EARLY ORDOVICIAN (ARENIG) BIVALVES FROM THE LLANGYNOG INLIER, SOUTH WALES

by JOHN C. W. COPE

ABSTRACT. The most diverse early Ordovician bivalve fauna yet known comprises 20 species belonging to 18 genera. It is from the early Arenig (Moridunian Stage) of the Llangynog Inlier, near Carmarthen, South Wales, and is dominated by actinodontoids, with palaeotaxodonts, cyrtodontoids and rarer modiomorphoids, anomalodesmatans, solemyoids and a pterioid. From the same locality a rostroconch is described and a nearby mid-Arenig (Whitlandian Stage) locality has yielded an ambonychiid. The following new taxa are described: *Pensarnia laeviformis* gen. et sp. nov., *Paulinea parva* gen. et sp. nov., *Ovatoconcha fragilis* gen. et sp. nov., *Glyptarca serrata* sp. nov., *Carminodonta crossi* gen. et sp. nov., *Fortowensia grandis* gen. et sp. nov., *Celtoconcha foveata* gen. et sp. nov., *Moridunia simplicidens* gen. et sp. nov., *Goniophora* (*Cosmogoniophorina*) *extensa* sp. nov., *Parallelodus dyfedensis* sp. nov., *Falcatodonta costata* gen. et sp. nov. and *Arenigomya carinata* gen. et sp. nov. The new genus *Hemiprionodonta* is introduced for forms previously described from the middle Ordovician of France and Iberia, and from the upper Ordovician of North Wales. The following higher level taxa are proposed: Superfamily Glyptarcoidea, Family Glyptarcidae, Order Cyrtodontida, Superfamily Falcatodontoidea and Family Falcatodontidae. The fauna includes the earliest known representatives of the solemyoids, pterioids and anomalodesmatans.

VERY few bivalves are known from rocks of pre-Arenig age. The earliest unequivocal records are from rocks of early Cambrian age. *Pojetaia* Jell, 1980 is undoubtedly an early palaeotaxodont bivalve; *Fordilla* Barrande, 1881 is of less certain affinities, and whilst it is regarded by most authorities as a bivalve (see Runnegar and Bentley 1983) not all agree with the views of Pojeta and Runnegar (1985) that it is a precursor of the modiolopsid bivalves of the Ordovician. Subsequently this view has been modified since the shell structure of these two genera has been shown to be remarkably similar (Runnegar and Pojeta 1992). Earlier than either of these is *Yangtzedonta* Yu, 1985 from the Meishucunian Stage of the Lower Cambrian; unfortunately this is known from only one valve, which has no muscle scars, and its bivalve affinities are thus uncertain. *Yangtzedonta* is just one example of a whole series of putative early Cambrian bivalves recorded in the literature; many of these were reviewed by Runnegar and Pojeta (1992) and all were assigned to other groups. Later Cambrian bivalves than these are unknown, and all recorded genera have been shown subsequently to belong to other phyla or molluscan classes (see Runnegar and Pojeta 1992). This was, for example, the fate of *Lamellodonta*, at the time of publication of the bivalve volume of the *Treatise on invertebrate paleontology* (Cox *et al.* 1969) the earliest supposed bivalve, later shown to be a distorted obolid brachiopod (Havlíček and Kříž 1978).

It is not until the early Ordovician that bivalves re-appear in the fossil record. From the Tremadoc Series, three records may be accepted unequivocally: those of Harrington (1938) from Satta Province, Argentina, of Pojeta and Gilbert-Tomlinson (1977) from the Amadeus Basin of Australia, initially recorded as of Arenig age, but subsequently shown to be of latest Tremadoc age (Shergold *et al.* 1991), and of Babin (1982) from the Montagne Noire. The record of a Tremadoc form from Afghanistan (Desparmet *et al.* 1971) is of uncertain early Ordovician age (Babin and Gutiérrez-Marco 1991). The nine or ten Tremadoc species include palaeotaxodonts, palaeoheterodonts and cyrtodonts. Thus Tremadoc bivalve faunas are exceptionally rare and of low diversity. From the lower part of the succeeding Arenig Series, bivalves have hitherto been described from four areas:

[Palaeontology, Vol. 39, Part 4, 1996, pp. 979–1025, 7 pls]

