, 1957, *B.? voraginosa* Siddiqui, 1971, *Oertliella* sp. A of Donze *et al.*, 1970, and Genus Indet. Sp. 1 of Dingle,

---

PLATE 25

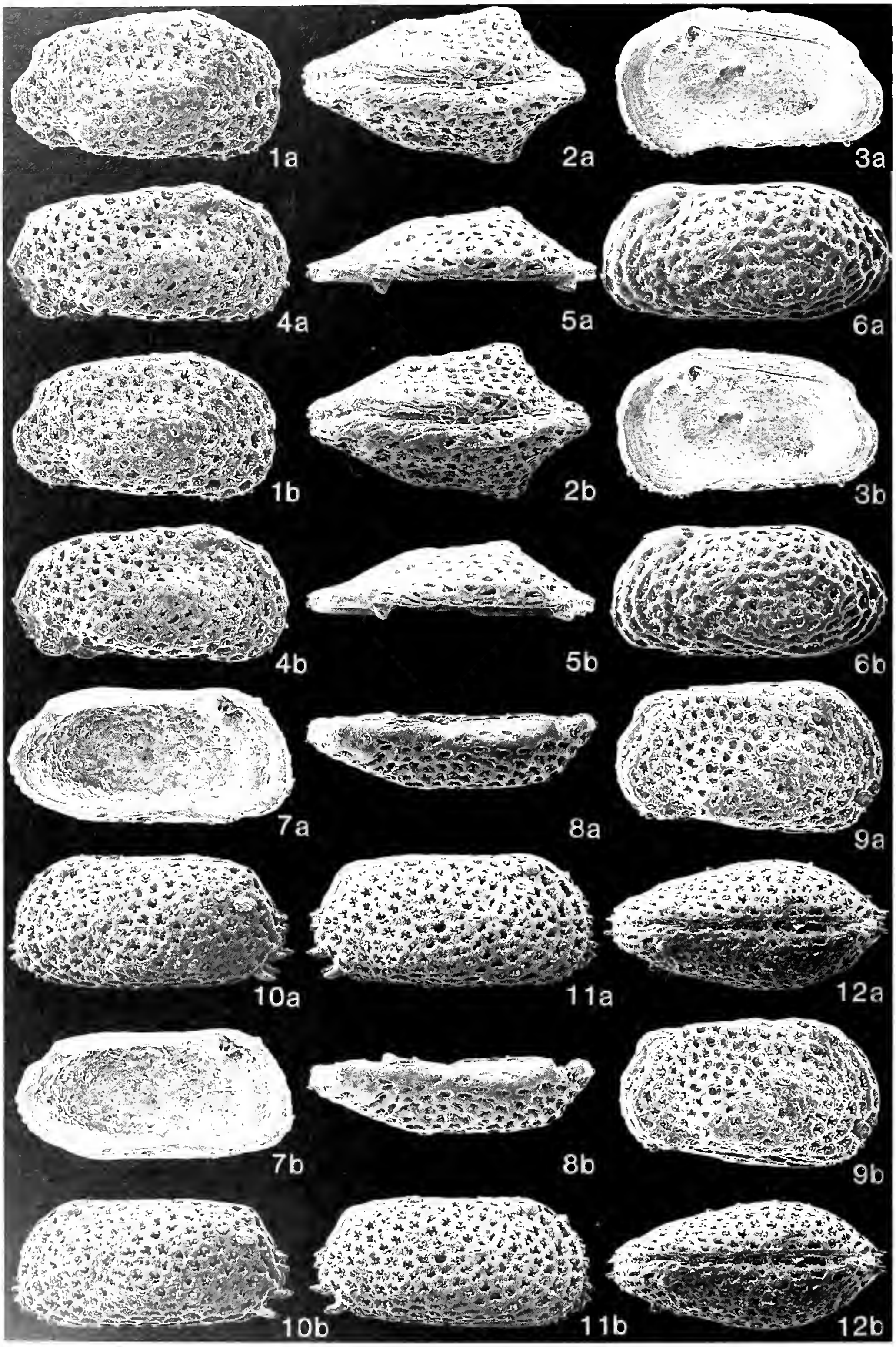
Figs 1–3 *Quadracythere distenta* sp. nov. Fig. 1, **holotype**, carapace, OS 8250, dorsal view, ×64; see also Pl. 24, fig. 12. Figs 2, 3, left valve, OS 8252; 2, external lateral view, ×61; 3, internal lateral view, ×66.

Figs 4–8 *Quadracythereis arcana* (Lubimova & Guha) *cornigera* subsp. nov. Fig. 4, paratype, male carapace, OS 7845, lateral view from right, ×72. Figs 5–7, subspecific **holotype**, female carapace, OS 7844; 5, lateral view from left, ×72; 6, lateral view from right, ×71; 7, dorsal view, ×82. Fig. 8, juvenile left valve, possibly not this species (see text, p. 231), OS 8257, external lateral view, ×85.

Fig. 9 *Quadracythere trijugis* Holden, 1976. Juvenile? right valve, OS 7843, external lateral view, ×76.

Figs 10, 11 *Quadracythere* sp. A. Carapace, OS 8244; 10, lateral view from left, ×53; 11, dorsal view, ×56.

Fig. 12 *Crenaleya tuberis* gen. et sp. nov. **Holotype**, female right valve, OS 8259, snap-knob as seen at mid-ventral margin, ×600. See also Pl. 26, figs 1, 3.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

1976 have a snap-knob mechanism or not, but on the basis of shape and ornamentation these species belong to *Crenaleya*.

Crenaleya tuberis sp. nov. Pl. 25, fig. 12; Pl. 26, figs 1–5, 9

Name. 'With a swelling', in reference to its ventrolateral swelling.

Diagnosis. A *Crenaleya* with elongate, subrectangular carapace, gently tapering posteriorly in lateral view; ventrolateral swelling terminating in a tubercle in the posterior third. Sexual dimorphism pronounced. Surface reticulate, with trifoliate pits.

Holotype. A female left valve, OS 8259. Ten specimens, OS 8260–1, 8263–70, are paratypes. Sample FCRM 1578, coastal cliff west of Ras Tapuri; Middle Oligocene.

Other material. 18 specimens from the locality and horizon above. Also occurs in FCRM 1575 and 1576.

Description. Carapace medium-sized to large, subrectangular in side view; dorsal and ventral margins subparallel, tapering slightly posteriorly. Anterior margin symmetrically rounded, posterodorsal margin concave; gently convex posteroventral margin slightly produced. There are 14–17 anteroventral and 4–6 posterior marginal denticles. Sexual dimorphism marked; presumed females higher in proportion to their length and wider than males. Lateral surface reticulate. The muri have short spines projecting into the fossae, giving them a crimped and trifoliate shape. Subcentral tubercle present, less prominent than a wide tuberculate ventrolateral swelling at about a third the length from posterior end, where carapace attains greatest width. Eye tubercle prominent and glassy. Duplicature moderately wide; line of concrescence coincides with inner margin so there is no vestibule. Right valve has a midventral snap-knob which rests against the mid-ventral margin of left. Hinge strongly holamphidont; in the right valve the conical anterior tooth has a post-jacent socket joined to an elongate elevated tooth by a smooth groove.

Dimensions (μm).	L	H	W
Holotype, female right valve OS 8259	700	410	220
Paratype, female carapace OS 8263	720	420	420
Paratype, male right valve OS 8260	810	425	255

Remarks. *C. tuberis* resembles Gen. Indet. 3 sp. 1 of Dingle, 1971, but the latter has a distinct marginal rim which the new species lacks.

Crenaleya sp. A Pl. 26, figs 10–12

Figured specimen. A carapace, OS 8271. Sample FCRM 2014, stream south-west of Mtwero; Lower Miocene. The only specimen.

Description. A distinctive rectangular species of *Crenaleya* with two very strong horn-like spines at the posteroventral angle. Carapace large, elongate; rectangular in side view with greatest width in posterior half. Dorsal and ventral margins parallel; anterior symmetrically rounded with about 14 marginal denticles. Posterodorsal margin makes a prominent cardinal angle with dorsal, meeting posteroventral margin at an obtuse angle at a point slightly below mid-height. Posterior margin has two posterodorsal and two much larger horn-like posteroventral spines. Lateral surface reticulate; muri have short spines which project into the fossae, giving them an ornate three- to six-rayed appearance. Eye tubercle well developed and glassy. A right valve, from Mafia SP/40′, kept at the BP Research Centre, Sunbury-on-Thames, has a moderately wide duplicature with line of concrescence separated from inner margin by a vestibule; there is a ventral snap-knob. There are four adductor scars and a V-shaped frontal scar as in the less calcified juveniles of the type species; hinge holamphidont.

Dimensions (μm).	L	H	W
Carapace OS 8271	1090	525	510

Crenaleya? sp. Pl. 26, figs 6–8

Figured specimen. A male left valve, OS 8262. Sample FCRM 1578, coastal cliff west of Ras Tapuri; Middle Oligocene. The only specimen.

Dimensions (μm).	L	H	W
Male left valve OS 8262	1070	520	325

Remarks. This specimen is placed in the genus *Crenaleya* with reservations because it differs markedly from the type species *C. tuberis* in lateral outline, particularly at the posterior margin. It is highest at the posterior third, in this differing from both *C. tuberis* and *C.* sp. A, which are highest at the anterior cardinal angle.

Genus *UROCYTHEREIS* Ruggieri, 1950

Type species. *Cytherina favosa* Roemer, 1838.

Urocythereis salebrosa sp. nov. Pl. 27, fig. 1

Name. 'Rough, rugged', with reference to the surface ornamentation.

Diagnosis. A species of *Urocythereis* with coarsely reticulate surface and fossae forming characteristic ventrolateral slits.

Holotype. A left valve, OS 7987. Two valves, OS 8272–3, are paratypes. Sample FCRM 2010, stream south-west of Mtwero; Lower Miocene.

Other material. Two single valves from the same locality and horizon.

Description. Carapace medium-sized, subrectangular in side view, with greatest height at anterior cardinal angle. Anterior

---

PLATE 26

Figs 1–5, 9 *Crenaleya tuberis* gen. et sp. nov. Figs 1, 3, **holotype**, female right valve, OS 8259; 1, external lateral view, ×61; 3, internal lateral view, ×63; see also Pl. 25, fig. 12. Figs 2, 9, paratype, female carapace, OS 8263; 2, dorsal view, ×62; 9, lateral view from right, ×66. Figs 4, 5, paratype, male right valve, OS 8260; 4, external lateral view, ×58; 5, dorsal view, ×58.

Figs 6–8 *Crenaleya*? sp. Male left valve, OS 8262; 6, external lateral view, ×43; 7, internal lateral view, ×43; 8, dorsal view, ×43.

Figs 10–12 *Crenaleya* sp. A. Carapace, OS 8271; 10, lateral view from left, ×41; 11, lateral view from right, ×41; 12, dorsal view, ×41.

margin well rounded, somewhat oblique below; posterior bluntly produced, with straight to concave posterodorsal margin; marginal denticles very few or absent. Dorsal and ventral margins straight and subparallel. Surface coarsely reticulate with some fossae joining to form prominent slits, especially ventrolaterally. Eye tubercle very weakly developed. Duplicature narrow, hinge typical of genus. No other internal features were seen.

DIMENSIONS (µm)	L	H	W
Holotype, left valve OS 7987	760	410	270

REMARKS. The shape and pattern of *U. salebrosa* have some affinity with those of *U. sorocula* (Seguenza) of Uliczny, 1969, but in other details the two are dissimilar. The most apparent difference is that *U. sorocula* has an elongate groove more or less parallel to the anterior margin and the Tanzanian species has not.

Urocythereis*? *apolegma sp. nov. Pl. 27, figs 2–4

NAME. 'Hem of a robe' (Greek), with reference to the marginal rim.

DIAGNOSIS. A species with a well-developed marginal rim and a single row of deep subquadrate fossae along the anterior and posterior margins.

HOLOTYPE. A male carapace, OS 8276. Five specimens, OS 8275, 8277, 8279–81, are paratypes. Sample FCRM 1578, coastal cliff west of Ras Tapuri; Middle Oligocene.

OTHER MATERIAL. Two specimens from the same locality and horizon, and one (OS 8278) from FCRM 2010, Lower Miocene. Also occurs in FCRM 1576.

DESCRIPTION. Carapace medium-sized to large, subrectangular-elongate in side view, with greatest width in front of posterior margin. Anterior margin rounded, posterior subrounded to angulate in the middle; anterior and posteroventral margins denticulate. Dorsal margin straight; ventral margin gently concave. Species dimorphic; in dorsal view, presumed females more swollen than presumed males. Lateral surface reticulate; a strong marginal rim is present all round the carapace, with a row of deep fossae just within the anterior and posterior parts. Elsewhere fossae are elongate, with muri bearing short spines giving them a crimped appearance. Eye tubercle more or less distinct. Duplicature moderately wide along anterior and posterior margins and considerably wider along ventral margin; duplicature coincides with inner margin. Selvage runs near, and parallel to, outer margin; selvage groove well developed. Muscle scars not visible; hinge weakly holamphidont.

DIMENSIONS (µm).	L	H	W
Holotype, male carapace OS 8276	870	400	355

REMARKS. Gen. Indet. 3 sp. 1 of Dingle (1976: 52, fig. 9(4)) is extremely similar to *U.*? *apolegma*, but Dingle's species has less well developed anterior and dorsal marginal ridges. The uncertainty about the muscle scars and the general external habitus make it doubtful that this species belongs to *Urocythereis*; however, no closer assignment is possible at present.

Subfamily **ORIONININAE** Puri, 1974

Genus ***ANTEROCYTHERE*** McKenzie & Swain, 1967

TYPE SPECIES. *Anterocythere purii* McKenzie & Swain, 1967

Anterocythere sp. B of Swain & Gilby, 1974

Pl. 27, figs 11–12; Pl. 28, fig. 1

1974 *Anterocythere* sp. B Swain & Gilby: 316; pl. 7, fig. 2.

FIGURED SPECIMEN. An immature right valve, OS 7813. Sample FCRM 1566, Mongo Stream, Lindi; Lower Miocene.

OTHER MATERIAL. Eight immature single valves, from FCRM 1566 (OS 7821), 1737, 1738, 1742, 1745, 1989, 2014, 2015.

DIMENSIONS (µm).	L	H	W
Right valve OS 7813	465	235	095

REMARKS. The genus *Anterocythere* seems to have been based on external ornamentation, which differs slightly from that of *Caudites* and *Orionina*, all three genera being identical internally. *Orionina* is well established and differs substantially from *Caudites*, being reticulate rather than smooth in the intercostal areas, but *Anterocythere* is neither well established nor much different from the other two. In fact an analogy may be drawn with some other genera which were erected a very long time ago on the basis of external ornament intermediate between that of two related genera, but which are still a source of considerable confusion. No adult specimens of *Anterocythere* were found in the Tanzanian sediments, hence Swain & Gilby's open nomenclature is retained; while the genus is retained here, grave doubt must attach to its value as a separate entity.

There is a striking resemblance between this taxon and *Caudites* cf. *rosaliensis* Swain, p. 240 (compare Pl. 28, fig. 1 with Pl. 27, fig. 7). However, in *Anterocythere* sp. B the principal posterior rib terminates in the middle of the posterior

---

PLATE 27

Fig. 1 *Urocythereis salebrosa* sp. nov. **Holotype**, left valve, OS 7987, external lateral view, ×60.

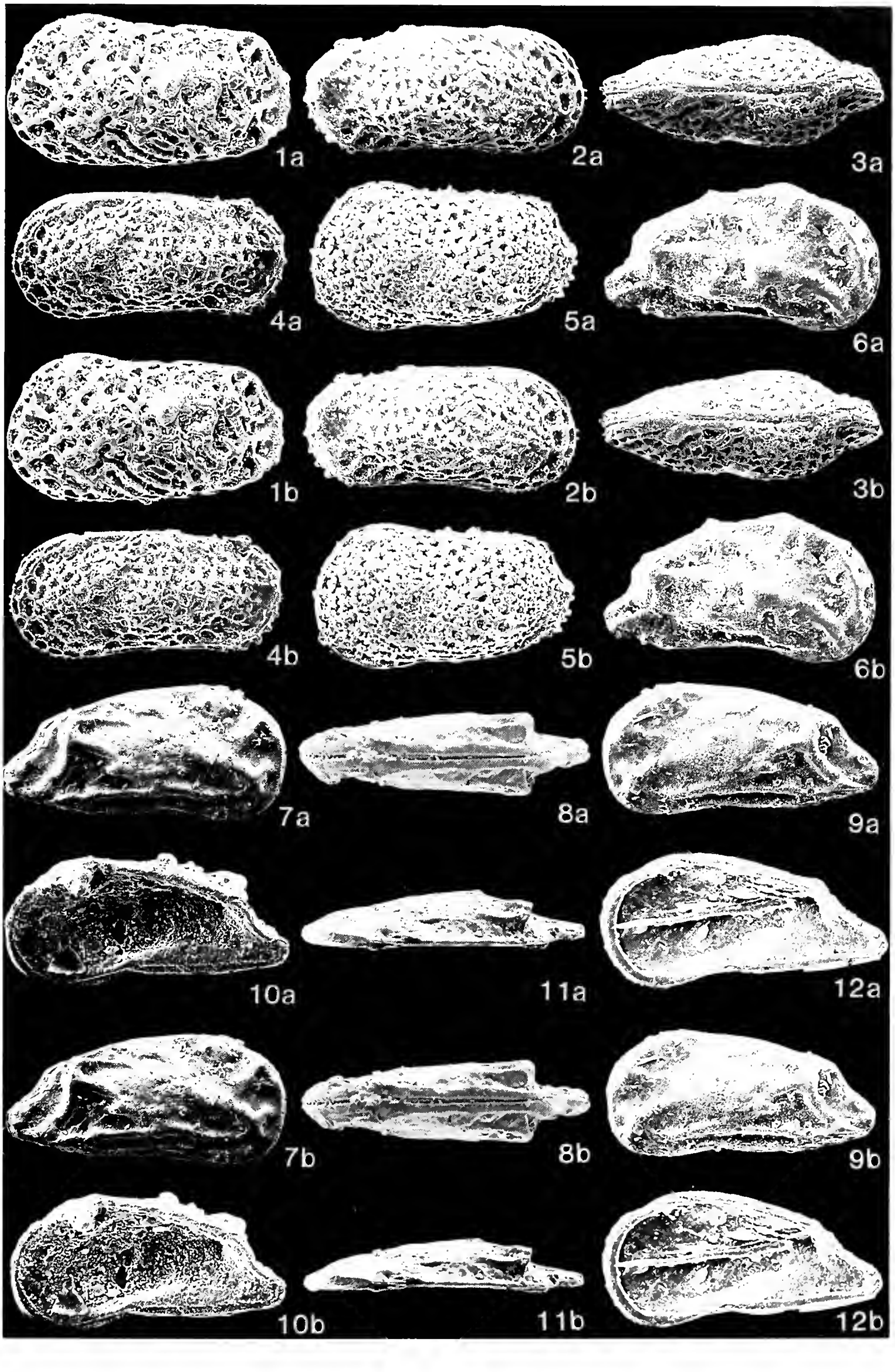
Figs 2–4 *Urocythereis*? *apolegma* sp. nov. **Holotype**, male carapace, OS 8276; 2, lateral view from right, ×53; 3, dorsal view, ×52; 4, lateral view from left, ×52.

Fig. 5 *Bythoceratina*? *asteria* sp. nov. **Holotype**, left valve, OS 8116, external lateral view, ×65.

Figs 6, 10 *Caudites* sp. Right valve, OS 7812; 6, external lateral view, ×92; 10, internal lateral view, ×94.

Figs 7–9 *Caudites* cf. *rosaliensis* Swain, 1967. Carapace, OS 7822; 7, lateral view from right, ×80; 8, dorsal view, ×82; 9, lateral view from left, ×79.

Figs 11, 12 *Anterocythere* sp. B of Swain & Gilby, 1974. Right valve, OS 7813; 11, dorsal view, ×99; 12, internal lateral view, ×101. See also Pl. 28, fig. 1.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

margin of the caudal process, whereas in *C.* cf. *rosaliensis* it terminates in the ventral margin of the caudal process. We consider that the one cannot be regarded as a juvenile of the other. Nevertheless, the similarity sustains our doubts about the distinction of *Anterocythere* as a seperate genus from *Caudites*.

Genus ***CAUDITES*** Coryell & Fields, 1937

TYPE SPECIES. *C. medialis* Coryell & Fields, 1937.

Caudites sp. Pl. 27, figs 6, 10

FIGURED SPECIMEN. A right valve, OS 7812. Sample FCRM 1661, near top of old garnet mine, Lindi; Lower Miocene.

OTHER MATERIAL. Four specimens, including one broken valve from FCRM 1989, and two valves (e.g. OS 7815) from FCRM 1566.

DESCRIPTION. Valves robust, tapering posteriorly, with gently sloping dorsal, and strongly concave posterodorsal, margins. Greatest height at anterior cardinal angle, greatest length below mid-height. Anterior margin gently rounded towards venter; posterior end drawn out, giving valves a subtriangular shape. Ventral margin slightly concave. External ornament consists of a number of strongly developed ridges; one runs from eye tubercle towards anteroventral margin; another runs from anteroventral margin to mid-length, where it forms a subcentral tubercle, then turns down and runs for a short distance parallel to ventral margin. The ventral ridge, less well developed than the upper one, runs parallel to the latter and joins it below the subcentral tubercle. There is a typical *Caudites* U-shaped ridge in the posterior half. Intercostal reticulation absent. Internally, marginal pore canals numerous, short, straight, and parallel to each other. No inframarginal pillar structures or muscle scars visible; hinge holamphidont.

DIMENSIONS (μm).	L	H	W
Right valve OS 7812	490	275	120

REMARKS. The subcentral tubercle-like knot formed by the median ridge distinguishes the Tanzanian species from most others; the intermarginal pillar structures so characteristic of this genus were not seen in this species.

Caudites cf. ***rosaliensis*** Swain, 1967 Pl. 27, figs 7–9

cf. 1967 *Caudites rosaliensis* Swain: 80; pl. 5, figs 9–11, 13.
cf. 1967 *Caudites rosaliensis* Swain; McKenzie & Swain: 295; pl. 20, fig. 17a–c; text-fig. 20.
cf. 1969 *Caudites rosaliensis* Swain; Swain: 467; pl. 3, figs 4a–c, 7a–b; pl. 10, figs 10a–b.
cf. 1969 *Caudites* sp. C Swain: 467; pl. 3, figs 6a–b.
cf. 1974 *Caudites rosaliensis* Swain; Swain & Gilby: 311; pl. 4, figs 10–11, 13.