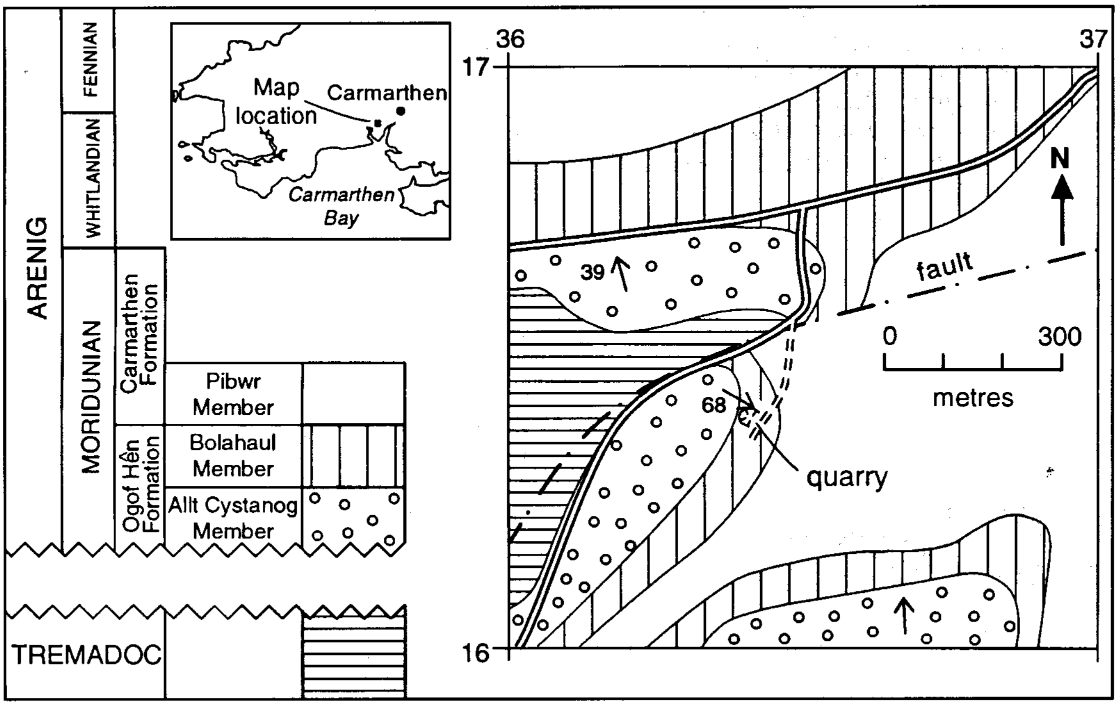
1. Ramsey Island, South Wales (Hicks 1873). The fauna, initially ascribed a Tremadoc age, was redescribed by Carter (1971) who reduced Hick's faunal list to five species. The specimens are very poorly preserved, and remain largely uninterpretable.
2. The Montagne Noire, southern France (Thoral 1935; Babin 1982). This fauna is generally well preserved and the Lower Arenig part contains seven species.
3. Salta Province, northern Argentina (Harrington 1938). An indifferently preserved fauna comprises three species.
4. The Moroccan Anti-Atlas (Babin and Destombes 1992). The early Arenig part of the fauna includes two specifically identifiable forms, both also known from the Montagne Noire.

Higher in the Arenig Series bivalves become more common, and have been reported from, in addition to localities 2. and 4. above, the Massif Armoricain, northern France (Barrois 1891; Babin 1966 – upper Arenig), Sweden (Soot-Ryen 1969 – upper Arenig), and Argentina (Sanchez and Babin 1993 – upper Arenig). The other early Ordovician bivalve occurrences listed by Pojeta (1971) (e.g. Billings 1865; Sardeson 1896; Butts 1941; Cloud and Barnes 1948) have proved either to be records of rostroconchs, or are not now considered to be early Ordovician. Because of this exceptional rarity, the discovery of a well preserved and diverse fauna from rocks of early Arenig (Moridunian Stage) age, consisting of 20 species, belonging to 18 genera, is clearly of considerable importance.