FIGURED SPECIMEN. A carapace, OS 7822; specimen lost. Sample FCRM 2010, stream south-west of Mtwero; Lower Miocene.

DIMENSIONS (μm).	L	H	W
Carapace OS 7822	570	255	170

REMARKS. The Tanzanian species is similar to Swain's in its outline and ornament. The only apparent difference between the two is that in the Tanzanian species the median ridge does not run from the posterior end towards the anteroventral margin; instead it is stepped, and joined to the ventral marginal ridge.

Family **LOXOCONCHIDAE** Sars, 1926
Subfamily **LOXOCONCHINAE** Sars, 1926

Genus ***LOXOCONCHA*** Sars, 1866

TYPE SPECIES. *Cythere rhomboidea* Fischer, 1855.

Subgenus ***LOXOCONCHA*** Sars, 1866

Loxoconcha (Loxoconcha) mbanjaensis sp. nov.
Pl. 28, figs 11–12; Pl. 29, figs 1–5

NAME. After the Mbanja river, the type locality.

DIAGNOSIS. A subrhomboidal species of *Loxoconcha*, with the greatest height and width in the middle. Surface with concentrically arranged pits.

HOLOTYPE. A female carapace, OS 8096. A female left valve OS 8097, and a male carapace, OS 8099, are paratypes. Sample FCRM 1746, Mbanja River; Lower Miocene.

OTHER MATERIAL. Seven specimens from FCRM 1566 (OS 8101–2), 1661 (OS 8100), 1989 (OS 8103–4), and 2015 (8105–6). Also occurs in FCRM 1737, 1745, 2010 and 2016.

DESCRIPTION. Carapace subrhomboidal in lateral view, with greatest height and width almost in the middle. Anterior margin obliquely rounded; posterior end slightly produced subdorsally, with concave posterodorsal margin and convex posteroventral margin. Dorsal margin concave to very gently curved, ventral straight to concave in anterior half and convex in posterior half. Sexual dimorphism marked, carapaces of presumed males being narrower and more elongate. Left valve overlaps right; overlap not pronounced. Lateral surface pitted; pits elongate and arranged concentrically along valve

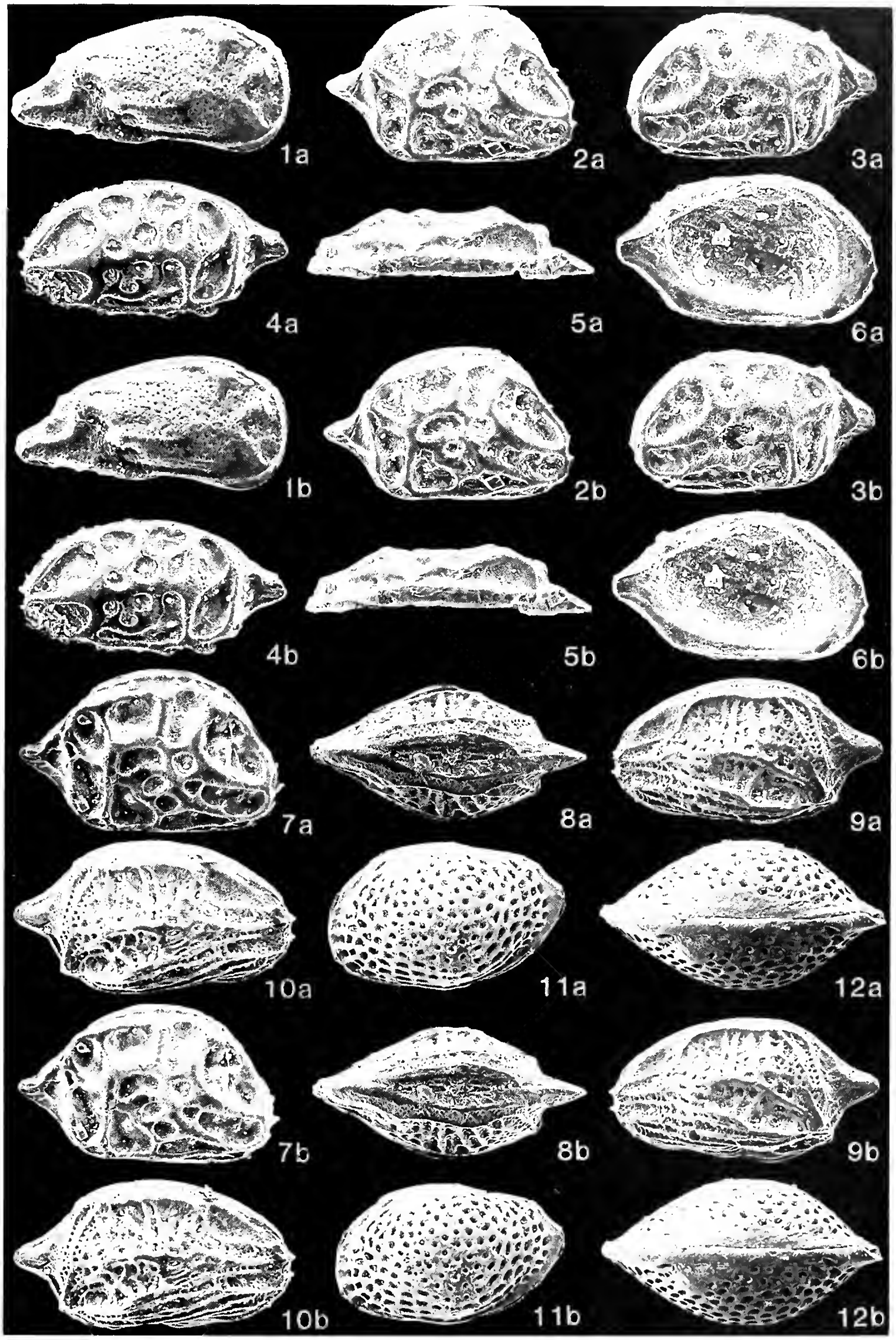
PLATE 28

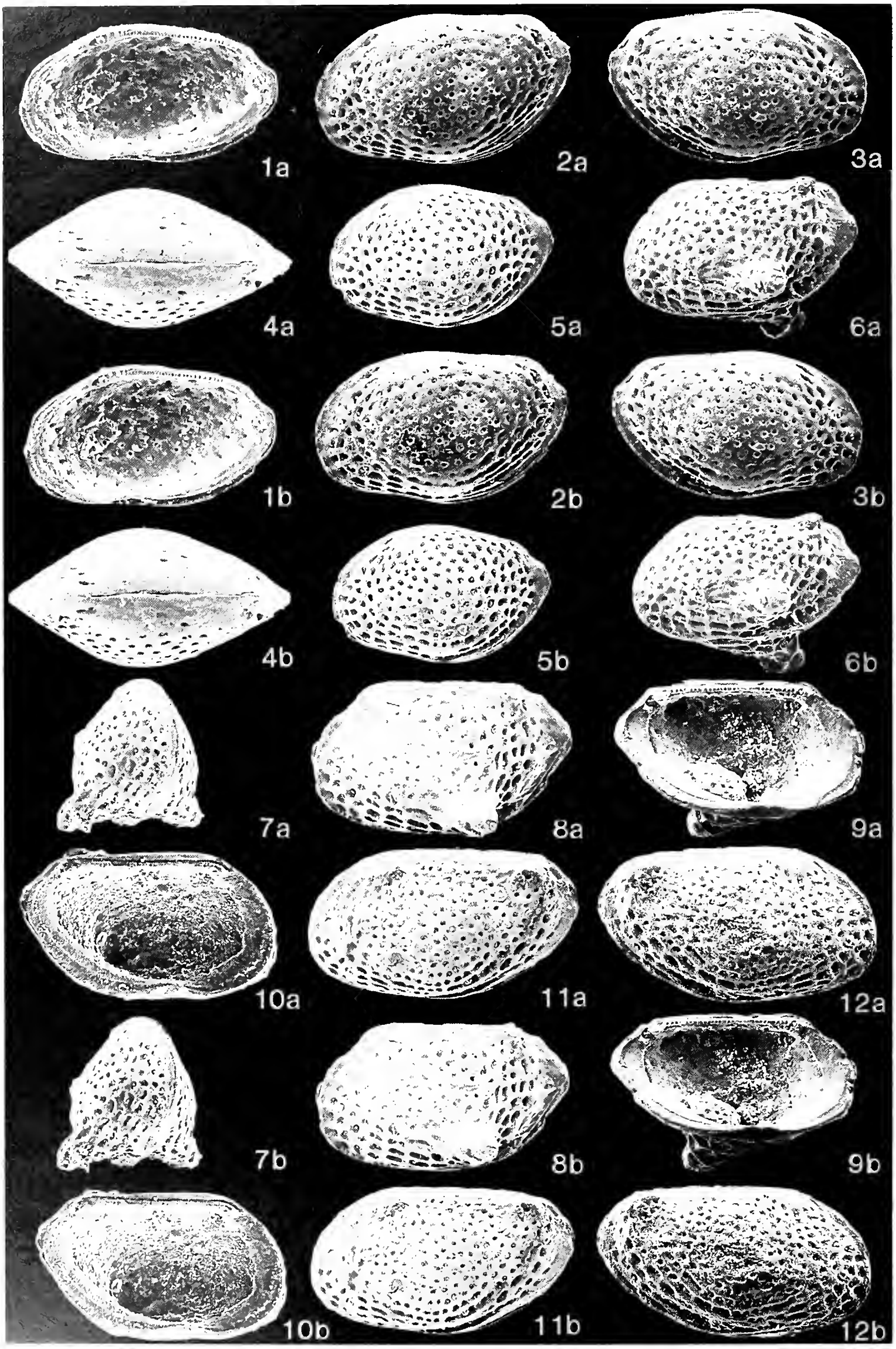
Fig. 1 *Anterocythere* sp. B of Swain & Gilby, 1974. Right valve, OS 7813, external lateral view, ×97. See also Pl. 27, figs 11–12.

Figs 2–7 *Hemicytherura subulata* sp. nov. Fig. 2, **holotype**, male right valve, OS 8300, external lateral view, ×126. Figs 3, 6, paratype, female left valve, OS 8301; 3, external lateral view, ×132; 6, internal lateral view, ×135. Fig. 4, male left valve, OS 8305, external lateral view, ×133. Figs 5, 7, paratype, female right valve, OS 8304; 5, dorsal view, ×147; 7, external lateral view, ×134.

Figs 8–10 *Kangarina* sp. Carapace, OS 7983; 8, dorsal view, ×134; 9, lateral view from left, ×131; 10, lateral view from right, ×137.

Figs 11, 12 *Loxoconcha (Loxoconcha) mbanjaensis* sp. nov. Fig. 11, paratype, female left valve, OS 8097, external lateral view, ×78. Fig. 12, holotype, female carapace, OS 8096, dorsal view, ×99; see also Pl. 29, fig. 5.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

margins, rounded on lateral surface. Eye spot very low, consisting of a large, opaque surface. Duplicature wide anteriorly and ventrally; inner margin and line of concrescence coincide except along anterior and posterodorsal margins where narrow vestibules are present. Selvage prominent. Marginal pore canals simple, straight and widely spaced. Normal pores moderately numerous, scattered and of various sizes. Hinge typically gongylodont, consisting of an anterior socket followed by a crenulate bar and an elongate posterior socket in the left valve.

DIMENSIONS (μm).	L	H	W
Holotype, female carapace OS 8096	465	305	255
Paratype, female left valve OS 8097	485	305	150
Paratype, male carapace OS 8099	610	375	315
Female right valve OS 8100	460	275	140

REMARKS. The present species is closest to *L. yazooensis* Huff 1970, but the less concentric arrangement of pits and the smooth muri of the Tanzanian species easily distinguish them.

Subgenus ***LOXOCORNICULUM*** Benson & Coleman, 1963

TYPE SPECIES. *Cythere fischeri* Brady, 1869*a*.

Loxoconcha* (*Loxocorniculum*) *postnodosa sp. nov.

Pl. 29, figs 11–12; Pl. 30, figs 1–4

NAME. A reference to the posterodorsal node.

DIAGNOSIS. A species of *Loxoconcha* with pronounced sexual dimorphism. In lateral view, the valves are rhomboidal, with the dorsal and ventral margins almost parallel to each other.

HOLOTYPE. A male carapace, OS 8092. A female carapace, OS 8093, is a paratype; specimen lost. Sample FCRM 1566, Mongo Stream, Lindi; Lower Miocene.

OTHER MATERIAL. Ten specimens from samples FCRM 1566 (e.g. OS 8091), 1575. Also occurs in FCRM 1574, 1576, 1578, 1628 and 1989.

DESCRIPTION. Carapace thickly calcified, rhomboidal, with greatest height and width in the middle. Anterior margin obliquely rounded towards the venter; posterior end upturned, forming a caudal process above mid-height. Dorsal margin straight and parallel to ventral, which is straight in the anterior half and curves upwards just behind mid-length. In dorsal view, carapace lens-shaped. Sexual dimorphism very pronounced, presumed males being more elongate than presumed females; females more tumid. Left valve larger than right; overlap not pronounced. Lateral surface coarsely pitted, pits being arranged almost parallel to outer margins. There is a prominent tubercle just below the posterior cardinal angle, also an eyespot. Internal features characteristic of genus.

DIMENSIONS (μm).	L	H	W
Holotype, male carapace OS 8092	540	305	250
Paratype, female carapace OS 8093	465	295	240

REMARKS. *Loxoconcha abrupta* Hornibrook 1952 is comparatively more ovate and has a stronger posterior tubercle; the posterior margin of *L. abrupta* is truncate in dorsal view whereas it is slightly produced in the new species. *L. pentockensis* Kingma 1948 is another species resembling *L. postnodosa* in some respects, but it differs in having a comparatively concave ventral margin and a more curved dorsal margin. *L. postdorsalata* Puri 1960 has a sinuous ventral margin with slight concavity anterior to the middle, whereas *L. postnodosa* has an almost straight ventral margin.

Two morphotypes are distinguished: see below.

Morphotype A

Pl. 30, fig. 5

FIGURED SPECIMEN. A male right valve, OS 8094. Sample FCRM 1575, shore south-west of Ras Tapuri; Middle Oligocene.

REMARKS. Morphotype A differs from typical *Loxoconcha* (*Loxocorniculum*) *postnodosa* in being more oblong, with a greater length/height ratio. The posteroventral curve is more gentle, and the posterodorsal tubercle is much reduced.

DIMENSIONS (μm).	L	H	W
Male right valve OS 8094	530	260	140

Morphotype B

Pl. 30, figs 6–7

FIGURED SPECIMEN. A male carapace, OS 8095. Sample FCRM 1575, shore south-west of Ras Tapuri; Middle Oligocene.

REMARKS. Morphotype B is like Morphotype A in most respects, but differs in having more and smaller pits, all of which are circular, and in the ventral margin being comparatively straight. In dorsal view it is more pencil-shaped than the lenticular *L. postnodosa*, s. str.

DIMENSIONS (μm).	L	H	W
Male carapace OS 8095	530	305	250

Loxoconcha* (*Loxocorniculum*) *tricornis sp. nov.

Pl. 30, figs 8–9

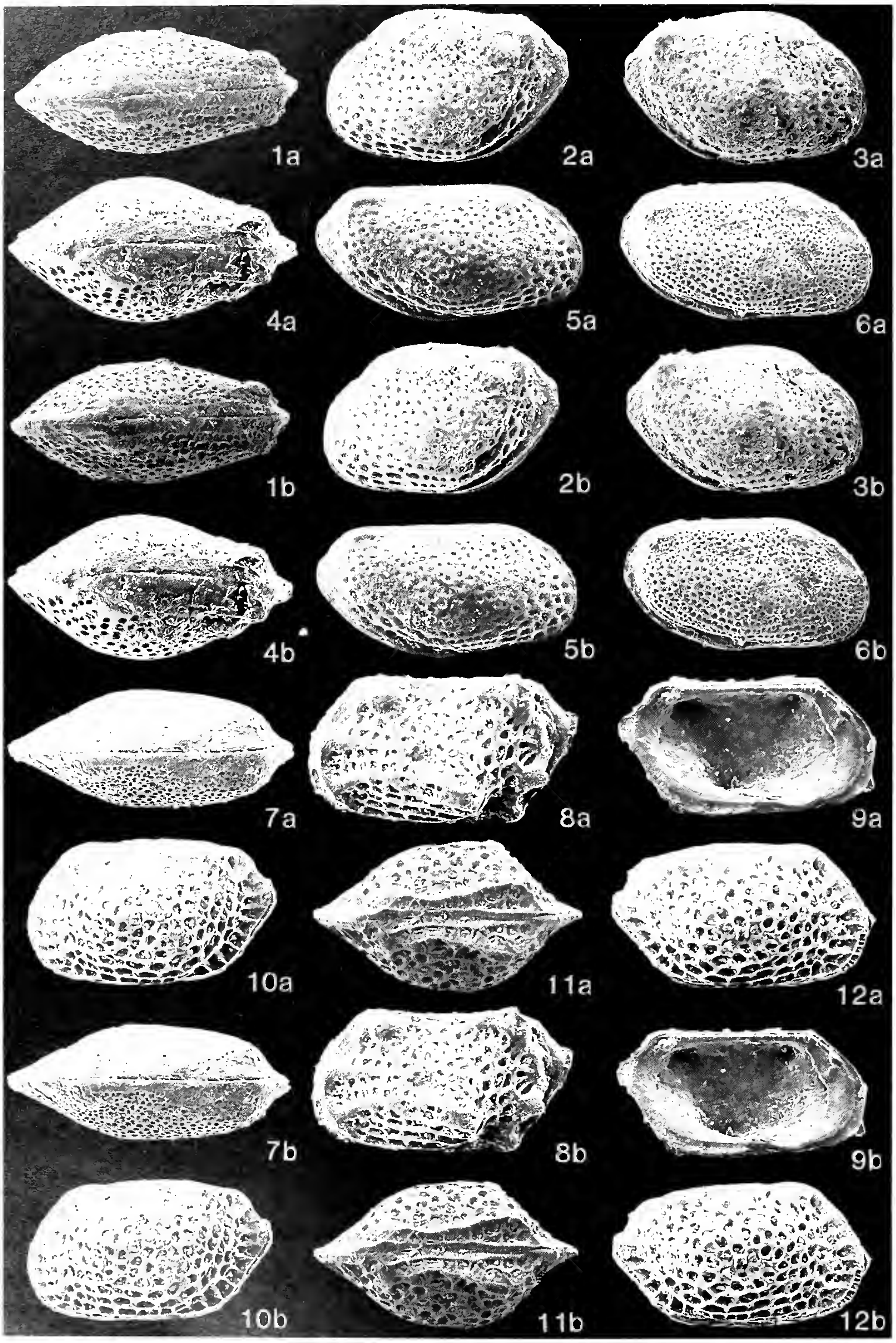
NAME. 'Three-horned', with reference to three tubercles in the posterior half of the valves.

PLATE 29

Figs 1–5 *Loxoconcha* (*Loxoconcha*) *mbanjaensis* sp. nov. Fig. 1, female right valve, OS 8100, internal lateral view, ×92. Figs 2–4, paratype, male carapace, OS 8099; 2, lateral view from left, ×69; 3, lateral view from right, ×69; 4, dorsal view, ×77. Fig. 5, **holotype**, female carapace, OS 8096, lateral view from left, ×77; see also Pl. 28, fig. 12.

Figs 6–10 *Loxoconcha* (*Loxocorniculum*) cf. *longispina* Keij, 1953. Figs 6, 7, female carapace, OS 7958; 6, ventrolateral view from left, ×81; 7, anteroventral view, ×81. Figs 8, 9, female left valve, OS 7959; 8, external lateral view, ×88; 9, internal ventrolateral view, ×86. Fig. 10, female left valve, OS 7960, internal lateral view, ×88.

Figs 11, 12 *Loxoconcha* (*Loxocorniculum*) *postnodosa* sp. nov. **Holotype**, male carapace, OS 8092; 11, lateral view from left, ×80; 12, lateral view from right, ×82. See also Pl. 30, fig. 1.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

DIAGNOSIS. Valves small and subrectangular. Surface with two prominent ridges in the anterior half and three tubercles in the posterior half.

HOLOTYPE. A female left valve, OS 8107. Three specimens, OS 8108–10, are paratypes. Sample FCRM 1566, Mongo Stream, Lindi; Lower Miocene.

MATERIAL. Five specimens from FCRM 1566, 2014 (e.g. OS 8111–2). Also occurs in FCRM 2015 and 2016.

DESCRIPTION. Carapace subrectangular in side view, with obliquely rounded anterior margin; posterodorsal margin concave to straight; posteroventral margin convex to straight. Dorsal and ventral margins subparallel. Sexual dimorphism marked, higher forms being interpreted as females. External surface strongly reticulate, with two prominent longitudinal ridges in anterior half and three tubercles in posterior half of each valve. Eye tubercle strongly developed. Duplicature moderately wide. Selvage strongly developed, running near outer margin. Muscle scars, hinge and other internal details characteristic of genus.

DIMENSIONS (μm).	L	H	W
Holotype, female left valve OS 8107	470	265	150
Paratype, male left valve OS 8108	450	235	–

REMARKS. *L. antillea* var. *rugosa* van den Bold, 1946, is related to *Loxoconcha tricornis*, but differs in having a rather irregular posteroventral margin; the two anterior ridges seem to be shorter and more convergent than in the Tanzanian species.

Loxoconcha (*Loxocorniculum*) cf. *longispina* Keij, 1953

Pl. 29, figs 6–10

cf. 1953 *Loxoconcha alata* Brady var. *longispina* Keij: 160; pl. 1, figs 10a, b.
cf. 1967 *Loxoconcha longispina* Keij; Holden: 32–34, figs 23a–d.
cf. 1976 *Loxoconcha longispina* Keij; Holden: F32; pl. 4, fig. 14; pl. 5, figs 3–6; pl. 14, figs 12–15.

FIGURED SPECIMENS. A female carapace, OS 7958; two valves, OS 7959, 7960. Sample FCRM 1578, coastal cliff west of Ras Tapuri; Middle Oligocene.

OTHER MATERIAL. Seven specimens, from the same sample. Also occurs in FCRM 1576, 2014 and 2016.

REMARKS. The Tanzanian specimens are very similar to Holden's from the Midway area, Hawaiian Islands, and may even be conspecific. Holden (1976) mentions that this species is very variable, the Pleistocene(?) specimens not being as strongly alate as his Miocene specimens. The Tanzanian specimens are strongly alate and come from the Mid-Oligocene. It seems therefore that the species originated as a strongly alate form on the western coast of the Indian Ocean.