The fauna occurs in a small quarry (Text-fig. 1) in the northern part of the Llangynog Inlier (Cope 1982), an area of rocks of Precambrian to Arenig age (Cope 1980), and is some 6 km to the south-west of Carmarthen, Dyfed, South Wales (Grid reference SN 3640 1639). The quarry was first mentioned by the Geological Survey (Strahan *et al.* 1909, p. 16) whose meagre faunal list reads '*Dictyonema*?, *Lingula* cf. *attenuata* J. de C. Sowerby, *Orthis calligramma* Dalman, *Orthis* sp., and a lamellibranch'. Here are exposed interbedded siltstones and mudstones of the early Arenig (Moridunian Stage) Bolahaul Member of the Ogof Hên Formation (Fortey and Owens 1978) which can be seen to overlie directly conglomerates of the Allt Cystanog Member of the same formation, and thin stringers of conglomerate and occasional pebbles are features of the sedimentary rocks in the quarry. Bioturbation is common and the rock is an intimate admixture of silt and clay fractions. The fauna is well dated by the trilobites *Merlinia murchisoniae* (Murchison) and *Neseuretus ramseyensis* Hicks, shown by Fortey and Owens (1987) to be characteristic of the Moridunian Stage. The unequivocal evidence of age of these rocks is important, for not only have they yielded the earliest known bryozoan (Taylor and Cope 1987) and parablastoid (Paul and Cope 1982), but representatives of the bivalve fauna include the earliest members of their family, order, or in some cases, subclass. Further new forms belonging to other classes of molluscs and to other phyla remain to be described; many of them too are the earliest representatives of their groups. The quarry has been scheduled as a Site of Special Scientific Interest (SSSI) under the protection of the Countryside Council for Wales (CCW). Anyone wishing to visit the locality, which is on private property, must first obtain permission from the CCW.

The reason for the preservation of this exceptionally diverse fauna may be briefly examined. Its extremely local nature is noteworthy; similar horizons, over a wide area around Carmarthen, have faunas dominated by brachiopods and contain few, if any bivalves. I have concluded that the exceptional diversity represented by the fauna in this one quarry is because it is from a close inshore environment, such as is not often preserved in the geological record. This habitat seems to have been the place where major evolutionary change was occurring, presumably in response to increased competition there. If it is indeed the case that the inshore environment was the source of much evolutionary pressure, it is not surprising that evolutionary intermediates are often lacking in the fossil record: they are to be found most often in the rarely preserved near-shore deposits, which, once identified, seem to have not only exceptionally diverse faunas, but to contain a significant number of first appearances of taxa at levels from specific up to class level.

Studies of the evolution of Phanerozoic marine communities by Sepkoski (1981) and Sepkoski and Miller (1985) have suggested that mollusc-dominated faunas are characteristic of the Mesozoic and Cenozoic. These 'modern faunas' displaced the brachiopod-dominated 'Palaeozoic faunas'



TEXT-FIG 1. Location of the source of the Arenig bivalve fauna in the Llangynog Inlier, its geological context and stratigraphical position.

progressively, from the Ordovician onwards, particularly in the near-shore environment. It is not until after the late Permian extinctions, however, that the 'modern faunas' are dominant. The Llangynog fauna is clearly the earliest mollusc-dominated fauna yet recorded (71·5 per cent. of the fauna), and for this reason alone is of considerable interest.

Although the fauna is exceptionally diverse, many horizons in the quarry proved virtually unfossiliferous, whereas others occasionally yielded abundant fossils belonging to many taxa. Altogether, almost 20 tonnes of rock were collected and split in the laboratory and have yielded a total of over 3100 fossils. Predominant amongst the fossils are bivalves (40·7 per cent.); also occurring are nautiloids (25·6 per cent.), brachiopods (17·9 per cent.), gastropods (4·5 per cent.), dendroids (3·9 per cent.), trilobites (2·4 per cent.), conulariids (1·6 per cent.), hyolithids (1·0 per cent.), monoplacophorans (0·7 per cent.), and parablastoids (0·6 per cent.). The remaining 1·1 per cent. consists of (in approximate descending order of abundance): a problematical coral-like organism, receptaculitids, gorgoniids, sponges, ostracods, eocrinoids, bryozoans and single specimens of graptoloid, rostroconch, crinoid and calcified red alga. In addition to being the most abundant, the bivalves are also the most diverse group in the fauna. In view of ideas about the completeness of the fossil record (e.g. Paul 1985) it is noteworthy that in this collection about ten taxa are each represented only by a single specimen.

The bivalve fauna is largely preserved as limonite-covered moulds; material from the more argillaceous horizons generally lacks the limonite coating and the moulds are pale grey in colour. Both form excellent material for investigation of the morphology of the shell. Dentition is commonly perfectly preserved and external moulds allow full appraisal of the external ornament. Unusually for deposits of this age, some bivalve taxa are represented by hundreds of specimens, thus allowing a study of intraspecific variability to be carried out on material which has not been significantly distorted. After hardening of the moulds with polyvinyl acetate, latex casts may be readily made which allow the full morphology of the shell to be reconstructed. A few bivalves have silicified shells; a few others are preserved as composite moulds (McAlester 1962), and most rarely some specimens have not been completely decalcified.