DIMENSIONS (μm).	L	H	W
Female carapace OS 7958	470	290	350
Female left valve OS 7959	475	285	220
Female left valve OS 7960	480	290	200

Subgenus ***MYRENA*** Neale, 1967

TYPE SPECIES. *Loxoconcha meridionalis* Müller, 1908.

Loxoconcha (*Myrena*) *loculus* sp. nov. Pl. 30, figs 10–12

NAME. 'Box' or 'purse', with reference to its shape in side view.

DIAGNOSIS. A species of *Loxoconcha* with a dorsal marginal ridge and strongly reticulate surface.

HOLOTYPE. A carapace, OS 8282. Six specimens, OS 8283–8, are paratypes. Sample FCRM 2033, Lindi Creek, east shore; Upper Eocene.

OTHER MATERIAL. Three specimens from samples FCRM 2034 and 2046. Also occurs in FCRM 2045.

DESCRIPTION. Carapace small, subrectangular, with almost uniform height but varying width. Anterior margin broadly rounded towards venter; posterior produced subdorsally. Dorsal and ventral margins straight and subparallel; posterodorsal and posteroventral margins straight to slightly concave. External surface reticulate, with comparatively large rectangular fossae arranged parallel to margin. Dorsal margin strongly modified by a wavy rim. Left valve overlaps right slightly. Eye tubercle well developed. Internal details not visible because of small size and poor preservation.

DIMENSIONS (μm).	L	H	W
Holotype, carapace OS 8282	370	220	220

REMARKS. The ornament and shape are somewhat akin to those of *Kuiperiana nystiana* (Bosquet) Keij 1957, but the Tanzanian species is much smaller and has a more produced posterior margin.

PLATE 30

Figs 1–4 *Loxoconcha* (*Loxocorniculum*) *postnodosa* sp. nov. Fig. 1, **holotype**, male carapace, OS 8092, dorsal view, ×86; see also Pl. 29, figs 11–12. Figs 2–4, paratype, female carapace, OS 8093 (specimen lost); 2, lateral view from left, ×84; 3, lateral view from right, ×86; 4, dorsal view, ×101.

Fig. 5 *Loxoconcha* (*Loxocorniculum*) *postnodosa*, Morphotype A. Male right valve, OS 8094, external lateral view, ×81.

Figs 6, 7 *Loxoconcha* (*Loxocorniculum*) *postnodosa*, Morphotype B. Male carapace, OS 8095; 6, lateral view from right, ×77; 8, dorsal view, ×88.

Figs 8, 9 *Loxoconcha* (*Loxocorniculum*) *tricornis* sp. nov. Fig. 8, **holotype**, female left valve, OS 8107, external lateral view, ×93. Fig. 9, paratype, male left valve, OS 8108, internal lateral view, ×93.

Figs 10–12 *Loxoconcha* (*Myrena*) *loculus* sp. nov. **Holotype**, carapace, OS 8282; 10, lateral view from left, ×109; 11, dorsal view, ×115; 12, lateral view from right, ×118.

Subgenus *PALMOCONCHA* Swain & Gilby, 1974

TYPE SPECIES. *Palmoconcha laevimarginata* Swain & Gilby, 1974.

Loxoconcha (*Palmoconcha*) *pinguis* sp. nov.

Pl. 31, figs 1–3

NAME. 'Fat', with reference to the ventral swelling.

DIAGNOSIS. A species of *Loxoconcha* with pronounced ventrolateral swelling and distinct eye tubercle.

HOLOTYPE. A carapace, OS 8289. A carapace, OS 8290, is a paratype. Sample FCRM 1746, Mbanja River; Lower Miocene.

OTHER MATERIAL. Two carapaces from the same locality and horizon. Also occurs in FCRM 1628.

DESCRIPTION. Carapace small, subrectangular in side view. Anterior margin obliquely rounded towards venter; posterior margin curved towards dorsum. Dorsal margin straight, ventral margin with concavity about one-third length from front, slightly modified by the overhanging ventrolateral swelling. In dorsal view lens-shaped, much like any other species of *Loxoconcha* at this angle, in contrast to the striking difference in outline in lateral view. Left valve overlaps right. Surface reticulate; central fossae largest and arranged concentrically. Muri on ventrolateral swelling are stronger than elsewhere. Eye tubercle prominent.

DIMENSIONS (µm).	L	H	W
Holotype, carapace OS 8289	390	235	200

REMARKS. From their size, these specimens might appear to be juveniles, but the other *Loxoconcha* species with similar shapes are all rather small in size. *L. watervalleyensis* Krutak 1961 is 0·40 long and 0·24 mm high; *L. angustata* Brady 1869*b*: 48 is 0·46 mm long (1/55 inch).

Carbonnel (1986) describes a number of *Loxoconcha* species from the Tertiary of the Senegal–Guinea Bissau Basin. Of these, only his Neogene (Serravallian?/Tortonian?) *L. kafountinensis* resembles any of our species. This differs from *L. pinguis* in that the accentuated horizontal costae in the central part of the shell continue to the dorsal margin, whereas in our species they are absent in the upper half of the shell which is occupied by fine pitting.

Genus *PHLYCTOCYTHERE* Keij, 1958

TYPE SPECIES. *Phlyctocythere eocaenica* Keij 1958.

Phlyctocythere reniformis sp. nov.

Pl. 31, figs 4–6

NAME. 'Kidney-shaped', with reference to its resemblance to a kidney.

DIAGNOSIS. A species of *Phlyctocythere* with a gently arched dorsal margin and compressed posteroventral margin.

HOLOTYPE. A carapace, OS 8292. Seven carapaces, OS 8291, 8293–8, are paratypes. Sample FCRM 1989, Likonga bridge; Lower Miocene.

OTHER MATERIAL. Five carapaces from the same sample. Also occurs in FCRM 1745.

DESCRIPTION. Carapace small to medium-sized, kidney-shaped to subrhomboidal in lateral view, with greatest height in middle and greatest width at mid-length or slightly in front of it. Anterior margin rounded, dorsal margin arched; ventral margin almost straight, curved posteroventrally; posterior produced subdorsally. In dorsal view, carapace lens-shaped with slightly elongate posterior margin. Left valve overlaps right, overlap being clearly visible along anterior and ventral margins. Eye tubercle lacking; lateral surface smooth. No internal details visible, since there are no single valves.

DIMENSIONS (µm).	L	H	W
Holotype, carapace OS 8292	425	265	240

REMARKS. This species resembles *Hemicytherura*? *nealei* Swain 1976 in general shape, but is 1·5 times larger and has a compressed zone which is confined to the posteroventral margin, instead of extending to the anterior, posterior and posteroventral margins as is the case in *H.*? *nealei*.

Family **PARACYTHERIDEIDAE** Puri, 1957*c*

Genus *PARACYTHERIDEA* Müller, 1894

TYPE SPECIES. *Paracytheridea depressa* Müller, 1894.

Paracytheridea anapetes Ahmad, 1977*a*

Pl. 31, figs 10–12; Pl. 32, figs 1–6

1977*a* *Paracytheridea anapetes* Ahmad: 41–42.

FIGURED SPECIMENS. Holotype, female carapace, OS 7757. Paratypes, female left valve, OS 7758; male right valve, OS 7760. Sample FCRM 2034, Lindi Creek, east shore; Upper Eocene. Also male left valve, OS 7759 (not a paratype) from sample FCRM 2033.

OTHER MATERIAL. Ten specimens from FCRM 1574 (e.g. OS 7764), 1575 (e.g. OS 7795), 1578, 1627, 1628, 1981, 2014, 2033 (e.g. OS 7759). Also occurs in FCRM 1661, 1989 and 2010.

DESCRIPTION. Carapace medium-sized, subtriangular to suboval in shape, with greatest height and width in posterior half. Anterior margin rounded, posterior produced into a sub-

---

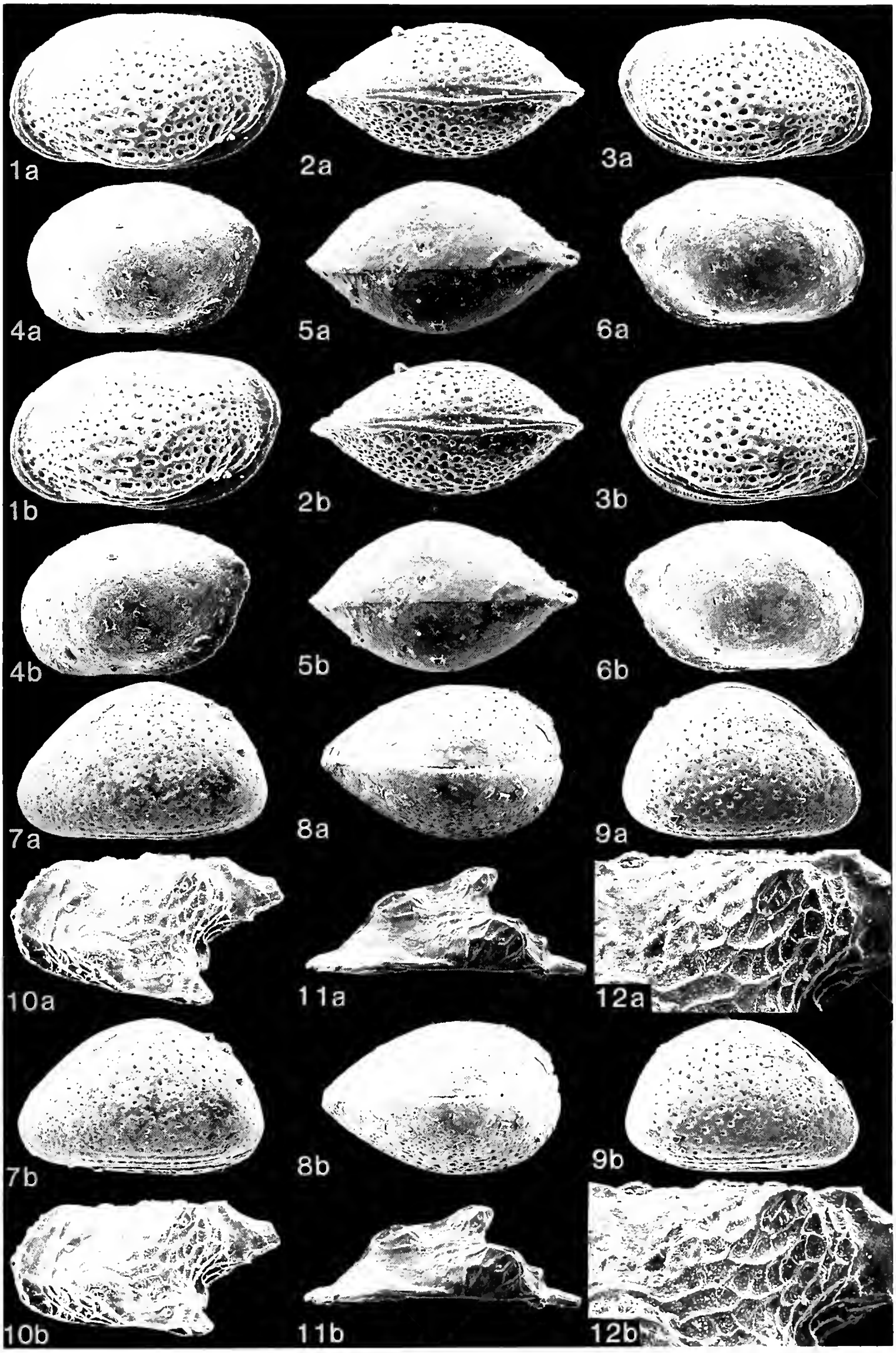
PLATE 31

Figs 1–3 *Loxoconcha* (*Palmoconcha*) *pinguis* sp. nov. **Holotype**, carapace, OS 8289; 1, lateral view from left, ×115; 2, dorsal view, ×115; 3, lateral view from right, ×105.

Figs 4–6 *Phlyctocythere reniformis* sp. nov. **Holotype**, carapace, OS 8292; 4, lateral view from left, ×89; 5, dorsal view, ×105; 6, lateral view from right, ×89.

Figs 7–9 *Uroleberis*? sp. Carapace, OS 8308; 7, lateral view from left, ×68; 8, dorsal view, ×66; 9, lateral view from right, ×65.

Figs 10–12 *Paracytheridea anapetes* Ahmad, 1977*a*. Fig. 10, 12, male left valve, OS 7759; 10, external lateral view, ×70; 12, details of ornament in the median area of the surface, ×300. Fig. 11, paratype, male right valve, OS 7760, dorsal view, ×86; see also Pl. 32, fig. 6.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

dorsal caudal process. Dorsal margin strongly modified in lateral view by a bulbous posterodorsal swelling, appearing straight to concave anteriorly and strongly convex posteriorly. In dorsal view dorsal margin straight, carapace broadly arrow-shaped. Sexual dimorphism marked, presumed females having a bulbous swelling and small alar prolongations posterodorsally, while males have a reduced swelling but larger alar prolongations. Lateral surface almost smooth anterodorsally and posteriorly; other areas covered with a characteristic pattern of ridges. A strong ridge runs from mid-anterior margin towards posterodorsal area, where it branches to form several small ones. Ornament completed by other small ridges meeting these branches almost at right angles. Internally, duplicature wide; line of concrescence and inner margin coincide throughout. A very narrow vestibule may be present along anterodorsal margin; this was impossible to verify. Only three anterior and one posterior marginal pore canals visible. There are four adductor muscle scars and a U-shaped frontal scar. Hinge varies slightly from typical *Paracytheridea*; right valve hinge has 14–15 additional small denticles in front of anterior cusped dental area; left hinge has corresponding sockets.

DIMENSIONS (µm).	L	H	W
Holotype, female carapace OS 7757	595	325	305
Paratype, female left valve OS 7758	560	280	195
Male left valve OS 7759	630	330	290
Paratype, male right valve (juvenile) OS 7760	525	270	220

REMARK. This species was originally described (Ahmad 1977*a*) on the present material.

Paracytheridea culmen sp. nov. Pl. 32, figs 8–12

NAME. 'Ridge', with reference to the ventrolateral ridge.

DIAGNOSIS. A species of *Paracytheridea* with a ventral alar ridge, notched posteriorly. Surface strongly reticulate.

HOLOTYPE. A female left valve, OS 7790. Three specimens, OS 7839–41, are paratypes. Sample FCRM 2010, stream south-west of Mtwero.

OTHER MATERIAL. Ten specimens from samples FCRM 1566, 1575 (e.g. OS 7788), 1578 (e.g. OS 7789), 1648, 2010 (e.g. OS 7791–3), 2014 (e.g. OS 7786–7). Also occurs in FCRM 1989.

DESCRIPTION. Carapace small, subtriangular in lateral view, with greatest height at anterior cardinal angle and greatest width in midventral region. Anterior margin symmetrically rounded; posterior produced into a subventral caudal process. Dorsal and ventral margins almost straight, converging posteriorly. Sexual dimorphism occurs, presumed males being lower in proportion to their length. Surface strongly reticulate, with thin ridges, irregular swellings and a prominent ventrolateral alar ridge; latter notched just before posterior end and merging gradually with the valve anteriorly. Duplicature moderately wide, not well differentiated. Line of concrescence and inner margin coincide. About eight straight, simple, parallel marginal pore canals occur anteriorly and two posteriorly. Muscle scar pattern obscure; a frontal V-shaped scar and two adductor scars can be seen. Hinge very weakly developed.

DIMENSIONS (µm).	L	H	W
Holotype, female left valve OS 7790	500	250	190
Paratype, female right valve OS 7788	440	230	140
Paratype, male left valve OS 7787	450	210	150

REMARKS. Compared with *P. gradata* (Bosquet) *emend.* Keij, 1957, *P. fenestrata* (Bosquet) *emend.* Keij, 1957, and *P. belhavensis* Howe & Chambers, 1935, *P. culmen* is more triangular and has a slightly different pattern of ornamentation.

A morphotype is distinguished: see below.

Morphotype A Pl. 32, fig. 7

FIGURED SPECIMEN. A male left valve, OS 7838. Sample FCRM 2010, stream south-west of Mtwero; Lower Miocene.

OTHER MATERIAL. One valve.

DESCRIPTION. Carapace elongate, subrectangular in side view, with greatest height at anterior cardinal angle and greatest length subventrally. Dorsal margin straight to slightly modified by posterodorsal swelling; ventral margin strongly modified externally by ventrolateral alar ridge, but straight when seen from inside. Anterior margin rounded, posterior margin truncate. Surface reticulate, with thin ridges, irregular swellings and a prominent anterolateral ridge which is divided in front of the posterior end. Smaller ridges arranged longitudinally below the ventrolateral alar ridge.

DIMENSIONS (µm).	L	H	W
Male left valve OS 7838	490	230	160

REMARK. Compared with typical *P. culmen*, Morphotype A is more elongate, less triangular and has a slightly different ornament.

Family **CYTHERURIDAE** Müller, 1894
Subfamily **CYTHERURINAE** Müller, 1894
Genus ***TANZANICYTHERE*** Ahmad, 1977*e*

TYPE SPECIES. *Cladarocythere pterota* Ahmad, 1977*b*.

Tanzanicythere pterota (Ahmad, 1977*b*) Pl. 33, figs 1, 2

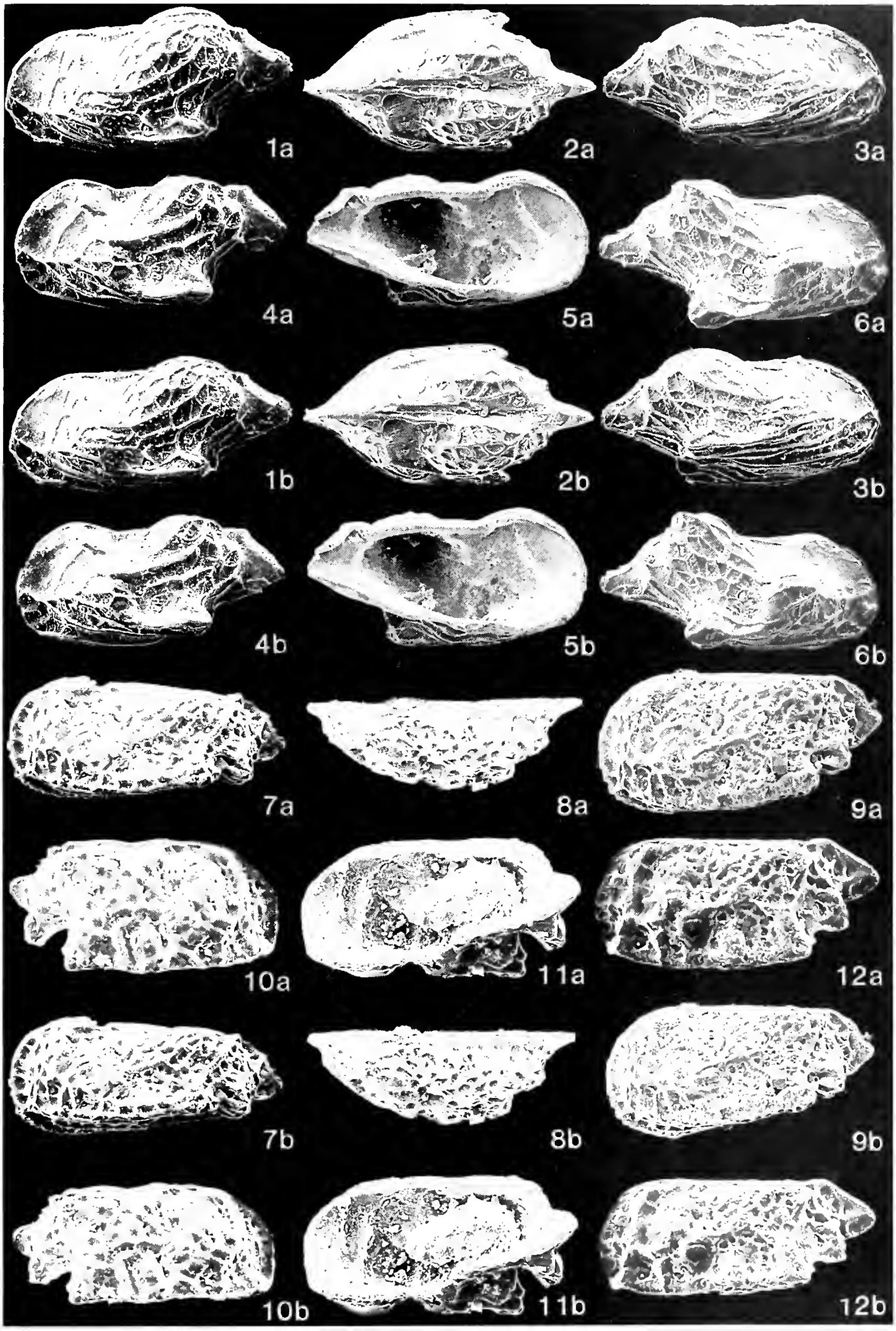
1977*b* *Cladarocythere pterota* Ahmad: 45–48.

PLATE 32

Figs 1–6 *Paracytheridea anapetes* Ahmad, 1977*a*. Figs 1–3, holotype, female carapace, OS 7757; 1, lateral view from left, ×79; 2, dorsal view, ×81; 3, lateral view from right, ×77. Figs 4, 5, paratype, female left valve, OS 7758; 4, external lateral view, ×80; 5, internal lateral view, ×82. Fig. 6, paratype, male right valve, OS 7760, external lateral view, ×91; see also Pl. 31, fig. 11.

Fig. 7 *Paracytheridea culmen* sp. nov., Morphotype A. Male left valve, OS 7838, external lateral view, ×93.

Figs 8–12 *Paracytheridea culmen* sp. nov. Figs 8, 9, **holotype**, female left valve, OS 7790; 8, dorsal view, ×90; 9, external lateral view, ×93. Figs 10, 11, paratype, female right valve, OS 7788; 10, external lateral view, ×101; 11, internal lateral view, ×101. Fig. 12, paratype, male left valve, OS 7787, external lateral view, ×102.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

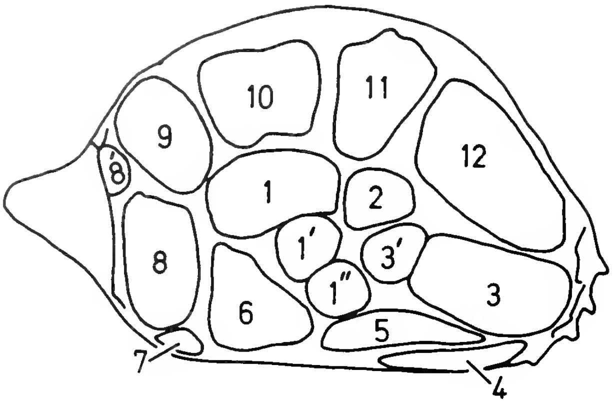


Fig. 9 *Hemicytherura subulata* sp. nov. Holotype OS 8300, ♀ right valve external lateral view, showing the arrangement of fossae. ×260.