The most obvious character of the bivalve fauna is that the vast majority of the material is very small, although little material appears to represent juvenile specimens. Only one or two species exceed 25 mm in length and much of the material is around 10 mm long. Disarticulated valves predominate, although a significant number of conjoined valves have been found for most species. From this one can conclude that the fauna represents a death assemblage. Although the specimens are disarticulated, they are, however, mostly devoid of signs of wear, suggesting that there has been no significant transport. This is emphasized by preservation of the most delicate structures on some of the fossils, such as the brachioles of the parablastoids (Paul and Cope 1982). Some species of bivalve are represented predominantly by conjoined valves, and it is probable that these were more deeply infaunal, with the specimens possibly representing an *in situ* death assemblage. In some cases the two disarticulated valves of the same specimen may be found in close proximity on the same bedding plane. It is clear that for the most part current activity was minimal and post-mortem drift, at least of the benthos, insignificant. Two occasional features do, however, indicate some degree of transport: in some cases two or three of the same valves of specimens of the same species have become stacked one within the other; in other cases the most prominent parts of the exterior of the shell appear to have suffered sufficient abrasion for growth increments to disappear.

SYSTEMATIC PALAEONTOLOGY

There are two classifications of bivalves which have more current use by palaeontologists than others; those of Cox *et al.* (1969) and of Pojeta (1987, which incorporates the latest modifications of his earlier (1978) classification). The two classifications differ significantly at subclass level. Since the publication of the *Treatise* much work has been published on Ordovician bivalves and the rostroconchs have been recognized as a separate class of molluscs. Pojeta has abandoned the subclass Cryptodonta because it contained a medley of taxa now properly assigned to other subclasses of bivalves and the class Rostroconchia; the order Solemyoida (*ex* Cryptodonta) is placed by Pojeta in the subclass Palaeotaxodonta. The modiomorphoids (*ex* Palaeoheterodonta) and mytiloids (*ex* Pteriomorphia) form the subclass Isofilibranchia Iredale, 1939; the Palaeoheterodonta and Heterodonta are combined in the subclass Heteroconchia Hertwig, 1895. As a result of conclusions drawn herein and by Cope (1995), it appears that the *Treatise* classification is closer to a true phylogenetic scheme, and the higher taxonomic subdivisions used are based on modifications to this.

Measurements are in millimetres, and were obtained using vernier calipers or a binocular microscope with eyepiece graticule. Length is the maximum length of the shell measured, as far as is possible to determine, parallel to the hinge-line; height is the maximum height of the shell measured at right angles to the length. For some of the palaeotaxodont bivalves the term hinge angle is used; this is the angle between the anterior and posterior parts of the hinge plate. For size description I describe as 'small' those specimens less than 10 mm long; 'medium-sized', lengths between 10 and 20 mm, and 'large' with length in excess of 20 mm.

Since a total of 1269 identifiable bivalves was collected, valid conclusions may be drawn concerning the relative abundance of the main groups. Since all evidence suggests that palaeotaxodonts were the earliest bivalves, it is perhaps surprising that they constitute only 12 per cent. of the fauna. In contrast, the palaeoheterodonts make up 78·3 per cent.: of these the dominant group is the actinodontoids (76·9 per cent.), whilst the modiomorphoids account only for some 1·4 per cent. Of the remaining groups, pteriomorphians account for 7·6 per cent., anomalodesmatans 1·7 per cent. and lipodontids 0·4 per cent. It is thus clear that if views on the history of the evolution of the filibranch gill are correct (Cope 1995), the evolutionary advantage of this gill as a feeding organ seems to have become immediately apparent after its origin in the earliest Ordovician, for not only are the non-palaeotaxodont groups abundant, they are also very diverse.

All the material from the Llangynog localities has been deposited in the collections of the Department of Geology, National Museum of Wales, Cardiff. The bivalves described herein are registered under accession number NMW 78. 17G. The prefix BGS refers to material in the British Geological Survey, Keyworth. Unless specifically mentioned, all material is from the Moridunian Stage of the Arenig Series and from the quarry described above. Under the heading '*Material*' the following abbreviations are used: LV, left valve(s); RV, right valve(s); CV, conjoined valve(s). The suffix E with any of these indicates an external mould only.

Class BIVALVIA Linnaeus, 1758
Subclass PALAEOTAXODONTA Korobkov, 1954
Order NUCULOIDA Dall, 1889
Superfamily NUCULOIDEA Gray, 1824
Family PRAENUCULIDAE Pfab, 1934

Remarks. The number and relationships of genera within the family is still in a state of flux. The *Treatise* lists five genera which occur in the Ordovician. To these can be added *Concavodonta* Babin and Melou, 1972; *Fidera* Pojeta and Gilbert-Tomlinson, 1977 and *Eritropis* Pojeta and Gilbert-Tomlinson, 1977. None of the existing genera can accommodate the species described here and thus new ones are proposed.

Genus PENSARNIA gen. nov.

Derivation of name. From Pensarn, south of Carmarthen.

Type species. Pensarnia laeviformis sp. nov.

Diagnosis. Praenuculid of rounded trapezoidal outline with strongly inflated valves of variable length and prominent umbones at anterior. Posterior part of dorsal margin and anterior ventral margin approximately parallel. Exterior with fine growth increments, occasional stronger increments in some. Taxodont dentition continuous beneath umbones; anteriormost teeth largest; those beneath umbones extremely small; posterior teeth largely equal in size posterior to umbones; 20–32 straight or chevron-shaped teeth. Hinge-line straight as far as posterior, where it follows curve of dorsal margin of valves. Anterior adductor circular, deeply inserted and with prominent triangular pedal retractor scar on dorsal side; posterior adductor larger, more shallowly inserted, subtrapezoidal. Umbones strongly curved over hinge-plate.

Stratigraphical range. Early–?mid Arenig, Moridunian–?Whitlandian stages.

Remarks. Pensarnia is similar to *Praenucula* Pfab, from the middle Ordovician of Bohemia, but differs in its orientation. Following the criteria of Bradshaw (1970), Bradshaw and Bradshaw (1971) and Tunnicliff (1982), it is clear that the umbones of *Praenucula* lie within the posterior half of the shell, whilst in *Pensarnia* they lie very much to the anterior. There are also differences in dentition. In *Praenucula* there is a gradational increase in the size of the teeth to the anterior and posterior of the umbones, and the subumbonal teeth are not markedly smaller. The anteriormost teeth of *Pensarnia* are also larger than in most species of *Praenucula*, and it may have been this latter feature which persuaded Morris (1978) to include this species in *Cardiolaria*, as *C. laevis*. However, in *Cardiolaria* the anterior teeth are larger still, and, more significantly, the anterior and posterior teeth belong to separate sets which overlap in the subumbonal region of the hinge plate. This latter feature was well illustrated by Babin and Gutiérrez-Marco (1991) and Bradshaw (1970). Nevertheless, the larger size of the anteriormost teeth of *Pensarnia* shows a superficial resemblance to *Cardiolaria*. The posterior adductor scar of *Praenucula* is of similar size to the anterior; both are circular and both have rounded pedal muscle scars associated with them. These features contrast with those of *Paulinea* gen. nov. (see below, p. 985) which has unequal-sized adductor muscle scars, a triangular anterior pedal scar and a scarcely impressed (and thus seldom visible) posterior pedal scar. *Paulinea* also has a more rounded ventral margin.

Pensarnia laeviformis sp. nov.

Plate 1, figures 1–10

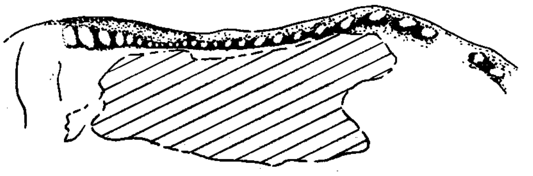
non 1824 *Nucula laevis* Say, p. 141, pl. 10, fig. 5.
1839 *Nucula*? *laevis* J. de C. Sowerby *in* Murchison, p. 635, pl. 22, fig. 1.
1902 *Nucula laevis* J. de C. Sowerby; Blake, p. 9.
1978 *Cardiolaria laevis* (J. de C. Sowerby); Morris p. 260, fig. 25.

Material. 59 specimens (32 LV, 23 RV, 4CV). Holotype: NMW 78. 17G. 1022. Paratypes: NMW 78. 1023–1077; Sowerby's material of *N.*? *laevis*, BGS Geological Society Collection 6849, three left valves from Pensarn, Carmarthen.

Diagnosis. As for genus (see above).

Derivation of name. Pro Sowerby's name *laevis* which is unavailable.