FIGURED SPECIMENS. Holotype, right valve OS 7772. Paratypes (unfigured here, but see Ahmad 1977*b*), left valve OS 7774, right valve OS 7773. Sample FCRM 2010, stream south-west of Mtwero; Lower Miocene.

OTHER MATERIAL. Sixteen single valves from samples FCRM 1738, 2010 (e.g. OS 7784–5 and paratypes OS 7775–6), 2015. Also occurs in FCRM 2014.

DESCRIPTION. Carapace small to medium-sized, with greatest height at anterior end and greatest width at middle; very fragile. Anterior margin modified externally by the ventrolateral frill but symmetrically rounded when seen from inside. Dorsal margin almost straight; posterior narrowly produced, giving a beaker-shaped appearance in internal view. Seen obliquely from inside, ventral margin almost straight, sub-parallel to dorsal margin, but in external view completely hidden by the overhanging lateral frill. Frill starts in ventral half of anterior margin, gradually increases in width and terminates abruptly anterior to caudal process. Lateral surface smooth except for frill. Three fine longitudinal ridges occur ventral to the frill. One runs just below top of the frill for its full length; the others are much shorter, and stronger in the posterior half than anteriorly. Internally, duplicature moderately wide; vestibule absent. Ten or eleven normal pore canals divide the frill into compartments; these canals are very much like marginal ones, and have been described by Maddocks (1966) as 'thick straight pore canals', while Hornibrook (1952) described those in *Manawa* as 'septa in the frill', and Ishizaki (1973) refers to them simply as 'marginal pore canals'. Three marginal pore canals visible. Four small adductor muscle scars in a vertical row, with three larger frontal scars placed dorsally, the lowest of which is V-shaped. Hinge very weak; crenulate anterior and posterior tooth plates in right valve, each with four or five teeth, connected by a crenulate bar. Left valve has complementary elements.

DIMENSIONS, including frill (µm).	L	H	W
Holotype, right valve OS 7772	490	270	235

REMARK. This species was originally described (Ahmad 1977*b*) on the present material.

Genus *HEMICYTHERURA* Elofson, 1941

TYPE SPECIES. *Cythere cellulosa* Norman, 1865.

Hemicytherura subulata sp. nov. Pl. 28, figs 2–7; Fig. 9

NAME. 'Awl-shaped, pointed', with reference to the shape and the pointed posterior end.

DIAGNOSIS. A small species of *Hemicytherura* with a marginal ridge running along the dorsal, anterior and ventral margins but slightly within the posterior margin. The fossae along the margins are large and of various shapes while those in the centre are small and round. The greatest height is at about mid-length.

HOLOTYPE. A female right valve, OS 8300. Four single valves, OS 8301–4, are paratypes. Sample FCRM 1566, Mongo Stream, Lindi; Lower Miocene.

OTHER MATERIAL. Two single valves from samples FCRM 1989 and 2015 (OS 8305).

DESCRIPTION. Anterior margin of carapace obliquely rounded towards the venter, with four or five denticles. Dorsal margin outline differs in the two valves, right being strongly arched, left with flatter curve. Ventral margin straight; posterior with caudal process just above mid-height. Sexual dimorphism marked, presumed females higher in proportion to length than males. Ornament typical of genus. For descriptive purposes the fossae have been numbered from 1 to 12, following Hoskin (1975). Fossa 1 is divided in some valves into 1, 1′, and 1″; 1 is rectangular, while 1′, 1″ and 2 are rounded. Fossa 3 is large, elongated, and broader anteriorly; fossa 3′ is narrowly separated from it and is semicircular to subtriangular. Fossae 4 and 5 are elongate and run along the ventral margin, separated from each other by a long murus. Fossa 6 is large, subtriangular, and separated from a small similar fossa 7. Fossa 8 is subrectangular and divided unequally into 8 and 8′. Fossa 9 is subrounded, 10 subquadrate, 11 narrow and subrectangular; these are large.

PLATE 33

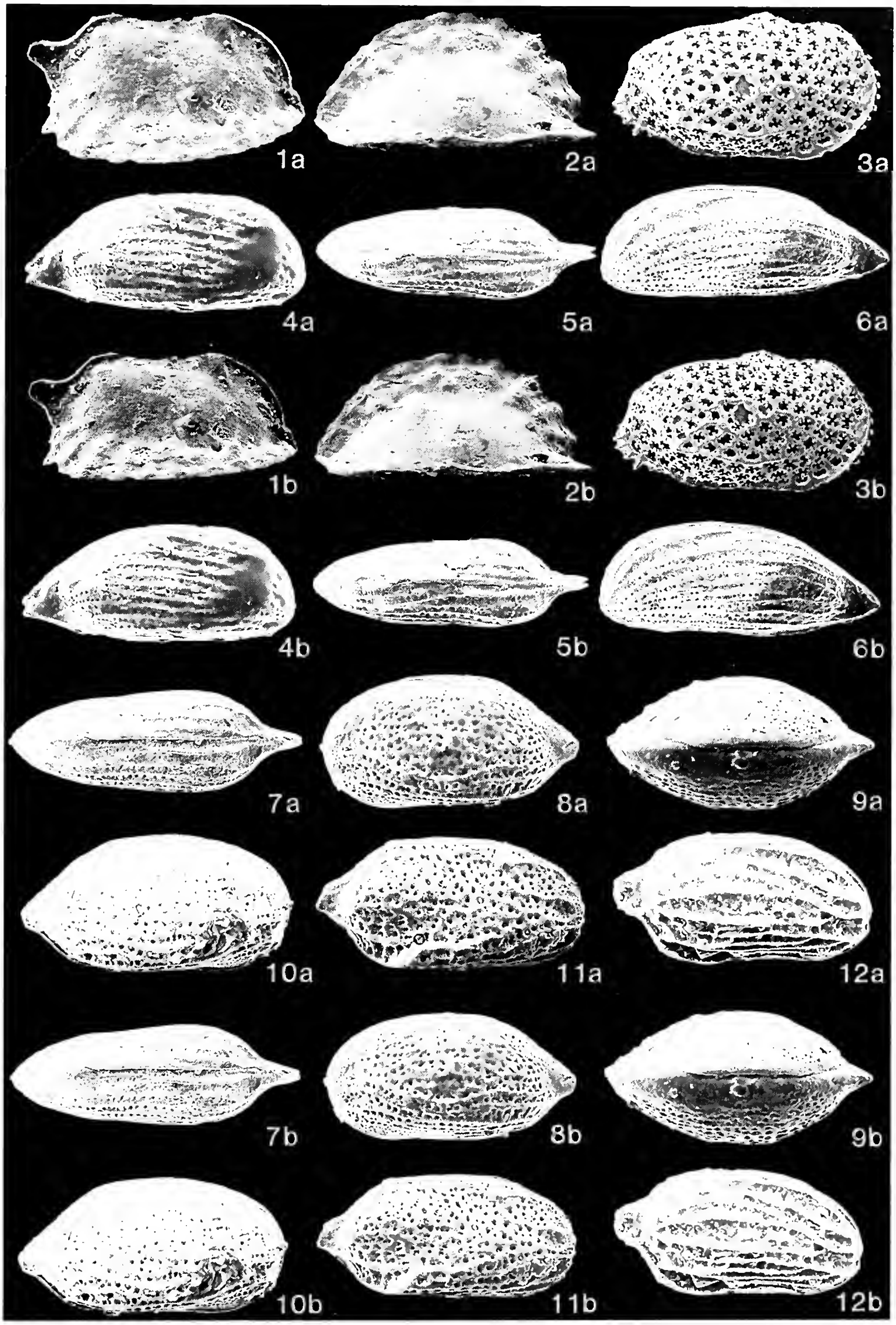
Figs 1, 2 *Tanzanicythere pterota* (Ahmad, 1977*b*). Holotype, right valve, OS 7772; 1, external lateral view, ×93; 2, dorsal view, ×95.

Fig. 3 Genus C sp. Right valve, OS 8320, external lateral view, ×78.

Figs 4–7 *Semicytherura opeata* sp. nov. Figs 4, 5, **holotype**, female carapace, OS 8313; 4, lateral view from right, ×94; 5, dorsal view, ×94. Figs 6, 7, paratype, male carapace, OS 8314; 6, lateral view from left, ×92; 7, dorsal view, ×93.

Figs 8–11 *Semicytherura emphysema* sp. nov. Figs 8–10, **holotype**, female carapace, OS 8309; 8, lateral view from left, ×116; 9, dorsal view, ×119; 10, lateral view from right, ×122. Fig. 11, paratype, male right valve, OS 8311, external lateral view, ×110.

Fig. 12 *Semicytherura* sp. A. Carapace, OS 8316, lateral view from right, ×110.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

Fossa 12, the largest, is subrectangular. The arrangement of the fossae is shown in Fig. 9.

A left valve from sample FRCM 2015, interpreted as a male dimorph, shows a slightly different pattern, but the overall arrangement of fossae is compatible with that of the holotype. The 25–30 normal pore canals are widely scattered. Six or seven marginal pore canals are visible along the posterior margin, but it is difficult to discern any at the anterior end. Hinge artiperatodont, as described by Bate (1972: 45).

DIMENSIONS (μm).	L	H	W
Holotype, female right valve OS 8300	325	205	085
Paratype, female left valve OS 8301	310	195	095
Paratype, female right valve OS 8304	320	200	085
Male left valve OS 8305	330	170	075

REMARKS. *Hemicytherura* sp. of McKenzie, 1974, from the Jangukian (Mid? Oligocene) of south-east Australia, has a very similar shape; fossae 8–12 have almost identical outlines, but fossae 1 and 3′ are missing in the Australian species. The Tanzanian species has the same pattern of ornament as *H. videns videns* (Müller, 1894), but the slightly different fossae, especially 6 and 8 which are shorter and more triangular in *H. subulata*, easily distinguish them.

Genus *SEMICYTHERURA* Wagner, 1957

TYPE SPECIES. *Cythere nigrescens* Baird, 1838.

Semicytherura emphysema sp. nov. Pl. 33, figs 8–11

NAME. 'Something inflated' (Greek), with reference to its ventral inflation.

DIAGNOSIS. A species of *Semicytherura* with ventrally inflated valves; the muri of the fossae are more developed in the ventral half than in the dorsal.

HOLOTYPE. A female carapace, OS 8309. Three specimens, OS 8310–2, are paratypes. Sample FCRM 1989, Likonga bridge; Lower Miocene.

OTHER MATERIAL. One specimen from the same sample. Also occurs in FCRM 1737 and 2010.

DESCRIPTION. Carapace rectangular to subrounded in side view, with subparallel dorsal and ventral margins, and straight to concave posterodorsal margin. Anterior margin symmetrically rounded, posterior produced into a median caudal process. Valves inflated ventrally; carapace lenticular and slightly acuminate posteriorly in dorsal view. Sexual dimorphism present; presumed females much shorter and more tumid than presumed males. External surface pitted to reticulate; pits smaller and muri not as well developed in the dorsal half as in the ventral half of the valves. Internal features could not be seen clearly, except for the hinge, which is typical of the genus.

DIMENSIONS (μm).	L	H	W
Holotype, female carapace OS 8309	390	190	190
Paratype, male carapace OS 8311	400	205	120

REMARKS. The difference in length between the presumed females and males suggests that the female carapace may represent the penultimate stage rather than the adult. The duplicature is not well developed in the single valves, which also suggests that the specimens may be juveniles. However, the sexual dimorphism can be clearly seen, and the size, though small, is within the limits of adults found in this genus. It was therefore thought better to name this species than to leave it under open nomenclature. *S. sella* (Sars, 1866) agrees in shape with the new species but differs from it in having coarser ridges and smaller pits.

Semicytherura opeata sp. nov. Pl. 33, figs 4–7

NAME. From Greek *opeas*, 'awl', with reference to the shape, especially in dorsal view.

DIAGNOSIS. A species of *Semicytherura* with 13 to 15 ridges, with lines of small rounded pits arranged longitudinally between them. The posterior is produced subventrally. Sexual dimorphism present.

HOLOTYPE. A female carapace, OS 8313. Two carapaces, OS 8314–5, are paratypes. Sample FCRM 1989, Likonga bridge; Lower Miocene. The only specimens.

DESCRIPTION. Carapace elongate-ovate in side view; dorsal margin strongly convex, almost continuous with the asymmetrically curved anterior margin and straight sloping posterodorsal margin. Ventral margin slightly concave in the middle and convex posteriorly; posterior produced into a ventral caudal process. Greatest height in the middle; greatest width just in front of posterior end. Sexual dimorphism present, presumed females being shorter and higher than males, and easily distinguished. In dorsal view, however, presumed males look more swollen than females. External surface ornamented with longitudinal ridges, about 13–15 in number when counted at mid-length; anteriorly and posteriorly the numbers decrease as adjacent ridges fuse. These ridges have lines of rounded pits arranged longitudinally between them. Lacking single valves, internal features were not seen.

DIMENSIONS (μm).	L	H	W
Holotype, female carapace OS 8313	490	210	170
Paratype, male carapace OS 8314	520	215	190

REMARKS. Since no internal features were seen placement of this species in *Semicytherura* and not *Cytherura* is based only on comparison with species such as *Semicytherura sulcata* (Müller, 1894). This resembles the new species in shape and ornament, but in *S. opeata* the caudal process is ventral while in *S. sulcata* it is located subdorsally.

Semicytherura sp. A Pl. 33, fig. 12

FIGURED SPECIMEN. A carapace, OS 8316. Sample FCRM 1575; shore south-west of Ras Tapuri; Middle Oligocene.

OTHER MATERIAL. One specimen from the same sample.

DESCRIPTION. Carapace subrectangular in side view; dorsal margin gently convex, anterior margin rounded. Posterodorsal and posteroventral margins concave, with a subdorsal caudal process. Ventral margin concave in the middle and strongly convex posteriorly, with greatest height in posterior third. Sexual dimorphism present, the presumed female being shorter than the male. External surface ornamented with 8 or 9 longitudinal ridges but no pits. Internally, hinge typical for the genus; other features cannot be seen clearly.

DIMENSIONS (µm).	L	H	W
Carapace OS 8316	390	200	160

REMARKS. *S. sella* (Sars, 1866) and *Semicytherura* sp. A are very similar but can be distinguished by the patterns of the ridges. In *S. sella* the ridges in the dorsal half curve strongly towards the mid-anterior region, whereas in *Semicytherura* sp. A the curvature of these ridges is less abrupt. *S. sella* also has thin transverse ridges meeting the stronger longitudinal ones; these are absent in the Tanzanian species.

Subfamily **CYTHEROPTERINAE** Hanai, 1957*b*

Genus ***CYTHEROPTERON*** Sars, 1866

TYPE SPECIES. *Cythere latissima* Norman, 1865.

Cytheropteron epelyx sp. nov. Pl. 34, figs 1–3

NAME. 'Overshadowing' (Greek), with reference to the overhanging ventrolateral part of the carapace.

DIAGNOSIS. A species of *Cytheropteron* with overhanging ventrolateral margin and an acuminate posterior margin.

HOLOTYPE. A right valve, OS 7849. 36 single valves, OS 7850–85, are paratypes. Sample FCRM 1578, coastal cliff west of Ras Tapuri; Middle Eocene.

OTHER MATERIAL. 21 specimens from the same sample (e.g. OS 7756). Also occurs in FCRM 1574, 1575 and 1576.

DESCRIPTION. Carapace medium-sized, well calcified, with greatest height slightly in front of the middle. Anterior margin obliquely rounded towards the venter; posterior acuminate. Dorsal margin asymmetrically arched, divisible into strongly sloping anterior, gently sloping middle and steeply sloping to concave posterior portions. Ventral margin strongly modified, especially about one-third from posterior end, by the overhanging ventrolateral ala. Lateral surface reticulate but not uniformly so; surface almost smooth dorsally, becoming gradually more reticulate ventrally. There are four weak longitudinal ridges, without reticulation, on the ventral surface between the margin and the alae. Another weak ridge runs along the ventral swelling. Marginal pore canals very few and widely separated. Muscle scars not clearly seen but consist of four adductor scars with a V-shaped frontal scar open towards ventral margin. Hinge like that in the *C. latissimum* (Norman, 1865) group of species. Right valve hinge has five denticles on either end with a crenulate bar between; left valve has corresponding elements.

DIMENSIONS (µm).	L	H	W
Holotype, right valve OS 7849	550	325	220
Paratype, right valve OS 7850	590	340	220

REMARKS. *Cytheropteron subreticulatum* Bold, 1946, is closely related to *C. epelyx*, but has a more strongly curved dorsal margin and less distinct posterior point.

Cytheropteron cf. ***nipeensis*** Bold, 1946 Pl. 34, figs 6–9

cf. 1946 *Cytheropteron nipeensis* Bold: 113; pl. 16, fig. 1.

FIGURED SPECIMENS. Male carapace, OS 7961; female carapace, OS 7962 (lost). Sample FCRM 2033, Lindi Creek, east shore; Upper Eocene.

OTHER MATERIAL. Eight specimens from the same sample (e.g. OS 7963).

DIMENSIONS (µm).	L	H	W
Female carapace OS 7962	385	205	150
Male carapace OS 7961	395	215	165

REMARKS. The Tanzanian species agrees with *C. nipeensis* Bold in outline; Bold's figure is not very informative, so it is not possible to say with certainty whether they are the same. Sexual dimorphism occurs in the Tanzanian species, the presumed males being longer and less high than the females; Bold does not mention dimorphism in *C. nipeensis*.

Cytheropteron sp. A Pl. 34, figs 4–5

FIGURED SPECIMEN. A carapace, OS 7846; the only well-preserved specimen. Sample FCRM 2033, Lindi Creek, east shore; Upper Eocene.

DESCRIPTION. Carapace strongly alate, highest in the middle. Anterior margin rounded towards venter, dorsal margin arched; posterior margin produced in a median caudal process. Ventral margin strongly modified by the ala in side view, but when seen obliquely from inside it is straight to slightly concave in anterior half and convex in posterior half. The strongly developed ventrolateral alae bifurcate at their posterior ends. Lateral surface smooth except for very fine hexagonal reticulations along the middle and four weak longitudinal ridges on ventral surface of ala. No internal details were seen.

DIMENSIONS (µm).	L	H	W
Carapace OS 7846	420	240	315

REMARKS. This species has a typical *Cytheropteron* shape but its bifurcated alae distinguish it from any other known species.

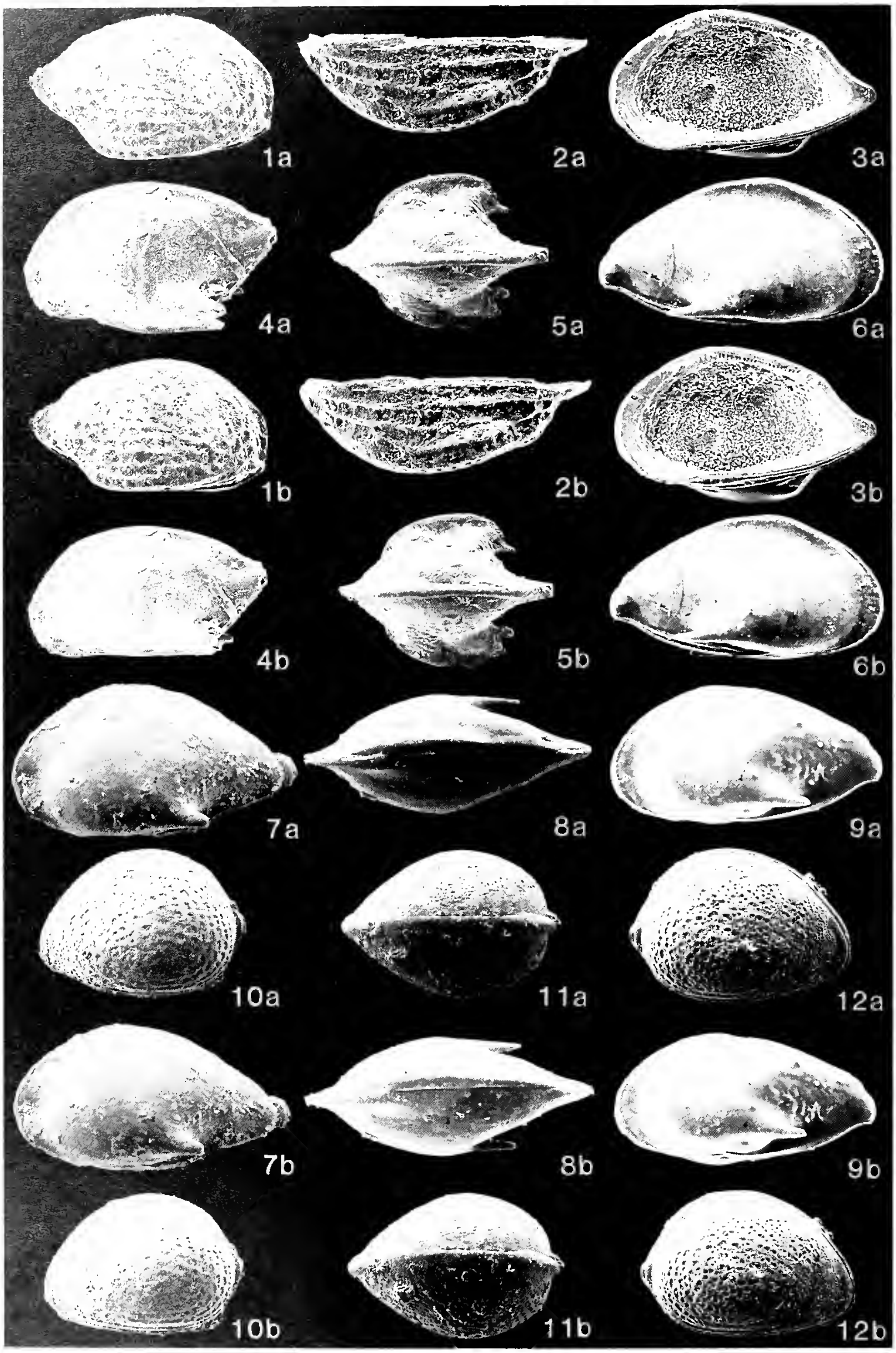
Genus ***KANGARINA*** Coryell & Fields, 1937

TYPE SPECIES. *K. quellita* Coryell & Fields, 1937.

Kangarina sp. Pl. 28, figs 8–10

FIGURED SPECIMEN. A carapace, OS 7983. Sample FCRM 2033, Lindi Creek, east shore; Upper Eocene. The only specimen.

DESCRIPTION. Carapace subtriangular in side view, with rounded anterior margin; posterior with a subcentral caudal process. Dorsal margin convex, posterodorsal concave, and ventral modified by the ventrolateral ridge. Ornament varies in different areas. Six ridges run back from the anterior end: two of them start above the middle and curve towards the dorsal margin; the other four start below the middle and tend to converge behind. Central dorsal area ornamented with transverse ridges; anterodorsal area reticulated with rounded fossae. The posteroventral and centroventral areas are reticulated with rounded fossae arranged longitudinally. No internal details visible.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

DIMENSIONS (µm).	L	H	W
Carapace OS 7983	335	175	165

REMARKS. Although the Tanzanian specimen has a shape which is comparable with that of some Tertiary *Kangarina* species, the ornament is completely different.

Family **XESTOLEBERIDIDAE** Sars, 1928

Genus ***UROLEBERIS*** Triebel, 1958

TYPE SPECIES. *Eocytheropteron parnensis* Apostolescu, 1955.

Uroleberis kyma sp. nov. Pl. 34, figs 10–12; Pl. 35, figs 1–3

1988 *Uroleberis kymus* Ahmad, MS; Neale & Singh: 89; pl. 1, figs 9, 13 ('*kynus*' on p. 87).

NAME. 'Swollen' (Greek), with reference to carapace.

DIAGNOSIS. A dimorphic species of *Uroleberis* with strongly convex dorsal margin and almost straight ventral margin.

HOLOTYPE. A female carapace, OS 8189. Four specimens, OS 8188, 8190–3, are paratypes. Sample FCRM 2033, Lindi Creek, east shore; Upper Eocene.

OTHER MATERIAL. Seven specimens from the same sample.

DESCRIPTION. Carapace ovate in female, ovate–elongate in male. Dorsal margin strongly convex, ventral margin almost straight. Anterior margin obliquely rounded below, posterior with laterally flattened caudal process slightly below mid-height. Left valve larger than right. Surface with concentrically arranged pits except along the ventral edge, where they are longitudinal. Eyesocket distinct from inside, with a reniform 'xestoleberis' spot behind it. Duplicature moderately wide; line of concrescence and inner margin separate throughout, forming an anterior vestibule. Marginal pore canals numerous, simple and straight, a few of them false. Four adductor muscle scars and a V-shaped frontal scar. Right valve hinge of crenulate terminal teeth, each with eight to ten denticles, connected by a narrow smooth groove. Left valve with corresponding terminal crenulate sockets connected by a narrow smooth ridge with a noticeable accommodation groove above.

DIMENSIONS (µm).	L	H	W
Holotype, female carapace OS 8189	485	385	360
Paratype, female carapace OS 8188	470	360	335
Paratype, male right valve (specimen lost) OS 8192	450	285	260

REMARKS. Sohn's genus and species indet. 4 from the Middle to Late Eocene of Pakistan (Sohn 1970: 68; pl. 4, figs 10–12) is most similar to *U. kyma*; however, the Tanzanian species has a less pitted surface and a straighter ventral margin. The present species is much smaller and has a better-developed caudal process than *Cythere ranikotiana* Latham, 1938, from Dandot, Pakistan. *Uroleberis armeniaca* Neale & Singh, 1985, is smaller and has a less arched dorsal margin than *Uroleberis kyma*.

***Uroleberis*?** sp. Pl. 31, figs 7–9

FIGURED SPECIMEN. A carapace, OS 8308. Sample FCRM 1989, Likonga bridge; Lower Miocene. The only specimen.

DESCRIPTION. Carapace rounded, subtriangular with greatest height two-fifths the length from posterior end. Greatest length below midline. Dorsal margin strongly arched, cardinal angles absent; ventral margin almost straight. Anterior and posterior margins both curve strongly towards the venter. Left valve overlaps right. Surface punctate centrally, becoming smooth peripherally; there are longitudinal ridges along the ventral margin.

DIMENSIONS (µm).	L	H	W
Carapace OS 8308	600	415	390

REMARKS. The present specimen shows some resemblance to *U. batei* Neale, 1975, but can easily be distinguished by its larger size and pitted surface.

Family **BYTHOCYTHERIDAE** Sars, 1866

Genus ***BYTHOCERATINA*** Hornibrook, 1952

TYPE SPECIES. *Bythoceratina mestayerae* Hornibrook, 1952.

Bythoceratina*? *asteria sp. nov. Pl. 27, fig. 5

NAME. 'Spotted with stars' (Greek); with reference to its ornamentation.

DIAGNOSIS. A species of *Bythoceratina*? with a very prominent eye-tubercle, and a ventrolateral swelling ending in a prominent sharp spine posteriorly.

HOLOTYPE. A left valve, OS 8116. Nine specimens, OS 8117–25, are paratypes. Sample FCRM 2010, stream south-west of Mtwero; Lower Miocene. No other material.

DESCRIPTION. Carapace quadrate in lateral view, tapering posteriorly, with the greatest height at the anterior cardinal angle. Anterior margin evenly rounded, posterior somewhat produced with straight posterodorsal margin. Dorsal and ventral margins almost straight. Marginal spines present at anterior and posterior margins, the posterior spines being

---

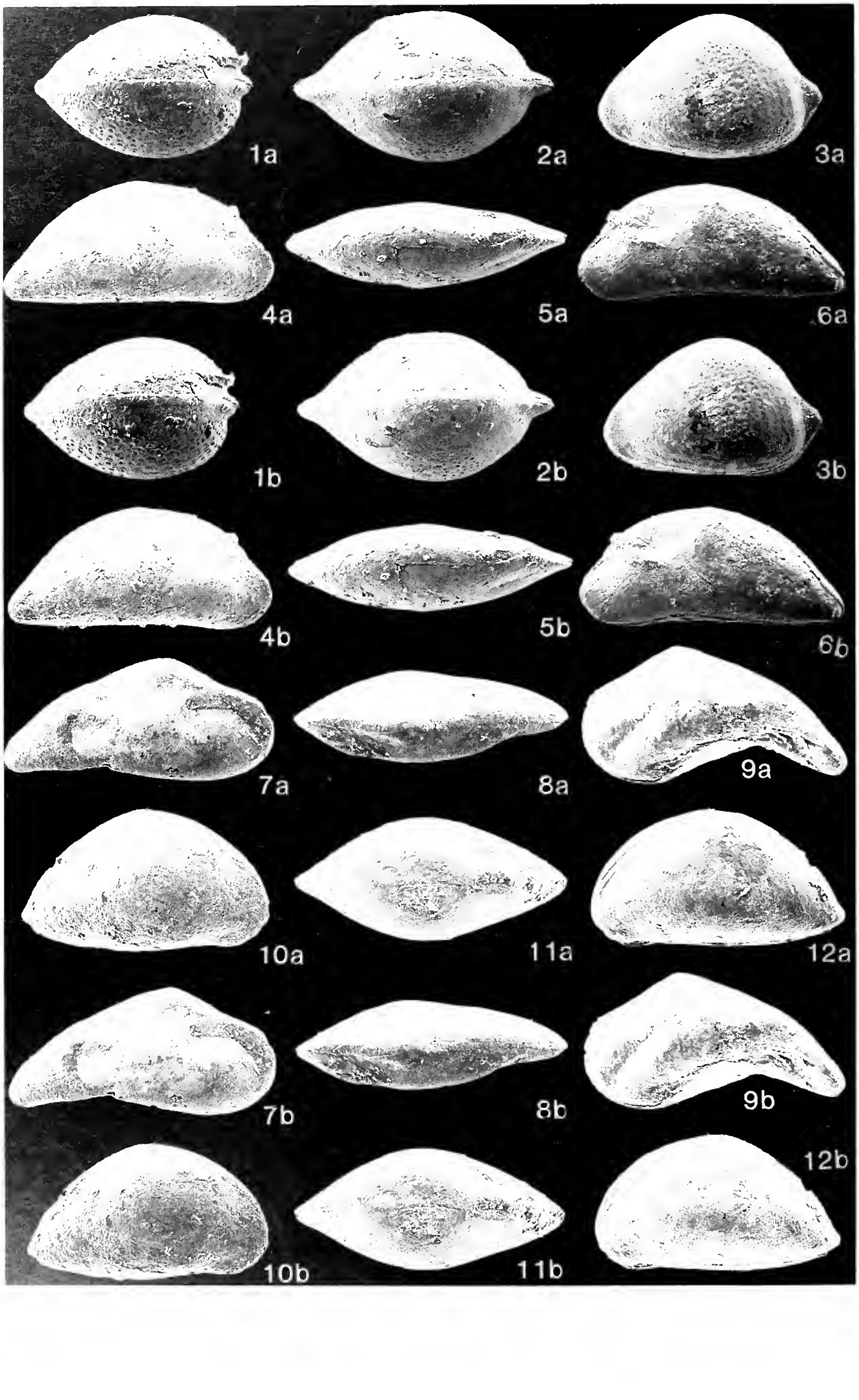
PLATE 34

Figs 1–3 *Cytheropteron epelyx* sp. nov. Figs 1, 2, **holotype**, right valve, OS 7849; 1, external lateral view, ×71; 2, ventral view, ×85. Fig. 3, paratype, right valve, OS 7850, internal oblique view, ×73.

Figs 4, 5 *Cytheropteron* sp. A. Carapace, OS 7846; 4, lateral view from left, ×96; 5, dorsal view, ×83.

Figs 6–9 *Cytheropteron* cf. *nipeensis* Bold, 1946. Figs 6–8, female carapace, OS 7962 (specimen lost); 6, lateral view from right, ×119; 7, lateral view from left, x119; 8, dorsal view, ×121. Fig. 9, male carapace, OS 7961, slightly ventrolateral view from left, ×111.

Figs 10–12 *Uroleberis kyma* sp. nov. Fig. 10, paratype, female carapace, OS 8188, lateral view from left, ×70; see also Pl. 35, fig. 1. Figs 11, 12, **holotype**, female carapace, OS 8189; 11, dorsal view, ×73; 12, lateral view from right, ×74.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
12b
10b
11b

strongly developed. A glassy round eye tubercle is present. External surface reticulate with trefoil-shaped ornamentation. Ventrolaterally each valve bears a hollow, sharp spine directed posteriorly. Median sulcus extremely shallow. Duplicature very narrow; radial pore canals very few and straight. Muscle scars not perfectly seen but probably the same as in *Bythoceratina*, consisting of five adductor scars arranged in a row. Right valve hinge consists of two elongate, crenulate terminal teeth with a crenulate median groove. Left valve has corresponding sockets and bar. The closure is additionally strengthened by a very weakly developed ventral snap-knob in the right valve and socket in the left valve.

DIMENSIONS (μm).	L	H	W
Holotype, left valve OS 8116	675	385	–

(Specimen cracked, too fragile to measure width.)

REMARKS. The distinct eye tubercle, snap-knob/socket mechanism, different hinge with crenulate terminal teeth, and slightly different shape distinguish this from other *Bythoceratina* species. However, the very narrow duplicature, suggesting that the specimens may be juveniles, and the imperfectly known muscle scars, do not justify the erection of a new genus. For the present this Tanzanian species is placed with doubt in *Bythoceratina*. *Leguminocythereis bisanensis* Okubo, 1975, agrees with this species in having similar spines directed posteriorly; internally, the marginal zone is equally narrow, and the terminal hinge elements are crenulate. However, the two can readily be distinguished. *Bythoceratina*? *asteria* is subrectangular in shape, has a well-developed eye tubercle, a shallow median sulcus and trefoil-shaped ornamentation, while *Leguminocythereis bisanensis* is more ovate, has an indistinct eye tubercle, no median sulcus, and rounded to subrectangular fossae.

***Bythoceratina* sp. A** Pl. 22, fig. 12

FIGURED SPECIMEN. A right valve, OS 8317. Sample FCRM 2010, stream south-west of Mtwero; Lower Miocene.

OTHER MATERIAL. Five single valves (none well preserved; all broken).

DESCRIPTION. Carapace oblong in lateral view with greatest height about one-quarter length from posterior end; greatest width in posterior half. Anterior margin narrowly rounded, posterior produced into a median caudal process. Dorsal and ventral margins run almost parallel for about one-third of the length and then diverge towards the posterior, the dorsal running almost straight and sloping upwards and the ventral strongly convex. Externally, the lateral surface has a shallow vertical sulcus at mid-length. The strong ventrolateral swelling terminates in a spine. Except for some sloping ridges on the swelling, the valve surface is smooth and punctate. Left valve hinge a crenulate median bar with weakly developed sockets at either end. Other internal features not clearly visible.

DIMENSIONS (μm).	L	H	W
Right valve OS 8317	575	345	280

REMARKS. All other species of *Bythoceratina* described so far have the caudal process in line with the hinge or just below it, but in *Bythoceratina* sp. A the caudal process is at mid-height. *Bythoceratina variabilis* Carbonnel 1969 is closely allied to *Bythoceratina* sp. A, but, besides the difference in the positions of the caudal processes, the two species have a different dorsal margin. The dorsal margin of Carbonnel's species is concave in the middle, whereas that of the Tanzanian species is concave in the anterior third.

Superfamily **CYPRIDACEA** Baird, 1846
Family **MACROCYPRIDIDAE** Müller, 1912

Genus ***MACROCYPRIS*** Brady, 1867

TYPE SPECIES. *Cythere minna* Baird, 1850.

***Macrocypris*? sp. A** Pl. 35, figs 10–12

FIGURED SPECIMEN. A carapace, OS 8306. Sample FCRM 1711, east flank of Kitulo Hill; Palaeocene. The only specimen.

DESCRIPTION. Carapace subtriangular in lateral view, with greatest height at about mid-length and valves tapering strongly posteriorly. Dorsal margin strongly curved in anterior half, sloping posteriorly; ventral margin almost straight. Anterior margin rounded, posterior acuminate. Right valve strongly overlaps left. No internal details visible.

DIMENSIONS (μm).	L	H	W
Carapace OS 8306	610	335	290

REMARKS. On the basis of shape this is not a typical *Macrocypris*, but no better assignment could be made in the circumstances so it is here doubtfully assigned to that genus. The only other described species which shows any resemblance to this specimen is the *Macrocypris*? sp. aff. *M.*? *dimorpha* Hazel & Holden, of Holden 1976; however the more acuminate posterior end of the Tanzanian specimen distinguishes it from Holden's species.

***Macrocypris* sp. B** Pl. 35, figs 4–6

FIGURED SPECIMEN. A carapace, OS 8307. Sample FCRM 1989, Likonga bridge; Lower Miocene. The only specimen.

DESCRIPTION. Carapace elongate, with dorsal margin arched; ventral margin slightly concave in the middle. Anterior end rounded, with some incurving below; posterior end narrowly

---

PLATE 35

Figs 1–3 *Uroleberis kyma* sp. nov. Fig. 1, paratype, female carapace, OS 8188, dorsal view, ×68; see also Pl. 34, fig. 10. Figs 2, 3, paratype, male carapace, OS 8192 (specimen lost); 2, dorsal view, ×98; 3, lateral view from left, ×84.

Figs 4–6 *Macrocypris* sp. B. Carapace, OS 8307; 4, lateral view from right, ×38; 5, dorsal view, ×40; 6, lateral view from left, ×38.

Figs 7–9 Genus A sp. Carapace, OS 7980; 7, lateral view from right, slightly oblique from dorsal, ×88; 8, dorsal view, ×90; 9, lateral view from left, slightly oblique from ventral, ×87.

Figs 10–12 *Macrocypris*? sp. A. Carapace, OS 8306; 10, lateral view from right, ×67; 11, dorsal view, ×75; 12, lateral view from left, ×67.

rounded. Left valve larger than right. No internal details visible.

DIMENSIONS (μm).	L	H	W
Carapace OS 8307	1170	545	370

REMARKS. *Macrocypris* sp. B strongly resembles *Macrocypris similis* Brady 1880, but the narrower anterior end and strongly concave ventral margin distinguish it from that species. This species differs from *M.*? sp. A in being more elongate and less triangular.

INCERTAE SEDIS

Genus A sp. Pl. 35, figs 7–9

FIGURED SPECIMEN. A carapace, OS 7980. Sample FCRM 1989, Likonga bridge; Lower Miocene.

OTHER MATERIAL. Five carapaces from the same locality and horizon.

DESCRIPTION. Anterior margin asymmetrically rounded, posterior end produced. Dorsal margin bent at mid-length, ventral margin concave. Right valve strongly overlaps left. No single valves found hence no internal details seen.

DIMENSIONS (μm).	L	H	W
Carapace OS 7980	510	270	170

REMARKS. Six specimens of this small new genus were found but naming it cannot be justified because of the absence of single valves. The specimens are unique in being very strongly bent at mid-length, behind which they narrow sharply. The smooth external surfaces and right-over-left overlap suggest that the genus is closely related to *Macrocypris*. *M. acuticaudata* Bate, *in* Bate & Bayliss 1969, from the Albian sediments of Kiwanga, Tanzania, is probably an ancestor of this Tertiary species.

Genus B sp. Pl. 11, figs 4–6

FIGURED SPECIMEN. A left valve, OS 8113. Sample FCRM 2010, stream south-west of Mtwero; Lower Miocene.

OTHER MATERIAL. Two specimens from the same locality and horizon. Also occurs in FCRM 2015.

DESCRIPTION. A species with concentrically arranged fossae; posteroventral complex consisting of three or four tubercles joined together. Anterior margin rounded, posterior subventrally produced, with a slightly concave posterodorsal margin; marginal spines present at both ends. Dorsal margin straight, ventral slightly concave; the two margins converge slightly behind. External surface reticulate with a few superimposed tubercles; eye tubercle present as an opaque spot. Muri thick and arranged concentrically, enclosing elongate fossae. Posteroventral complex conspicuously raised. Internally, duplicature fairly wide, with line of concrescence and inner margin slightly separated to give a narrow anterior vestibule. Selvage well developed at anterior and anteroventral margins. Marginal pore canals not visible; four adductor scars and a V-shaped frontal scar. Hinge holamphidont.

DIMENSIONS (μm).	L	H	W
Left valve OS 8113	570	330	160

REMARKS. While Genus B sp. is trachyleberine, it differs completely from *Trachyleberis* and cannot be placed in any of the other genera. It is here left under open nomenclature.

Genus C sp. Pl. 33, fig. 3

FIGURED SPECIMEN. A right valve, OS 8320. Sample FCRM 1738, South Mtwero; Lower Miocene.

OTHER MATERIAL. Two single valves from FCRM 1737 (OS 8319) and 1738.

DESCRIPTION. A species with reticulate surface, the muri being crimped. The right valve has a snap-knob which fits into the snap-socket of the left. Carapace subquadrate in lateral view, with greatest height near anterior cardinal angle. Anterior rounded, with marginal denticles; posterior margin truncated in upper half, rounded below and slightly produced. Dorsal and ventral margins straight and subparallel, slightly converging towards posterior end. Surface ornament consisting of a reticulate pattern of ridges, the muri being strongly crimped. Position of adductor muscle scars marked by an ovoid subcentral depression; eye tubercle elongate and not clearly developed. Three ridges are especially prominent; one, beginning near the posterior cardinal angle, runs forward parallel to the dorsal margin until it turns downwards about two-thirds of the way along and merges into other small ridges. The other two ridges are ventrolateral, the lower one running along the ventral margin and the upper one, about the same length and running parallel to it, ending in a small spine just in front of the posterior margin. Duplicature moderately wide. Line of concrescence and inner margin coincide throughout, so there is no vestibule. Selvage prominent along anterior and posterior margins, running at a little distance from outer margin. There is a unique snap-knob/socket mechanism; four small toothlike knobs in the right valve, behind the strong mid-ventral knob, correspond with sockets in the left. Marginal pore canals short, parallel and numerous, about 30 anteriorly and 8–9 posteriorly. Normal pore canals present all over the surface. Four adductor muscle scars, in a vertical row, with a fused V-shaped frontal scar which cannot be seen clearly. Hinge holamphidont; right valve has a smooth knob-like anterior tooth followed by a crenulate posterior tooth.

DIMENSIONS (μm).	L	H	W
Right valve OS 8320	545	335	160

REMARKS. Only one of the three specimens found is adult so the genus is left under open nomenclature. There is little in the literature with which this species can be compared. At the generic level, *Agulhasina* Dingle 1971 resembles it in outline and ornament, but has surface spines, no eye tubercle, and fewer marginal pore canals. *Australileberis* Dingle, 1976, agrees with this genus in some details but has different ornament. *Stigmatocythere* Siddiqui, 1971, has similar dorsal and ventral ridges and the hinge and marginal pore canals are similar also, but the frontal scar in *Stigmatocythere* is oval. The surface ornament is also different, the fossae in *Stigmatocythere* being subrectangular and shallow, while those of the new genus are trifoliate, crimped and deeper. The new genus differs from all the others in its snap-knob/socket mechanism. Palaeoecologically, Genus C has only been found in silty shaly clays, and is associated with deeper water genera such as *Krithe* and *Parakrithe*.

PALAEOECOLOGY

When the ecology at the species level is unknown, certain limitations are placed upon the interpretation of palaeocology. Based on the generally accepted habitat of certain genera, however, it has been possible to reach conclusions which are given below. We make the following assumptions.

(1) Certain genera with a strongly reticulate or ornamented lateral surface, strongly calcified carapace and well-developed eye tubercle inhabit shallow marine water. These genera are *Aurila*, *Quadracythere*, *Haughtonileberis*, *Leguminocythereis*, *Stigmatocythere*, *Cytheropteron* (thick shelled), *Callistocythere*, *Costa*, *Hermanites* and *Hemicytherura*.

(2) A second group of shallow-water marine genera is almost confined to tropical and subtropical waters, only living in or around reefs. This group includes *Triebelina*, *Paranesidea* and *Loxoconcha* (*Loxocorniculum*). The genera *Cytherelloidea*, *Uroleberis*, *Kangarina* and *Triebelina* may also be taken as indices for warm temperatures, above the 10°C isocryme according to Sohn (1964) for *Cytherelloidea*, and about 20°–25°C for all four genera according to McKenzie (1974).

(3) A third group of genera is often regarded as indicating moderately deep marine waters (>75 m). This includes *Krithe*, *Parakrithe*, *Paijenborchella* and *Henryhowella*.

Based on these assumptions, the following grouping of sample localities is suggested:

(1) Shallow water: FCRM 2010.
(2) Shallow water but indicating an approach to a reef environment: FCRM 1566, 1574, 1575, 1576, 1578, 1627, 1628, 1661, 1689, and 1692.
(3) Deep water: FCRM 1737, 1738; and less deep, FCRM 1742, 1745.
(4) Mixed fauna: FCRM 2033, 2034; these have a mixed fauna mostly indicating a shallow reef environment but with some deeper water incursions. For other samples nothing conclusive can be said except that they contain mostly shallow-water genera.