Description. All the material is of small size; the holotype is 9·0 mm long and 7·2 mm high. The anterior adductor is circular on the holotype, but other material shows that it can be subtriangular. It is deeply inserted and arising from its dorsal margin is a long triangular scar extending to the umbonal regions; in some specimens this scar is divided down its mid-line. The posterior adductor is not so deeply impressed and is subtrapezoidal rather than circular; a few specimens show a faint trace of posterior pedal muscle scar running dorsally from the posterior adductor.



TEXT-FIG. 2. *Pensarnia laeviformis*; NMW 78. 17G. 1063; *camera lucida* drawing of hinge region of left valve, internal mould; shaded area is matrix exposed by removal of umbo; × 10.

The holotype is a right valve internal mould which shows five teeth anterior to and 15 posterior to the umbo, where the hinge-plate is damaged; other material shows up to ten anterior and 22 posterior teeth. In specimens where the umbo has been removed (e.g. Pl. 1, fig. 9) the teeth continue beneath the umbones, where, however, they become much smaller; it is not possible to see these teeth with the umbo in place as the hinge-plate lies so closely beneath the umbones. Up to ten teeth may be hidden from view in this way. The hinge-line is essentially straight and the hinge-angle is close to 180° on the holotype and on the majority of specimens. In forms where the hinge-line appears essentially straight, curvature is confined to its posterior extremity, where it follows the curve of the dorsal margin of the valves.

There is considerable variation in shape. Some examples are strongly truncated posteriorly, so that the hinge-line curves strongly at a point very much closer to the umbonal region than is normal for this species. Because these are so distinct it was thought they belonged to a separate species, but enough material was collected to establish that this is simply a posteriorly very abbreviated form, with intermediates occurring between it and the more usual morphologies. With this shortened hinge, the species appears to have a high hinge angle; this is the result of transposing the normal angle of the posterior part of the hinge-line closer to the umbo. In these posteriorly truncated forms (e.g. Pl. 1, figs 5–6) the posterior part of the hinge-line bends through an angle approaching 50°. Others are intermediate in shape (e.g. Pl. 1, fig. 7). Notwithstanding these differences in length, the posterior part of the dorsal margin remains closely parallel to the anterior part of the ventral margin. The teeth in any specimen may be straight or chevron-shaped.

The exterior of the shell is basically smooth, but some specimens show fairly regular, stronger growth increments, giving a coarse concentric ornament.

Remarks. *Nucula*? *laevis* (Sowerby *in* Murchison, 1839) is a junior homonym of *N. laevis* Say, 1824, from the Miocene of Chesapeake Bay, Maryland, and remained unused until its quotation by Morris (1978). Sowerby's material is a mudstone block with three palaeotaxodonts (BGS, Geol. Soc. Coll. 6849) which was identified as 'the type' by Blake (1902). No holotype was designated by Sowerby, who described the species as being three-and-a-half lines long and nearly two lines high (a line is equivalent to 2·1 mm). Dimensions of the largest specimen (Pl. 1, fig. 8) are 7·2 mm long and 4·0 mm high, a close correspondence with Sowerby's measurements; this is identified as the one that he described and is here designated the lectotype of his (unavailable) species. The label is badly faded, but the specimen is stated by Sowerby (*in* Murchison 1839, p. 635) to be from 'Pensarn, near Caermarthen in black schist' and the lithology is consistent with that exposed in the Roman Road section there, described in *The Silurian System*. The locality was re-collected by Fortey and Owens (1978) who assigned it to the Bolahaul Member of the Ogof Hên Formation, of the same age as the Llangynog fauna.

Sowerby's species was not referred to by Carter (1971) in his revision of the Ramsey Island fauna. *Ctenodonta menapiensis* Hicks, refigured by Carter (1971, pl. 38, figs 1–2) as *Praenucula menapiensis*, was described as being anteriorly elongated, with the umbones at the posterior; if it is a *Praenucula*, this orientation is correct, but it is possible that it was wrongly oriented by Carter. In that case, the pronounced anterior adductor impression could suggest that it belongs instead to *Pensarnia*. In view of the similar age and relative proximity of Ramsey Island, the two may well be congeneric, but as Hicks' material is so poorly preserved and considerably distorted, specific comparisons are meaningless.

Mr S. P. Tunnicliff has drawn to my attention specimens of *Pensarnia* from the Mytton Flags of Shropshire in the British Geological Survey collections. These clearly belong to the genus, but may represent a new species. They are of early or mid-Arenig age.

Genus PAULINEA gen. nov.