Ostracods are sensitive to many factors in the environment and consideration of various ecological parameters suggests that the Lindi fauna comes from waters with the following characteristics:

1. *Depth*: Apparently shallow water with some deep water incursion in Lower Miocene (FCRM 1737, 1738).
2. *Oxygen*: Generally well oxygenated. As the water was warm it would have held less oxygen, but no reducing environments are evident and none of the ostracods are pyritized. The ostracods are generally robust, indicating fairly high energy waters; this may also account for the lack of pyritization of the fauna.
3. *Salinity*: All the Lindi ostracod genera which are still living at the present time are now restricted to water with salinities in the range of 30 to 40%; Lindi ostracods probably lived in waters of this salinity range.
4. *Clarity:* Well-developed eye tubercles suggest that the waters were extremely clear. The deep-water genus *Krithe*, with its numerous species, is blind but its close relative *Ommatokrithe*, which occurs here, has eye tubercles and was separated from *Krithe* for that very reason.
5. *Temperature*: The size of these ostracods is generally small which suggests that waters were warm, temperatures at times reaching 20°–25°C.

An attempt was made to deduce the comparative rate of sedimentation on the basis of the ratio of single valves to carapaces. Pokorný (1964*b*) had observed that, in the case of *Karsteneis karsteni* (Reuss) and *Cythereis longaeva* Pokorný, the percentage of closed carapaces was higher in regions of rapid sedimentation. Oertli (1971), working on abundant ostracod material, concluded that in conditions of slow sedimentation the carapace opens because of bacterial decomposition of muscles and ligaments, but in rapid sedimentation conditions the dead ostracods quickly sink by their own weight far enough into the sediment for the valves not to be separated. Comparing the ostracods from the surface samples of Lindi with those from borehole samples of Lamu (Kenya), where the rate of sedimentation was almost the same (Kent, *in* Kent *et al.* 1971), the percentage of closed carapaces was found to be higher in the Lamu samples than in those from Lindi. It was also found that the ratio depended on the genera or species concerned. For example, in the Lindi area, species of *Costa*, *Paracytheridea* and *Tanzanicythere* were mostly found as single valves, but species of *Xestoleberis*, *Clithrocytheridea*?, *Phlyctocythere*, and *Incongruellina* were mostly present as entire carapaces, the two groups occurring together.

Based on the ten most productive samples from the three periods, we deduced that the maximum rate of sedimentation occurred during the Lower Miocene; the rate was slightly less for the Eocene. For the Oligocene, however, it was about half of the maximum deduced for the Lower Miocene. These results corroborate the comparative rates of sedimentation calculated by Kent *et al.* (1971: 89); a comparative chart is given in Fig. 6, p. 184. It is therefore concluded that during the Upper Eocene the water was mostly shallow with some deeper water incursions at times, and the rate of sedimentation was faster than in the overlying Oligocene. During the Oligocene there was a general regression, the water becoming shallower but with a greater development of reefs and much slower sedimentation. During the Lower Miocene a transgression occurred, the water being shallow near reefs but deeper in other places, and with a greater rate of sedimentation than previously. The greater diversity of the fauna in Lower Miocene times supports this speculation.

FAUNAL ASSEMBLAGES

During the Upper Eocene, *Paijenborchella*, *Hermanites*, *Uroleberis*, *Clithrocytheridea*?, *Quadracythere*, *Stigmatocythere*, *Triebelina*, *Paranesidea*, *Cytherella*, *Bairdia* and *Cytherelloidea* became well established. Some of the *Cytherelloidea* species are distinctive in having the selvage of the left valve grown out behind the anterior part of the hinge to form a tooth. Most of these genera continued to exist during the Oligocene, only *Cytherelloidea* and *Clithrocytheridea*? being absent in sediments younger than Eocene. *Paijenborchella* disappeared for a while, to reappear in the Lower Miocene. A number of new genera appeared during this time, including *Loxoconcha* (*Loxocorniculum*), *Leguminocythereis*, *Haughtonileberis*, *Crenaleya*, *Carinocythereis* and *Semicytherura*. *Paracytheridea* became rare.

It appears that *Aitkenicythere* Bate (1976), which existed in Tanzania during the Bajocian–Tithonian (Jurassic), may be a distant ancestor of *Haughtonileberis*, which appeared during the Campanian in South Africa and during the Oligocene at

Table 1 Range table of ostracod species. This table also includes data from the BP ostracod collection kept at Sunbury-on-Thames; see p. 264. • < 10 specimens. ● 11–20 specimens. ⬤ > 20 specimens.

	LOWER MIOCENE												?L.–M. OLIGOCENE					UPPER EOCENE						
	ASSEMBLAGE ZONES																							
	Cytherella mediocalva												*Leguminocythereis dinglei*					*Cytherella lindiensis*						
	FCRM SAMPLE NUMBER																							
OSTRACODS	1566	1661	1989	2010	2014	2015	2016	1746	1745	1742	1738	1737	1574	1575	1576	1578	1628	1689	1692	2033	2034	2045	2046	1711
Cytherella mediocalva	⬤		⬤	●		⬤		⬤	⬤	●														
Ambocythere sp.	•																							
Bradleya ? sp. A	•																							
Callistocythere jugosa A	●																							
Falsocythere maccagnoi	•																							
Procythereis radiata	•																							
Caudites sp.	•	•	•																					
Leptocythere fastigata	•		•																					
Quadracythere distenta	•		•																					
Hemicytherura subulata	•		•			•																		
Loxoconcha (Loxocorniculum) tricornis	•				•	•	•																	
Krithe burdigalia			•																					
Aurila concentrica A	•							•																
Paijenborchella cf. *iocosa*	•		•								•													
Hermanites mongoensis	•			⬤					•															
Loxoconcha (L.) mbanjaensis	•	•	•	•	●	●	•	●	⬤	•		•												
Anterocythere sp. B	•		•		•	•			•	•	•	•												
Tanella sp. A		•																						
Tanella sp. B		•																						
Macrocypris sp. B			•																					
Phlyctocythere reniformis			●						•															
Quadracythere kenti			•																					
Semicytherura opeata			•																					
Uroleberis ? sp.			•																					
Occultocythereis africana			•	•																				
Trachyleberidea ? *cirrata*				•										•			•							
Trachyleberis duplex				•																				
Gujaratella ? *tanzaniensis*				•																				
Bythoceratina ? *asteria*				●																				
Bythoceratina sp. A				•																				
Semicytherura emphysema			•	•								•												
Caudites cf. *rosaliensis*				•																				
Procythereis aligera				•																				
Quadracythere trijugis				•										•		•								
Urocythereis salebrosa				•																				
Henryhowella sentosa				•			•																	
Bairdia cf. *attenuata*			•																					
Costa trudis			•	•	⬤	•	•		•															
Incongruellina tonsa				●				•	•															
Tanzanicythere pterota				●	●	●					•													
Bairdia cf. *schulzi*			•			•			•	•										•				
Genus B sp.				•		•																		
Crenaleya sp. A					•																			
Paijenborchella quasimalaiensis dilata					•																			
Idiocythere sp. A		•						•																
Ruggieria furcilla					⬤	•		•	•															
Loxoconcha (Palmoconcha) pinguis								•									•							
Aurila concentrica B	•															•								
Paijenborchella disadunca C									•	•	•													
Paijenborchella disadunca			•							•														
Paijenborchella disadunca A											•													
Parakrithe cicatricosa			•		•		•			•	•	•												
Ommatokrithe prolata											•	●												
Krithe liebaui										•	●	⬤												
Crenaleya sp.																•								

Table 1 Range table of ostracod species. This table also includes data from the BP ostracod collection kept at Sunbury-on-Thames; see p. 264. • < 10 specimens. ● 11–20 specimens. ⬤ > 20 specimens.

	LOWER MIOCENE												?L.-M. OLIGOCENE					UPPER EOCENE						
	ASSEMBLAGE ZONES																							
	Cytherella mediocalva												*Leguminocythereis dinglei*					*Cytherella lindiensis*						
	FCRM SAMPLE NUMBER																							
OSTRACODS	1566	1661	1989	2010	2014	2015	2016	1746	1745	1742	1738	1737	1574	1575	1576	1578	1628	1689	1692	2033	2034	2045	2046	1711
Genus A sp.			•																					
Genus C sp.											•	•												
Callistocythere jugosa	•		•											•										
Buntonia sp.									•	•							•							
Paracytheridea culmen	•		•	•	●									•	•									
Paracytheridea culmen A				•																				
Aurila concentrica	⬤		•	⬤		•		•	•			•	•	•	•	•		•	•					
Loxoconcha (Loxocorniculum) postnodosa	•		•										●	●	⬤	•	●							
Stigmatocythere bornhardti								•	•	•				•		•								
Urocythereis ? *apolegma*				•											●	•								
Leguminocythereis dinglei													●	⬤	•	•								
Loxoconcha cf. *longispina*					•		•								●	●								
Loxoconcha postnodosa B														•								•		
Cytheropteron epelyx													•	•	•	⬤								
Haughtonileberis rastapuriensis													•	•	•	•								
Quadracythere subquadra													•	•	●	⬤								
Loxoconcha postnodosa A														•										
Crenaleya tuberis														•	•	●								
Acanthocythereis postcornis														•	•	•								
Semicytherura sp. A														•										
Leptocythere amoena														•	•	•								
Carinocythereis sp.														•	•	•	•							
Quadracythere vanga																•								
Haughtonileberis radiata															•	•								
Quadracythere ? *acuta*																•				•				
Hermanites mongoensis A																•								
Bradleya ? sp. B																•								
Paijenborchella disadunca B																	•	•	•					
Stigmatocythere intexta									•					•			•					•		
Quadracythere arcana cornigera	•		•		•			•	•					•		•				●				
Bairdia amygdaloides oblongata														•		•	•			•				•
Cytherella lindiensis																				⬤	●	•		•
Paracytheridea anapetes		•	•	•	•								•			•	•			●	●			
Triebelina howei															•	•								
Hermanites carchesium																				•				
Hermanites percultus																				•				
Clithrocytheridea ? *semiluna*																				•		•		
Cytherelloidea gemellata																				•				•
Cytherelloidea patagiata																				•				
Cytherelloidea sp. B																				•				
Cytheropteron cf. *nipeensis*																				•				
Cytheropteron sp. A																				•				
Kangarina sp.																				•				
Paijenborchella disadunca D																				•				
Costa ? *hullina*																				•	•			
Loxoconcha (Myrena) loculus																				●	•	•	•	
Paijenborchella quasimalaiensis																				•	•			
Paranesidea fracticorallicola																				•				
Paranesidea nigrescens																				•				
Paranesidea cf. *fortificata*			•																	•			•	
Quadracythere sp. A																				•				
Rostrocytheridea ? sp.																				•				
Uroleberis kyma																				•				
Cytherelloidea sp. A																					•			
Krithe medioelata																					•			
Paranesidea sp. A																								•
Macrocypris ? sp. A																								•

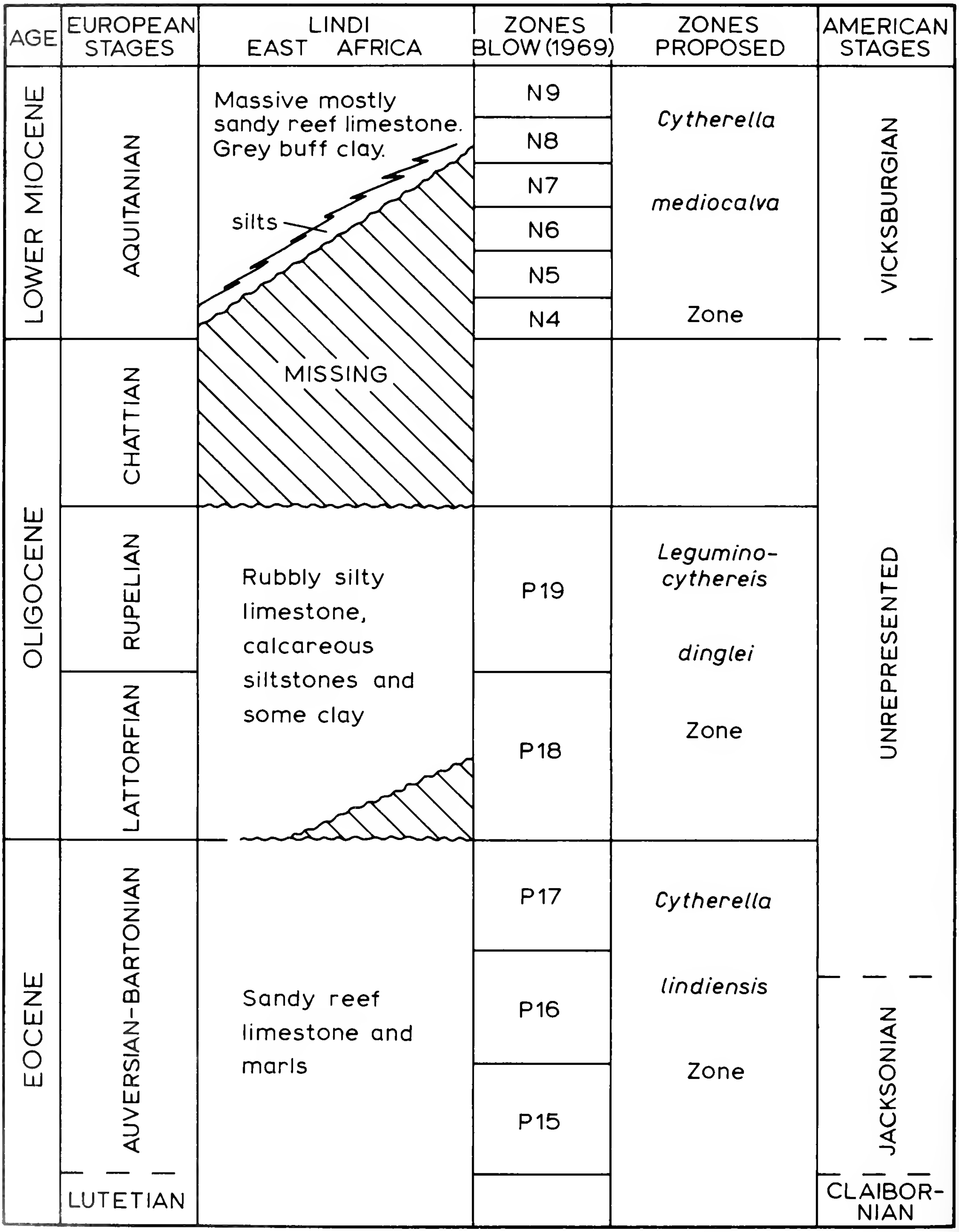


Fig. 10 Correlation of proposed ostracod biozones with those of Blow (1969).

Lindi; it is not known if it existed in Tanzania during the intervening time.

The Lower Miocene was a time of strong transgression, resulting in a very diverse fauna. New species appeared in the genera *Ommatokrithe*, *Bythoceratina*, *Ruggieria*, *Costa*, *Hemicytherura*, *Phlyctocythere*, *Tanzanicythere*, *Incongruellina* and *Xestoleberis*. Species of *Cytherella* and *Aurila* became abundant; *Paijenborchella* and *Krithe*, which first appeared in the Eocene and disappeared in the Oligocene, became re-established.

OSTRACOD BIOZONES

Planktonic foraminiferal biozones of the Lindi area and their relationships elsewhere in the world have been established by Eames *et al.* (1962) and Blow (1969). The ostracod zones suggested here are local Assemblage Zones; their correlation with Blow's Zones are shown in Fig. 10.

(1) *Cytherella lindiensis* Zone (= Upper Eocene). Corresponding roughly with Blow's Zones P15 to P17, this zone is defined by the abundance of *Cytherella lindiensis* sp. nov. and by the presence of the following species. (The species marked * are also known to occur elsewhere):

Cytherelloidea gamellata sp. nov.
Cytherelloidea patagiata sp. nov.
Clithrocytheridea? *semiluna* sp. nov.
Hermanites carchesium sp. nov.
Hermanites percultus sp. nov.
Krithe medioelata sp. nov.
Loxoconcha (*Myrena*) *loculus* sp. nov.
Paijenborchella (Eopaijenborchella) quasimalaiensis sp. nov.
Uroleberis kyma sp. nov.
* *Paracytheridea anapetes* Ahmad, 1977
* *Paranesidea* cf. *reticulopunctata* (Benson)
* *Stigmatocythere intexta* sp. nov.

The type locality for the *Cytherella lindiensis* Zone is the Lindi Creek, east shore, Tanzania, at FCRM 2033.

(2) *Leguminocythereis dinglei* Zone (= ?Lower to Middle Oligocene). This zone corresponds with Blow's Zones P18 and P19 and is characterized by the absolute range of the nominate taxon and by the presence of the following species:

Crenaleya tuberis gen. et sp. nov.
Cytheropteron epelyx sp. nov.
Haughtonileberis rastapuriensis sp. nov.
Hermanites mongoensis, Morphotype A
Leptocythere amoena sp. nov.
Quadracythere subquadra Siddiqui, 1971
Quadracythere vanga sp. nov.
* *Acanthocythereis postcornis* (Siddiqui, 1971)
* *Loxoconcha* (*Loxocorniculum*) cf. *longispina* Keij, 1953
* *Loxoconcha* (*Loxocorniculum*) *postnodosa* sp. nov.
* *Triebelina howei* (Stephenson)

There is an absence of such deeper-water genera as *Krithe* and *Ommatokrithe*.

The type locality for this zone is the shore south-west of Ras Tapuri, Tanzania, at FCRM 1576, which is also jointly the type locality for the *Globigerina oligocaenica* Zone of Blow & Banner (*in* Eames *et al.* 1962).

(3) *Cytherella mediocalva* Zone (= Lower Miocene). This zone corresponds roughly with Blow's Zones N4 to N9 and is defined by the presence of *Cytherella mediocalva* sp. nov., which is limited in range to this zone, and by the presence of the following species:

Bythoceratina? *asteria* sp. nov.
Tanzanicythere pterota (Ahmad, 1977)
Costa trudis Ahmad, 1977
Hemicytherura subulata sp. nov.
Hermanites mongoensis sp. nov.
Incongruellina tonsa sp. nov.
Krithe liebaui sp. nov.
Occultocythereis africana sp. nov.
Leptocythere fastigata sp. nov.
Loxoconcha (*Loxoconcha*) *mbanjaensis* sp. nov.
Loxoconcha (*Loxocorniculum*) *tricornis* sp. nov.
Ommatokrithe prolata Ahmad, 1977
Phlyctocythere reniformis sp. nov.
Paijenborchella (*Eopaijenborchella*) *disadunca* sp. nov.
Ruggieria (*Ruggieria*) *furcilla* sp. nov.
* *Aurila concentrica* sp. nov.
* *Callistocythere jugosa* sp. nov.
* *Paracytheridea culmen* sp. nov.

The type locality is the Mongo Stream, Lindi, at FCRM 1566.

CONCLUSIONS

The Tanzanian fauna forms part of the West Indian Ocean Ostracod Province. The fauna is linked to that of Pakistan by the presence of *Quadracythere subquadra*, *Q. arcana*, *Acanthocythereis postcornis*, and *Stigmatocythere bornhardti* (closely related to *S. obliqua* from Pakistan). Many more species common to the two regions may be found when the younger (Oligocene–Miocene) Pakistan fauna is fully documented. The Lindi fauna is related to the South African fauna by the presence of *Occultocythereis africana* (=Gen. Indet. 5, sp. 1 of Dingle, 1976), *Haughtonileberis radiata*, *H. rastapuriensis* (very similar to *H. fissilis*), and a number of other species. The Malagasy ostracod fauna is not well known, but the presence of the genus *Tanzanicythere*, so far found only in these two regions, suggests that they have close connections.

McKenzie's (1973: 479) suggestion that 'the Caribbean, Mediterranean, Indo–West Pacific and Australasian marine provinces are the spoor of Tethys' is supported by the Tanzanian ostracod fauna, which is linked to the Caribbean by the presence of *Triebelina howei* (Stephenson), and to Nicaragua by *Anterocythere* sp. B of Swain & Gilby. The presence of *Paijenborchella* (*Eopaijenborchella*) *quasimalaiensis* sp. nov. (closely related to *P. malaiensis* Kingma from Indonesia, and to *P. cymbula* Ruggieri from the Mediterranean), indicates a link, albeit rather tenuous, with all these areas. Similarly, the presence of *Quadracythere trijugis* Holden suggests a link with the Pacific. The biogeographv of these species supports Keij's (1976) view that Tertiary to Recent tropical, shallow marine ostracods show a wide geographical distribution. No links, however, have been found with the West African, South American or Atlantic ostracod faunas. Palaeontologically, too, the relationships are closer with faunas of the southern hemisphere; for example for south-eastern Australia and New Zealand high temperatures have been documented for the Upper Eocene and Oligo-Miocene (Gill 1968, Jenkins 1968 and McKenzie 1973). During this time the absence of any cold water taxa combined with the small size of ostracods, a factor normally attributed to tropical environments, suggests warm water temperatures for the Lindi area. If one accepts the suggestion by McKenzie (1973) that the presence of *Cytherelloidea* and *Uroleberis* indicates 20°–25° C, then the temperature during the Upper Eocene was at times as high as that. The strengthening of carapace closure by a snap-knob/socket mechanism in species such as *Bythoceratina*? *asteria*, *Trachyleberidea*? *cirrata*, *Crenaleya tuberis* and Genus C sp. suggests that the water may have been turbulent.

Another interesting feature of this fauna is the appearance of eye tubercles in genera which usually lack them, e.g. *Bythoceratina*, *Idiocythere* and *Ommatokrithe* (closely related to *Krithe*). This may indicate unusually clear water, which indeed occurs around tropical reefs.

Eames *et al.* (1962) mention the presence of laterally discontinuous reef-like conditions for only short periods during the Upper Eocene and Oligocene, and more widespread reef conditions during the Lower Miocene. The presence of *Triebelina*, *Paranesidea* and *Loxoconcha* (*Loxocorniculum*) is often associated with reef conditions. The presence of *Krithe* and *Parakrithe* is often associated with deep water; they occur in samples FCRM 1737 and 1738, but no other evidence of deep water sediments has yet been found.

As in some other areas changes in the ostracod distribution closely follow regional geological events. The Mid-Oligocene regression resulted in a great number of specimens and species, whilst the Lower Miocene transgression resulted in a very diverse fauna. This corroborates Kent's (1974) chronology of East African tectonic events (Fig. 5c, p. 183). Moreover, the rates of sedimentation calculated on valve/carapace ratios also show some agreement with Kent's (*in* Kent *et al.* 1971) estimates.

In summary, it is suggested that the Lindi Tertiary ostracod fauna may be regarded as indicative of a warm, clear-water deposit laid down in a shallow shelf area, whose depth may have been mostly less than 50 m but sometimes deepened to well over 75 m, and whose minimum temperature was not less than 10° C. During the Oligocene there was a general regression which was followed by a widespread Miocene transgression.

Three ostracod biozones corresponding roughly to well-established Planktonic Foraminifera zones occur (Fig. 10, p. 262).

FCRM SAMPLE DATA

The sample prefix FCRM refers to material collected by the BP-Shell geologist F.C.R. Martin in 1951–57 (Eames *et al.* 1962: 62); the locality and lithological information was given by him in a private report to BP-Shell in 1957. See Fig. 3, p. 181.

More than one-third of the samples were provided as washed residues; from some others only the ostracods which had been picked out and placed in the BP Research Centre, Sunbury-on-Thames, were available. Consequently most of the sample descriptions are based on the original accounts by Martin and other BP-Shell geologists. Wherever enough material was available, thin sections were made and studied and the descriptions amended where necessary.

Sample	Location	Lithology	Age
FCRM 1566	Mongo Stream, Lindi	Sandy detrital fossiliferous limestone	Lower Miocene
FCRM 1574	Shore south-west of Ras Tapuri, *c.* 6 km north of Lindi	Grey-buff silty sandstone	Mid-Oligocene
FCRM 1575	Shore south-west of Ras Tapuri, as above	Grey calcareous siltstone with quartz grains; some bivalve & echinoid remains; abundant orbitoids	Mid-Oligocene
FCRM 1576	Shore south-west of Ras Tapuri, about 18 m north of FCRM 1575	Buff-grey biomicrite with abundant orbitoids	Mid-Oligocene
FCRM 1578	Shore south-west of Ras Tapuri, as above	Hard sandy limestones and grey-buff silty sands	Mid-Oligocene
FCRM 1627	Kitunda Jetty road, near bottom of slope	Green-grey shaley clays	Mid-Oligocene
FCRM 1628	Kitunda Jetty road, *c.* 3 m above FCRM 1627	Shelly calcareous sand & orbitoidal clay with thin ribs of cemented orbitoidal rock	Mid-Oligocene
FCRM 1644 & 1645	North end of Kitunda slope, just above shore level	Grey-green clays with interbedded thin marly limestones	Upper Eocene
FCRM 1647 & 1648	Kitunda slope, from *c.* 3 m to *c.* 15 m above shore level	Grey-green silty clays with some thin-bedded marly foraminiferal limestones	Upper Eocene
FCRM 1661	Near top of old garnet mine, north Lindi	Dark grey-brown gypseous clays	Lower Miocene
FCRM 1689	Old quarry above road, east of Mchole salt works	Dark buff-grey silty clays	Upper Eocene
FCRM 1692	Old quarry below road, east of Mchole salt works	Dark grey-brown clays	Upper Eocene
FCRM 1711	Stream south-west of upper Wireless Station, Kitulo Hill	Massive rotten soft marly limestone; micrite	Palaeocene?

Sample	Location	Lithology	Age
FCRM 1737 & 1738	South Mtwero, in sisal waste gully	Bedded grey silty shaly clays with thin modular clay-stones	Lower Miocene
FCRM 1742	Mbanja River	Buff-grey silty foraminiferal clay	Lower Miocene
FCRM 1745 & 1746	Mbanja River, upstream of FCRM 1742	Fine-grained limestone	Lower Miocene
FCRM 1792	Beside Mingoya Road, about 1g miles from the Lindi bridge	Buff-grey, slightly gypsiferous clay	Upper Eocene
FCRM 1963	Lindi–Mingoyo road, south-west of Lindi (not covered by Fig. 3)	Soft buff-grey sands	?
FCRM 1964	Kitunda slopes	Dark grey, brown-stained shaly clay	Upper Eocene
FCRM 1981	Kikwetu factory refuse gully	Thin bedded micritic limestone with a little quartz	Lower Miocene
FCRM 1989	On west side of road bridge, 9° 49.4′S, 39° 43.8′E, south of Likonga estate	Foraminiferal lime-stone, about 95% carbonate material	Lower Miocene
FCRM 2010	Cliff on left bank of stream south-west of Mtwero Estate	Buff-grey highly fossiliferous carbon-ate muddy sands	Lower Miocene
FCRM 2014 –2016	Location given as 'various points up-stream of FCRM 2010'	Buff-grey silty nodular shaly clays	Lower Miocene
FCRM 2033	East shore of Lindi Creek	Brown silty clay with foraminifera and shell fragments	Upper Eocene
FCRM 2034	East shore of Lindi Creek, about 10 m south of FCRM 2033	Grey buff-stained clay	Upper Eocene
FCRM 2045 & 2046	Lindi–Mingoyo road, above 2g km south of Lindi	Fragmented buff-grey clay (reworked?)	Upper Eocene

ACKNOWLEDGEMENTS. We wish to thank Dr R. H. Bate, formerly of the British Museum (Natural History), for providing the samples which formed the basis of this study, and Dr C. G. Adams, Dr F. T. Banner and Mr R. L. Hodgkinson for access to material in the British Museum (Natural History). Dr W. J. Clarke, formerly of the British Petroleum Company, Sunbury-on-Thames, and Dr D. A. L. Jenkins, BP Exploration Co. Ltd., supplied various maps and allowed the examination of the BP ostracod collection and private reports. We are also grateful to Professor W. A. van den Bold for the loan of a paratype of *Parakrithe robusta* and Dr J. E. Whittaker for measurements of the widths of some specimens; Dr Whittaker also compiled the systematic index. Finally we would like to record our appreciation of the editorial help afforded by Mrs U. M. Grigg, Halifax, Nova Scotia, and Mr D. L. F. Sealy, British Museum (Natural History), and the technical assistance of Mr J. Garner, Mr P. McSherry and Mr T. Sinclair, of the University of Hull.

REFERENCES

Ahmad, M. 1977*a–e*. On *Paracytheridea anapetes* Ahmad sp. nov. *Stereo-Atlas of Ostracod Shells*, Leicester, 4 (7): 41–44 (1977*a*). On *Cladarocythere pterota* Ahmad gen. et sp. nov. *Ibid.* 4 (8): 45–48 (1977*b*). On *Costa trudis* Ahmad sp. nov. *Ibid.* 4 (21): 127–130 (1977c). On *Ommatokrithe prolata* Ahmad gen. et sp. nov. *Ibid.* 4 (22): 131–134 (1977*d*). On *Tanzanicythere* Ahmad nom. nov. *Ibid.* 4 (27): 153 (1977*e*).

Alexander, C. I. 1927. The stratigraphic range of the Cretaceous ostracod *Bairdia subdeltoidea* and its allies. *J. Paleont.*, Chicago, **1**: 29–33.

—— 1929. Ostracoda of the Cretaceous of North Texas. *Bull. Univ. Texas*, Austin, **2907**: 1–137.

—— 1934. Ostracoda of the Midway (Eocene) of Texas. *J. Paleont.*, Menasha, **8**: 206–237.

Al-Sheikhly, S. S. J. 1982. Some new species of the genus *Occultocythereis* H. V. Howe, 1951 (Trachyleberidinae, Ostracoda) from the Maastrichtian–Eocene of north and western Iraq. *J. geol. Soc. Iraq*, Baghdad, **15**: 69–83.

Anderson, F. W. 1964. A new species of the Ostracod Genus *Paijenborchella* Kingma. *Geol. Mag.*, Hertford, **101**: 40–43.

Apostolescu, V. 1955. Description de quelques Ostracodes du Lutétien du Bassin de Paris. *Cah. géol. Thoiry*, **28–29**: 241–279.

Babinot, J. F. 1981. Ostracodes du Crétacé supérieur – Cenozoïque de Côte d'Ivoire. *Cah. Micropaléont.*, Paris, **1981** (2): 53–70, 4 pls.

Baird, W. 1837–38. The Natural History of the British Entomostraca. *Mag. Zool. Bot.*, Edinburgh, London & Dublin, **1**: 35–41, 309–333, 514–526; **2**: 132–144, 400–412.

—— 1846. Arrangement of the British Entomostraca, with a List of Species, particularly noticing those which have as yet been discovered within the bounds of the Club. *Hist. Berwicksh. Nat. Club*, **2** (13): 145–158.

—— 1850. *The Natural History of the British Entomostraca.* 364 pp (ostracods 138–182). London (Ray Society).

Barbeito-Gonzales, P. J. 1971. Die Ostracoden des Küstenbereiche von Naxos (Griechenland) und ihre Lebensbereiche. *Mitt. hamburg. Zool. Mus. Inst.*, Hamburg, **67**: 255–326.

Bate, R. H. 1969. *In* Bate, R. H. & Bayliss, D. D., An outline account of the Cretaceous and Tertiary Foraminifera and of the Cretaceous ostracods of Tanzania. *Proc. 3rd African micropalaeont. Colloquium*, Cairo: 113–164.

—— 1972. Upper Cretaceous Ostracoda from the Carnarvon Basin, Western Australia. *Spec. Pap. Palaeont.*, London, **10**: 1–85.

—— 1975. Ostacods from Callovian to Tithonian sediments of Tanzania, East Africa. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **26** (5): 161–223.

—— 1976. New name for *Rhadinocythere* Bate, 1975. *Geol. Mag.*, Cambridge, **113**: 489.

Benson, R. H. 1972. The *Bradleya* problem, with descriptions of two new psychrospheric ostracode genera, *Agrenocythere* and *Poseidonamicus* (Ostracoda: Crustacea). *Smithson. Contr. Paleobiol.*, Washington, **12**: 1–138.

—— **R. H., Berdan, J. M., Bold, W. A. van den, Hanai, T., Hessland, I., Howe, H. V., Kesling, R. V., Levinson, S. A., Reyment, R. A., Moore, R. C., Scott, H. W., Shaver, R. H., Sohn, I. G., Stover, L. E., Swain, F. M., Sylvester-Bradley, P. C. & Wainwright, J.** 1961. Arthropoda 3. Crustacea, Ostracoda. *In* Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology*, **Q**. 422 pp., textfigures. Kansas.

—— **& Coleman, G. L.** 1963. Recent marine ostracodes from the eastern Gulf of Mexico. *Paleont. Contr. Univ. Kansas*, Lawrence, Arthropoda Art. **2**: 1–52, 8 pls.

Blow, W. H. 1969. *In* Brönnimann, P. & Renz, H. H. (eds), Planktonic Foraminiferal Biostratigraphy. *Proc. First International Conference on Planktonic Microfossils*, Geneva, **1**: 1–442.

Bold, W. A. van den 1946. *Contribution to the study of Ostracoda, with special reference to the Tertiary and Cretaceous micro-fauna of the Caribbean Region.* 167 pp. Amsterdam (Reprinted 1970).

—— 1958*a*. Ostracoda of the Brasso Formation of Trinidad. *Micropaleontology*, New York, **4**: 391–418.

—— 1958*b*. *Ambocythere*, a new genus of Ostracoda. *Ann. Mag. nat. Hist.*, London, (12) **10** (119): 801–813.

—— 1965. Middle Tertiary Ostracoda from northwestern Puerto Rico. *Micropaleontology*, New York, **11**: 381–414.

—— 1966. Ostracoda of the Pozon Section, Falcon, Venezuela. *J. Paleont.*, Tulsa, **40** (1): 177–185.

—— 1974. Ornate Bairdiidae in the Caribbean. *Geosci. Man*, Baton Rouge, **6**: 29–40.

Bonaduce, G., Ciampo, G. & Masoli, M. 1975. Distribution of Ostracoda in the Adriatic Sea. *Pubbl. Staz. zool. Napoli*, Naples, **40** (Suppl.): 1–304.

Bosquet, J. 1852. Description des entomostracés fossiles des terrains Tertiares de la France et de la Belgique. *Mém. Acad. r. Sci. Lett. Belg.*, Brussels, **24**: 1–142.

Bowen, R. N. C. 1953. Ostracoda from the London Clay. *Proc. Geol. Ass.*, London, **64**: 276–292.

Brady, G. S. 1867. A synopsis of the British Ostracoda. *Intellect. Obs.*, London, **12**: 110–130.

—— 1869*a*. *In* Folin, L. de & Périer, L. 1867–1871. *Les Fonds de la Mer*, **1**. 316 pp., 32 pls.

—— 1869*b*. Contributions to the study of the Entomostraca. IV. Ostracoda from the River Scheldt and the Grecian Archipelago. *Ann. Mag. nat. Hist.*, London, (4) **3**: 45–50.

—— 1880. Report on the Ostracoda dredged by H.M.S. Challenger during the years 1873–1876. *Rep. scient. Results Voy. Challenger*, London, (Zool.) **1**: 1–184.

—— 1898. On new or imperfectly known species of Ostracoda, chiefly from New Zealand. *Trans. zool. Soc. Lond.*, **14**: 429–452.

——, **Crosskey, H. W. & Robertson, D.** 1874. A monograph of the Post-Tertiary Entomostraca of Scotland including species from England and Ireland. 232 pp. *Palaeontogr. Soc. [Monogr.]*, London.

Carbonnel, G. 1969. Les Ostracodes du Miocene Rhodanien. *Docum. Lab. Géol. Fac. Sci. Lyon*, **33**: 1–469.

—— 1986. Ostracodes tertiares (Paléogène à Néogène) du bassin sénégalo-guinéen. *Docums Bur. Rech. géol. minières*, Orléans, **101** (2): 33–243.

Ciampo, G. 1971. Gli ostracodi delle argille pleistoceniche del Mar Piccolo (Taranto). *Boll. Soc. Nat. Napoli*, **80**: 49–88.

Coryell, H. N. & Fields, S. 1937. A Gatun ostracode fauna from Cativa, Panama. *Am. Mus. Novit.*, New York, **956**: 1–18.

Crane, M. J. 1965. Upper Cretaceous ostracodes of the Gulf Coast area. *Micropaleontology*, New York, **11**: 191–254.

Crouch, R. W. 1949. Pliocene Ostracoda from Southern California. *J. Paleont.*, Tulsa, **23**: 594–599.

Deroo, G. 1966. Cytheracea (Ostracodes) du Maastrichtien de Maastricht (Pays-Bas) et des régions voisines; résultats stratigraphiques et paléontologiques de leur étude. *Meded. geol. Sticht.*, Maastricht, (C) **2**: 1–197.

Devoto, G. 1965. Lacustrine Pleistocene in the Lower Liri Valley (southern Latium). *Geologica romana*, Rome, **6**: 291–368.

Dingle, R. V. 1969*a*. Marine Neocomian Ostracoda from South Africa. *Trans. R. Soc. S. Afr.*, Cape Town, **38**: 139–163.

—— 1969*b*. Upper Senonian ostracods from the coast of Pondoland, South Africa. *Trans. R. Soc. S. Afr.*, Cape Town, **38**: 347–385.

—— 1971. Some Cretaceous ostracodal assemblages from the Agulhas Bank (South African continental margin). *Trans. R. Soc. S. Afr.*, Cape Town, **39**: 393–418.

—— 1976. Palaeogene ostracods from the continental shelf off Natal, South Africa. *Trans. R. Soc. S. Afr.*, Cape Town, **42**: 35–79.

Donze, P., Porthault, B., Thomel, G. & Villoutreys, O. de 1970. Le Sénonien inférieur de Puget-Théniers (Alpes-Maritimes) et sa microfaune. *Géobios*, Lyon, **3**: 41–106.

Eames, F. E., Banner. F. T., Blow, W. H. & Clarke, W. J. 1962. *Fundamentals of Mid-Tertiary Stratigraphical Correlation.* 163 pp., 17 pls, folding tables. Cambridge.

—— **& Kent P. E.** 1955. Miocene beds of the East African coast. *Geol. Mag.*, Hertford, **92**: 338–344.

Elofson, O. 1941. Zur Kenntnis der marinen Ostracoden Schwedens mit besonderer Berücksichtigung des Skageraks. *Zool. Bidr. Uppsala*, **19**: 215–534.

Esker, G. C. 1968. Danian ostracodes from Tunisia. *Micropaleontology*, New York, **14**: 319–333.

Fischer, S. 1855. Beitrag zur Kenntnis der Ostracoden. *Abh. bayer. Akad. Wiss.*, Munich, **7** (3): 635–666, pls XIX–XX.

Gill, E. D. 1968. Oxygen isotope palaeotemperature determinations from Victoria, Australia. *In* Dawson, J. W. (ed.), *The Tertiary Climate of New Zealand*, **16**: 56–61. Tuatara.

Hanai, T. 1957–59. Studies on the Ostracoda from Japan. I. Subfamily Leptocytherinae n. subfam. *J. Fac. Sci. Tokyo Univ.*, (II) **10**: 431–468 (1957*a*). III. Subfamilies Cytherurinae G. W. Müller (emend. G. O. Sars 1925) and Cytheropterinae n. subfam. *Ibid.* **11**: 11–36 (1957*b*). IV. Family Cytherideidae Sars 1925. *Ibid.* **11**: 291–308 (1959).

Hartmann, G. 1964. Zur Kenntnis der Ostracoden des Roten Meeres. *Kieler Meeresforsch.*, Kiel, **20**: 35–127.

—— **& Puri, H. S.** 1974. Summary of Neontological and Paleontological Classification of Ostracoda. *Mitt. hamburg. zool. Mus. Inst.*, **70**: 7–73.

Hazel, J. E. 1967. Classification and distribution of the Recent Hemicytheridae and Trachyleberididae (Ostracoda) off northeastern North America. *Prof. Pap. U.S. geol. Surv.*, Washington, **564**: 1–45.

Holden, J. C. 1967. Late Cenozoic Ostracodes from the drowned terraces in the Hawaiian Islands. *Pacific Sci.*, Hawaii, **21**: 1–50.

—— 1976. Late Cenozoic Ostracoda from Midway Island Drill Holes. *Prof. Pap. U.S. geol. Surv.*, Washington. **680F**: 1–43.

Hornibrook, N. de B. 1952. Tertiary and Recent marine Ostracoda of New Zealand. Their origin, affinities, and distribution. *Palaeont. Bull. Wellington*, **18**: 1–82.

—— 1953. Some New Zealand Tertiary marine Ostracoda useful in stratigraphy. *Trans. R. Soc. N. Z.*, Dunedin, **81**: 303–311.

Hoskin, I. R. 1975. Comparison of valve ornamentation in various species of *Hemicytherura* from western Ireland, the Mediterranean and the Red Sea. *Revta esp. Micropaleont.*, Madrid, **7**: 91–98.

Howe, H. V. 1951. New Tertiary ostracode fauna from Levy County, Florida. *Geol. Bull. Fla*, Tallahassee, **34** (1): 1–43.

—— 1955. *Handbook of Ostracod Taxonomy.* 386 pp. Baton Rouge, La. (Louisiana Univ. Studies Phys. Sci. No. 1.)

—— 1961. *In* Benson, R. H. *et al.* (q.v.)

—— 1963. Type saline Bayou Ostracoda of Louisiana. *Bull. geol. Surv. La*, Baton Rouge, **40**: 1–62.

—— **& Chambers, J.** 1935. Louisiana Jackson Eocene Ostracoda. *Geol. Bull. La*, New Orleans, **5**: 1–65.

—— **& Law, J.** 1936. Louisiana Vicksburg Oligocene Ostracoda. *Geol. Bull. La*, New Orleans, **7**: 1–96, 6 pls.

Huff, W. J. 1970. The Jackson Eocene Ostracoda of Mississippi. *Bull. Miss. geol. econ. topogr. Surv.*, Jackson, **114**: 1–289.

Ishizaki, K. 1973. Discovery of the Family Punciidae, Ostracoda (Crustacea), from Okinawa Island, Japan. *Sci. Rep. Tôhoku Univ.*, Sendai, (2 ser., geol.) spec. vol. **6**: 403–405.

Jenkins, D. G. 1968. Variations in the numbers of species and subspecies of planktonic Foraminiferida as an indicator of New Zealand Cenozoic paleotemperatures. *Paleogeogr. Palaeoclimat. Palaeoecol.*, Amsterdam, **5**: 309–313.

Jones, T. R. 1849. A Monograph of the Entomostraca of the Cretaceous Formation of England. 40 pp. *Palaeontogr. Soc. [Monogr.]*, London.

—— **& Sherborn, C. D.** 1889. A supplemental monograph of the Tertiary Entomostraca of England. 55 pp. *Palaeontogr. Soc. [Mongr.]*, London.

Keen, M. C. 1974. Some *Ruggieria*-like ostracods from the Tertiary and Recent of West Africa. *Proc. Vth African micropaleont. Colloquium*, Addis Ababa, (1972): 451–469.

Keij, A. J. 1953. Preliminary note on the Recent Ostracoda of the Snellius expedition. *Proc. K. ned. Akad. Wet.*, Amsterdam, (B) **56**: 155–168.

—— 1957. Eocene and Oligocene Ostracoda of Belgium. *Mem. Inst. r. Sci. nat. Belg.*, Brussels, **136**: 1–210.

—— 1958. Note on the Lutetian Ostracoda of Damery (Marne), France. *Proc. K. ned. Akad. Wet.*, Amsterdam, (B) **61**: 63–73.

—— 1966. Southeast Asian Neogene and Recent species of *Paijenborchella* (Ostracoda). *Micropaleontology*, New York, **12**: 343–354.

—— 1976. Notes on *Havanardia* and *Triebelina* species (Ostracoda). *Proc. K. ned. Akad. Wet.*, Amsterdam, (B) **79**: 36–44.

Kent, P. E. 1974. Continental margin of East Africa—A Region of vertical movements. *In* Burk, C. A. & Drake, C. L. (eds), *The Geology of Continental Margins*: 313–320. Berlin, Heidelberg, New York.

——, **Hunt, J. A. & Johnstone, D. W.** 1971. The geology and geophysics of coastal Tanzania. *Geophys. Pap. Inst. geol. Sci.*, London, **6**: 1–101.

Khosla, S. C. 1978. Lower Miocene Ostracoda from Jamnagar and Porbandar Districts, Gujarat, India. *Micropaleontology*, New York, **24**: 251–290.

Kingma, J. T. (1948). *Contributions to the Knowledge of the Young-Caenozoic Ostracoda from the Malayan Region.* 119 pp. Thesis, Univ. Utrecht (unpubl.).

Krutak, P. R. 1961. Jackson Eocene Ostracoda from the Cocoa Sand of Alabama. *J. Paleont.*, Tulsa, **35**: 769–788.