Derivation of name. For my wife, Pauline.

Type species. *Paulinea parva* sp. nov.

Diagnosis. Moderately inflated praenuculids with shape ventral to hinge semicircular to subcircular and prominent, generally blunt umbones within anterior half of shell, not strongly curved over hinge-plate. Hinge-line with graded series of peg-like taxodont teeth smaller beneath umbones and increasing in size outwards (gradidentate); hinge plate curved ventrally anteriorly and posteriorly. Anterior adductor circular, rather shallowly inserted, with dorsally situated pedal retractor scar visible in some; posterior adductor very shallowly inserted, larger, subcircular, often not discernible. Exterior of shell smooth or with occasional strong growth increments. Ventral margin of shell very thin.

Stratigraphical range. Early Arenig, Moridunian Stage.

Remarks. This genus is more rounded in outline than *Pensarnia*, has more gradually graded tooth size (gradidentate of Cope 1995) and the umbones are less pronounced on internal moulds and are not so strongly curved over the hinge-plate as in *Pensarnia*. The adductor muscles are also less deeply inserted than in the latter. *Paulinea* does not compare easily with any other praenuculid, and is readily distinguished by its shape, outline, and hinge-line.

Paulinea parva sp. nov.

Plate 1, figures 11–22

Derivation of name. From the Latin *parva* (= small), alluding to the small size of this species.

Material. 96 specimens (49 LV, 46 RV, 1 CV). Holotype: NMW 78. 17G. 1078. Paratypes: NMW 78. 17G. 1079–1173.

Diagnosis. As for genus.

Description. Moderately inflated praenuculid varying in shape from ovoid to subcircular, with well-defined umbo. The holotype, a right valve internal mould, is 6·5 mm long and 4·8 mm high and lies towards the larger end of the size range. Many of the paratypes are between 5·0 and 6·5 mm long, but some are even smaller. Morphologies vary from elongated forms (length: height ratio approaches 1·5:1; e.g. Pl. 1, fig. 11) through to those in which the ratio approaches 1:1 (Pl. 1, fig. 12). Thus NMW 78. 17G. 1110 is 7·7 mm long and 5·2 mm high and NMW 78. 17G. 1081 (Pl. 1, fig. 19) is 4·3 mm long and 4·2 mm high. The holotype shows a lightly impressed circular anterior adductor muscle scar, dorsal to which is a faint triangular impression of the anterior pedal retractor. The posterior adductor scar is quite faintly impressed and is subcircular; its area is about twice that of the anterior scar. A very faint area extending dorso-anteriorly from this scar may be a posterior pedal retractor. In many specimens the posterior adductor scar is not visible, but in the occasional specimen it may be pronounced.

The greatest length is achieved about half-way between the hinge-line and the ventral margin; both anterior and posterior margins are rounded. The hinge-line is generally significantly shorter than the shell length and a series of peg-like taxodont teeth are present. On the holotype there are five anterior to the umbo and seven behind; subumbonal teeth are not visible on the holotype, but other specimens show that teeth are continuous beneath the umbo, where they are smaller. The teeth may number up to 20; they follow the curve of the hinge-line anteriorly and posteriorly. The hinge-angle is close to 180°, but because the ends of the hinge-plate curve ventrally in many specimens the impression gained is of a smaller hinge angle.

The exterior of the shell is generally smooth, but a few forms have accentuated growth increments and in a further few these are so pronounced that the shell appears to have a pronounced commarginal ornament.

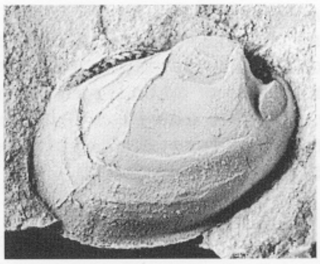
Remarks. This species differs from any described hitherto. The ovoid morphotype superficially resembles *Ctenodonta cambriensis* Hicks from the Arenig of Ramsey Island, which, however, has a length:height ratio approaching two and has less prominent umbones. I have examined Carter's (1971) lectotype of Hicks' species (Manchester Museum MM 10042) and agree that it is a palaeotaxodont. Like much of Hicks' material it is so badly preserved and distorted by cleavage that I recommend restricting the name to the type material. It is impossible to compare the dentition of any of Hicks' material with the Llangynog palaeotaxodonts.