Latham, M. H. 1938. Some Eocene Ostracoda from North-West India. *Proc. R. Soc. Edinburgh*, **59**: 38–48.

Latreille, P. A. 1806. Cohors secunda. Ostracoda. *In*: *Genera crustaceorum et insectorum*, **1**: 17–18. Paris.

Lubimova, P. S., Guha, D. K. & Mohan, M. 1960. Ostracoda of Jurassic and Tertiary deposits from Kutch and Rajasthan (Jaisalmer), India. *Bull. geol. min. metall. Soc. India*, Calcutta, **22**: 1–61.

M'Coy, F. 1844. *A Synopsis of the Characters of the Carboniferous Limestone Fossils of Ireland*. 207 pp. (ostracods 163–168). Dublin.

McKenzie, K. G. 1973. Cenozoic Ostracoda. *In* Hallam, A. (ed.), *Atlas of Palaeobiogeography*: 477–487. Amsterdam.

—— 1974. Cainozoic Ostracoda of Southeastern Australia with the description of *Hanaiceratina* new genus. *Geosci. Man*, Baton Rouge, **6**: 153–182.

—— **& Swain, F. M.** 1967. Recent Ostracoda from Scammon Lagoon, Baja California. *J. Paleont.*, Tulsa, **41**: 281–305.

Maddocks, R. F. 1966. Distribution patterns of living and subfossil podocopid ostracodes in the Nosy Bé area. *Paleont. Contr. Univ. Kansas*, Lawrence, **12**: 1–72.

—— 1969. Revision of Recent Bairdiidae (Ostracoda). *Bull. Smithson. Inst.*, Washington, **295**: 1–126.

Mandelstam, M. I. 1960. *In*: Ostracoda. *In* Chernousova, H. E. (ed.), *Osnovy Paleontologii* 8 (Chenistonogie,Trilobitoobraznie i Rakoobraznie): 264–413, pl. 17. Moscow.

Morkhoven, F. P. C. M. van 1963. *Post-Palaeozoic Ostracoda. Their Morphology, Taxonomy and Economic Use*. **2**, *Generic descriptions*. 478 pp. Amsterdam.

Müller, G. W. 1894. Die Ostracoden des Golfes von Neapel und abgrenzenden Meeres-Abschnitte. *Fauna und Flora des Golfes von Neapel*, **21**. 404 pp. Berlin.

—— 1908. Die Ostracoden der Deutschen Südpolar-expedition 1901–1903. *In* Drygalski, E. von (ed.), *Deutsch Südpolar-expedition*, **10** (Zool. II): 51–181, 19 pls. Berlin.

—— 1912. Ostracoda. *In* Schulze, F. E. (ed.), *Das Tierreich*, **31**. xxxiiix+434 pp. Berlin.

Neale, J. W. 1967. An ostracod fauna from Halley Bay, Coats Land, British Antarctic Territory. *Scient. Rep. Br. Antarct. Surv.*, London, **58**: 1–50.

—— 1975. The Ostracod Fauna from the Santonian Chalk (Upper Cretaceous) of Gingin, Western Austalia. *Spec. Pap. Palaeont.*, London, **16**: 1–88.

—— **& Singh, P.** 1985. Ostracoda from the Middle Eocene of Assam. *Palaeontology*, London, **28**: 355–385.

—— —— 1988. Some problems associated with the genus *Uroleberis*. *In*: Hanai, T., Ikeya, M. & Ishizaki, K. (eds), Evolutionary Biology of Ostracoda. *Dev. Palaeont. Stratigr.*, Amsterdam, **11**: 81–92.

Neviani, A. 1928. Ostracodi fossili d'Italia. I: Vallebiaja (Calabriano). *Memorie pont. Accad. Sci. nuovi Lincei*, Rome, (2) **11**: 1–120, 2 pls.

Norman, A. M. 1865. Report on the Crustacea. *In* Brady, G. S., Report of Deep Sea Dredging on the Coasts of Northumberland and Durham, 1862–4. *Nat. Hist. Trans. Northumb.*, Newcastle, **1** (1): 12–29, pls V–VII.

Oertli, H. J. 1961. Ostracodes du Langhien-type. *Riv. ital. Paleont.*, Milan, **67**: 17–44.

—— 1971. The aspect of Ostracode faunas—A possible new tool in petroleum sedimentology. *In* Oertli, H. J. (ed.), Paléoécologie des Ostracodes. *Bull. Cent. Rech. Pau*, **5 suppl.**: 137–151.

Okubo, I. 1975. *Callistocythere pumila* Hanai, 1957 and *Leguminocythereis bisanensis* sp. nov. in the Inland Sea, Japan (Ostracoda). *Proc. jap. Soc. syst. Zool.*, Tokyo, **11**: 23–31.

Omatsola, M. E. 1972. Recent and Subrecent Trachyleberididae and Hemicytheridae (Ostr., Crust.) from the western Niger Delta, Nigeria. *Bull. geol. Instn* Univ. Upsala, (N.S.) **3**: 37–120.

Poag, C. W. 1974. Ostracode biostratigraphy and correlation of the Chickasawhay stage (Oligocene) of Mississippi and Alabama. *J. Paleont.*, Tulsa, **48**: 344–356.

Pokorný, V. 1955. Contribution to the morphology and taxionomy of the Subfamily Hemicytherinae Puri. *Acta Univ. Carol.*, Prague, **1955** (3): 1–36.

—— 1964*a*. *Oertliella* and *Spinicythereis*, new ostracod genera from the Upper Cretaceous. *Vest. ústřed. Úst. geol.*, Prague, **39**: 283–284.

—— 1964*b*. Some palaeoecological problems in marine ostracode faunas, demonstrated on the Upper Cretaceous ostracodes of Bohemia, Czechoslovakia. *Pubbl. Staz. zool. Napoli.*, **33 suppl.**: 462–479.

Puri, H. S. 1953. The ostracode genus *Hemicythere* and its allies. *J. Wash. Acad. Sci.*, Washington, **43**: 169–179.

—— 1954. Contribution to the study of the Miocene of the Florida Panhandle. *Bull. Fla St. geol. Surv.*, Tallahassee, **36** [for 1953]: 215–309.

—— 1955. *Hermanites*, new name for *Hermania* Puri, 1954. *J. Paleont.*, Tulsa, **29**: 558.

—— 1957*a*. Postscript notes on the ostracode subfamily Brachycytherinae. *J. Wash. Acad. Sci.*, Washington, **47**: 306–308.

—— 1957*b*. *Henryhowella*, new name for *Howella* Puri 1956. *J. Paleont.*, Tulsa, **31**: 982.

—— 1957*c*. Notes on the ostracode subfamily Cytherideidinae Puri, 1952. *J. Wash. Acad. Sci.*, Washington, **47**: 305–306 (precedes 1957*a*).

—— 1960. Recent Ostracoda from the West Coast of Florida. *Trans. Gulf Cst Ass. geol. Socs*, New Orleans, **10**: 107–149.

—— 1974. Normal pores and the phylogeny of Ostracoda. *Geosci. Man*, Baton Rouge, **6**: 137–151.

Ramsay, V. W. 1968. A new morphological aspect of the Ostracod genus *Cytherelloidea* Alexander. *Micropaleontology*, New York, **14**: 348–356.

Roemer, F. A. 1838. Die Cytherinen der Molasse-Gebirges. *Neues Jb. Min. Geogn. Geol. Petrefakt.*, Stuttgart, **1838**: 514–519, pl. VI.

—— 1840–41. *Die Versteinerungen des norddeutschen Kreidegebirges*. 145 pp., 16 pls. Hannover.

Rome, R. 1962. Ostracodes. *In*: *Exploration hydrobiologique du Lac Tanganyika (1946–1947). Résultats Scientifiques* **3** (8). 305 pp. Brussels (Inst. R. Sci. nat. Belg.).

Ruggieri, G. 1950. Gli Ostracodi delle sabie grigie quaternarie (Milazziano) di Imola. I. *G. Geol.*, Bologna, (2) **21**: 1–57.

—— 1951. Una nuova *Paijenborchella* del Pliocene della Calabria. *G. Geol.*, Bologna, (2) **21**: 59–63.

—— 1953. Eta e faune di un terrazzo marino sulla Costa Ionica della Calabria. *G. Geol.*, Bologna, (2) **23**: 17–168.

—— 1956. La suddivisione degli Ostracodi gia compresi nel genere *Cythereis* proposta da Neviani nel 1928. *Atti Soc. ital. Sci. nat.*, Milan, **95**: 161–175.

—— 1958. Alcuni Ostracodi del Neogene italiano. *Atti Soc. ital. Sci. nat.*, Milan, **97**: 127–146.

—— 1961. Alcuni Ostracodi Quaternari e Recenti pertinenti al genere *Costa* Neviani. *Boll. Soc. paleont. ital.*, Modena, **1**: 3–9.

—— 1962. Gli Ostracodi marini del Tortoniano (Miocene medio-superiore) di Enna, nella Sicilia centrale. *Palaeontogr. ital.*, Pisa, **56**: 1–68.

—— 1967. Due Ostracofaune del Miocene alloctono della Val Marecchia (Appennino settentrionale). *Riv. ital. Paleont.*, Milan, **73**: 351–384.

—— 1972. Su alcuni Ostracodi marini plio-pleistocenici mediterranei. *Atti Soc. ital. Sci. nat.*, Milan, **113**: 89–113.

Sars, G. O. 1866. Oversigt af Norges marine ostracoder. *Forh. VidenskSelsk. Krist.*, Kristiana, **7**: 1–130.

—— 1888. Nye Bidrag til Kundskaben om Middlehavets Invertebratfauna. 4. Ostracoda Mediterranea. *Arch. Math. Naturv.*, Oslo, **12**: 173–324.

—— 1910. Zoological results of the Third Tanganyika Expedition, conducted by W. A. Cunnington, F. Z. S., 1904–1905. Report on the Ostracoda. *Proc. zool. Soc. Lond.*, **1910**: 732–760.

—— 1925–8. *An account of the Crustacea of Norway*. **9** *Ostracoda*. Parts IX & X, Cypridae (concluded), Cytheridae (part): 137–176 (1925). Parts XIII & XIV, Cytheridae (continued): 209–240 (1926). Parts XV & XVI, Cytheridae (concluded): 241–277 (1928). Bergen.

Sexton, J. W. 1951. The ostracode *Cytherelloidea* in North America. *J. Paleont.*, Tulsa, **25**: 808–816.

Siddiqui, Q. A. 1971. Early Tertiary Ostracoda of the Family Trachyleberididae from West Pakistan. *Bull. Br. Mus. nat. Hist.*, London, (Geol. suppl.) **9**: 1–98.

Sissingh, W. 1972. Late Cenozoic Ostracoda of the South Aegean Island Arc. *Utrecht micropaleont. Bull.*, **6**: 1–187.

Skogsberg, T. 1928. Studies on marine ostracods Part II. External Morphology of the genus *Cythereis* with descriptions of twenty-one new species. *Occ. Pap. Calif. Acad. Sci.*, San Francisco, **15**: 1–155.

Sohn, I. G. 1964. The ostracode genus *Cytherelloidea*, a possible indicator of paleotemperature. *Pubbl. Staz. zool. Napoli*, **33 suppl.**: 529–534.

—— 1970. Early Tertiary ostracodes from West Pakistan. *Mem. geol. Surv. Pakist.*, Quetta, **3** (1): 1–91, 4 pls.

Stephenson, M. B. 1936. Shell structure of the ostracode genus *Cytheridea*. *J. Paleont.*, Menasha, **10**: 695–703.

—— 1946. *Glyptobairdia*, a new genus of Ostracoda. *J. Paleont.*, Tulsa, **20**: 345–347.

—— 1947. Notes on the ostracode genus *Triebelina*. *J. Paleont.*, Tulsa, **21**: 577–579.

Swain, F. M. 1955. Ostracoda of San Antonio Bay, Texas. *J. Paleont.*, Tulsa, **29**: 561–646.

—— 1967. Ostracoda from the Gulf of California. *Mem. geol. Soc. Am.*, Washington, **101**: 1–139.

—— 1969. Taxonomy and ecology of near-shore Ostracoda from the Pacific Coast of North and Central America. *In* Neale, J. W. (ed.), *The Taxonomy, Morphology and Ecology of Recent Ostracoda*: 423–474. Edinburgh.

—— 1971. Pleistocene Ostracoda from deep-sea sediments in the southeastern Pacific Ocean. *In* Funnell, B. M. & Riedel, W. R. (eds), *The Micropalaeontology of Oceans*: 487–492. Cambridge.

—— 1976. Lower and Middle? Cretaceous Ostracoda from the Atlantic Ocean off Guiana and off West Africa. *J. Paleont.*, Tulsa, **50**: 734–753.

—— **& Gilby, J. M.** 1974. Marine Holocene Ostracoda from the Pacific Coast of North and Central America. *Micropaleontology*, New York, **20**: 257–352.

Sylvester-Bradley, P. C. 1948. The Ostracode Genus *Cythereis*. *J. Paleont.*, Tulsa, **22**: 792–797.

Triebel, E. 1949. Zur Kenntnis der Ostracoden-Gattung *Paijenborchella*. *Senckenbergiana*, Frankfurt a.M., **30**: 193–203.

—— 1958. Zwei neue Ostracoden-Gattungen aus dem Lutet des Pariser Beckens. *Senckenberg. leth.*, Frankfurt a.M., **39**: 105–117.

Uliczny, F. (1969). *Hemicytheridae und Trachyleberididae (Ostracoda) aus dem Pliozän der Insel Kephallinia (Westgriechenland)*. 152 pp. Dissertation, Univ. Munich (unpubl.).

Ulrich, E. O. & Bassler, R. S. 1904. Superorder Ostracoda. *In*: Systematic paleontology, Miocene, Arthropoda. *Md geol. Surv. stratigr. Mem.*, Baltimore, **Miocene**: 98–130.

Wagner, C. W. 1957. *Sur les ostracodes du Quaternaire–Récent des Pays-Bas et leur utilisation dans l'étude géologique des dépôts holocènes*. 257 pp. The Hague.

SYSTEMATIC INDEX

New taxonomic names and page numbers of the principle references are printed in bold type. Asterisks denote illustrations.

Bulletin of the British Museum (Natural History)

Geology Series

Most earlier Geology *Bulletins* are still in print. A full list of available titles can be obtained from Publication Sales (address inside front cover).

Vol. 36 No. 3 The Ordovician Graptolites of Spitsbergen. R. A. Cooper & R. A. Fortey. 1982. Pp. 157–302, 6 plates, 83 figs, 2 tables. £20.50

Vol. 36 No. 4 Campanian and Maastrichtian sphenodiscid ammonites from southern Nigeria. P. M. P. Zaborski. 1982. Pp. 303–332, 36 figs. £4.00

Vol. 37 No. 1 Taxonomy of the arthrodire *Phlyctaenius* from the Lower or Middle Devonian of Campbellton, New Brunswick, Canada. V. T. Young. 1983. Pp. 1–35, 18 figs. £5.00

Vol. 37 No. 2 *Ailsacrinus* gen. nov., an aberrant millericrinid from the Middle Jurassic of Britain. P. D. Taylor. 1983. Pp. 37–77, 48 figs, 1 table. £5.90

Vol. 37 No. 3 Miscellanea: Permian *Glossopteris* in Turkey—Wealden *Theriosuchus*—Wealden conifer—Permian plants of Saudi Arabia—Carboniferous Edrioasteroidea—British cicadas—Dittonian cephalaspids. 1983. Pp. 79–171. £13.50

Vol. 37 No. 4 The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. B. G. Gardiner. 1984. Pp. 173–428, 145 figs, 4 plates. 0 565 00967 2. £39.00

Vol. 38 No. 1 New tertiary pycnodonts from the Tilemsi valley, Republic of Mali. A. E. Longbottom. 1984. Pp. 1–26, 29 figs, 3 tables. 0 565 07000 2. £3.90

Vol. 38 No. 2 Silicified brachiopods from the Viséan of County Fermanagh, Ireland. (III) Rhynchonellids, Spiriferids and Terebratulids. C. H. C. Brunton. 1984. Pp 27–130, 213 figs. 0 565 07001 0. £16.20

Vol. 38 No. 3 The Llandovery Series of the Type Area. L. R. M. Cocks, N. H. Woodcock, R. B. Rickards, J. T. Temple & P. D. Lane. 1984. Pp. 131–182, 70 figs. 0 565 07004 5. £7.80

Vol. 38 No. 4 Lower Ordovician Brachiopoda from the Tourmakeady Limestone, Co. Mayo, Ireland. A. Williams & G. B. Curry. 1985. Pp. 183–269, 214 figs. 0 565 07003 7. £14.50

Vol. 38 No. 5 Miscellanea: Productacean growth and shell shape—Jurassic alga *Palaeosiphonium*—Upper Ordovician brachiopods and trilobites—Lower Devonian Osteostraci from Podolia—*Hipparion* from Diavata—Preparation and study of Singa skull—Carboniferous and Permian bryozoa—Lower Eocene trionychid—Montsech fossil insects. 1985. Pp. 271–412. 0 565 07004 5. £24.00

Vol. 39 No. 1 Upper Cretaceous ammonites from the Calabar region, south-east Nigeria. P. M. P. Zaborski. 1985. Pp. 1–72, 66 figs. 0 565 07006 1. £11.00

Vol. 39 No. 2 Cenomanian and Turonian ammonites from the Novo Redondo area, Angola. M. K. Howarth. 1985. Pp. 73–105. 33 figs. 0 565 07006 1. £5.60

Vol. 39 No. 3 The systematics and palaeogeography of the Lower Jurassic insects of Dorset, England. P. E. S. Whalley. 1985. Pp. 107–189, 87 figs, 2 tables. 0 565 07008 8. £14.00

Vol. 39 No. 4 Mammals from the Bartonian (middle/late Eocene) of the Hampshire Basin, southern England. J. J. Hooker. 1986. Pp. 191–478, 71 figs, 39 tables. 0 565 07009 6. £49.50

Vol. 40 No. 1 The Ordovician graptolites of the Shelve District, Shropshire. I. Strachan. 1986. Pp. 1–58, 38 figs. 0 565 07010 X. £9.00

Vol. 40 No. 2 The Cretaceous echinoid *Boletechinus*, with notes on the phylogeny of the Glyphocyphidae and Temnopleuridae. D. N. Lewis. 1986. Pp. 59–90, 11 figs, 7 tables. 0 565 07011 8. £5.60

Vol. 40 No. 3 The trilobite fauna of the Raheen Formation (upper Caradoc), Co. Waterford, Ireland. A. W. Owen, R. P. Tripp & S. F. Morris. 1986. Pp. 91–122, 88 figs. 0 565 07012 6. £5.60

Vol. 40 No. 4 Miscellanea I: Lower Turonian cirripede—Indian coleoid *Naefia*—Cretaceous–Recent Craniidae—Lectotypes of Girvan trilobites—Brachiopods from Provence—Lower Cretaceous cheilostomes. 1986. Pp. 125–222. 0 565 07013 4. £19.00

Vol. 40 No. 5 Miscellanea II: New material of *Kimmerosaurus*—Edgehills Sandstone plants—Lithogeochemistry of Mendip rocks—Specimens previously recorded as teuthids—Carboniferous lycopsid *Anabathra*—*Meyenodendron*, new Alaskian lepidodendrid. 1986. Pp. 225–297. 0 565 07014 2. £13.00

Vol. 41 No. 1 The Downtonian ostracoderm *Sclerodus* Agassiz (Osteostraci: Tremataspididae). P. L. Forey. 1987. Pp. 1–30. 11 figs. 0 565 07015 0. £5.50

Vol. 41 No. 2 Lower Turonian (Cretaceous) ammonites from south-east Nigeria. P. M. P. Zaborski. 1987. Pp. 31–66. 46 figs. 0 565 07016 9. £6.50

Vol. 41 No. 3 The Arenig Series in South Wales: Stratigraphy and Palaeontology. I. The Arenig Series in South Wales. R. A. Fortey & R. M. Owens. II. Appendix. Acritarchs and Chitinozoa from the Arenig Series of South-west Wales. S. G. Molyneux. 1987. Pp. 67–364. 289 figs. 0 565 07017 7. £59.00

Vol. 41 No. 4 Miocene geology and palaeontology of Ad Dabtiyah, Saudi Arabia. Compiled by P. J. Whybrow. 1987. Pp. 365–457, 54 figs. 0 565 07019 3. £18.00

Vol. 42 Cenomanian and Lower Turonian Echinoderms from Wilmington, south-east Devon. A. B. Smith, C. R. C. Paul, A. S. Gale & S. K. Donovan. 1988. 244 pp., 80 figs, 50 pls. 0 565 07018 5. £46.50

Vol. 43 A Global Analysis of the Ordovician–Silurian boundary. Edited by L. R. M. Cocks & R. B. Rickards. 1988. 394 pp., figs. 0565 07020 7. £70.00

Vol. 44 No. 1 Miscellanea: Palaeocene wood from Mali—Chapelcorner fish bed—*Heterotheca* coprolites—Mesozoic Neuroptera and Raphidioptera. 1988. Pp. 1–63. 0 565 07021 5. £12.00

Vol. 44 No. 2 Cenomanian brachiopods from the Lower Chalk of Britain and northern Europe. E. F. Owen. 1988. Pp. 65–175. 0 565 07022 3. £21.00

Vol. 44 No. 3 The ammonite zonal sequence and ammonite taxonomy in the *Douvilleiceras mammillatum* Superzone (Lower Albian) in Europe. H. G. Owen. 1988. Pp. 177–231. 0 565 07023 1. £10.30

Vol. 44 No. 4 Cassiopidae (Cretaceous Mesogastropoda): taxonomy and ecology. R. J. Cleevely & N. J. Morris. 1988. Pp. 233–291. 0 565 07024 X. £11.00

Vol. 45 No. 1 Arenig trilobites—Devonian brachiopods—Triassic demosponges—Larval shells of Jurassic bivalves—Carboniferous marattialean fern—Classification of Plectambonitacea. 1989. Pp. 1–163. 0 565 07025 8. £40.00

Vol. 45 No. 2 A review of the Tertiary non-marine molluscan faunas of the Pebasian and other inland basins of north-western South America. C. P. Nuttall. 1990. Pp. 165–371. 456 figs. 0 565 07026 6. £52.00

Vol. 46 No. 1 Mid-Cretaceous Ammonites of Nigeria—new amphisbaenians from Kenya—English Wealden Equisetales—Faringdon Sponge Gravel Bryozoa. 1990. Pp. 1–152. 0 565 070274. £45.00

CONTENTS

Bulletin British Museum (Natural History)

GEOLOGY SERIES

Vol. 46, No. 2, January 1991