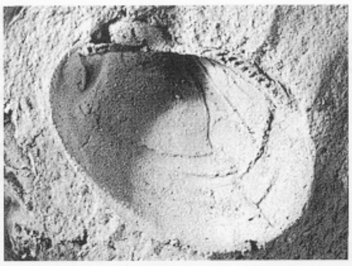
EXPLANATION OF PLATE 1

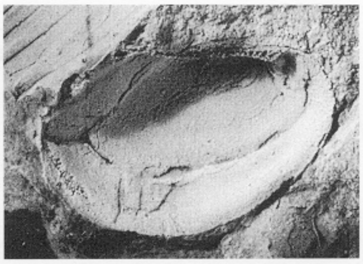
Figs 1–10. *Pensarnia laeviformis* gen. et sp. nov. 1, NMW 78. 17G. 1022, holotype; internal mould of right valve. 2, latex cast of holotype. 3, NMW 78. 17G. 1071; latex cast of left valve. 4, NMW 78. 17G. 1055; right valve, internal mould. 5, NMW 78. 17G. 1051; left valve, internal mould of extremely shortened form. 6, latex cast of specimen shown in fig. 5. 7, NMW 78. 17G. 1060; left valve, internal mould. 8, BGS Geol. Soc. Coll. 6849; left valve, internal mould, figured by Sowerby (*in* Murchison 1839, pl. 22, fig. 1) as *Nucula*? *laevis*, Roman Road, Pensarn. 9, NMW 78. 17G. 1063; left valve, internal mould, umbo removed to show dentition, posterior end of hinge-plate missing. 10, NMW 78. 17G. 1057; latex cast of left valve external mould. 1–8, 10, ×4; 9×6·5.

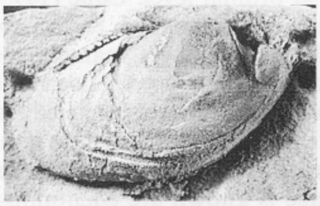
Figs 11–22. *Paulinea parva* gen. et sp. nov. 11, NMW 78 17G. 1078, holotype; right valve internal mould. 12, NMW 78. 17G. 1151; left valve, internal mould of shortened form. 13, NMW 78. 17G. 1114; latex cast of left valve. 14, NMW 78. 17G. 1098; right valve, composite mould, showing growth increments. 15, NMW 78. 17G. 1117; enlarged view of gradidentate dentition, right valve, internal mould with umbo removed. 16–17, NMW 78. 17G. 1161; left valve, internal mould and latex cast. 18, NMW 78. 17G. 1172; left valve, internal mould. 19, NMW 78. 17G. 1081; right valve, internal mould of shortened form. 20, NMW 78. 17G. 1164; internal mould, right valve with prominent umbo. 21, NMW 78. 17G. 1091; left valve, internal mould with pronounced growth increment. 22, NMW 78. 17G. 1151; left valve, internal mould, small circular form. 11–14, 16–22, ×4; 15, ×6·5.

PLATE 1

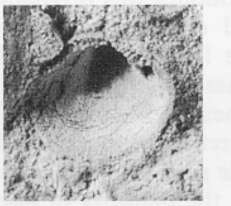

1


2

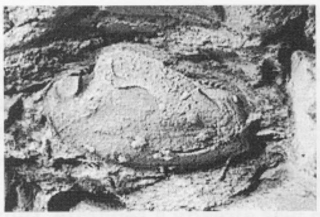

3

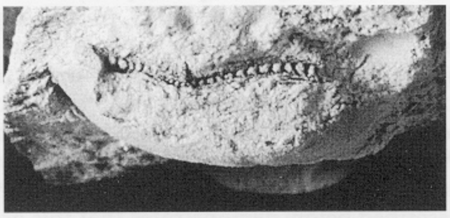

4

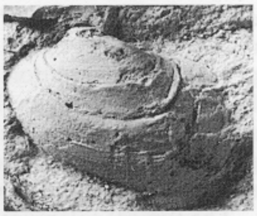

5

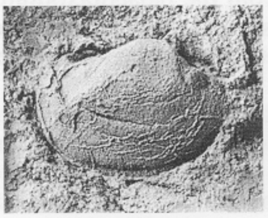

6


7


8


9


10

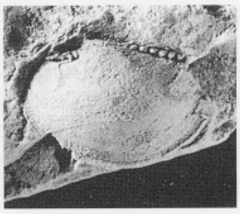

11

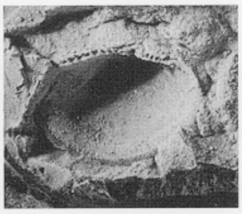

12

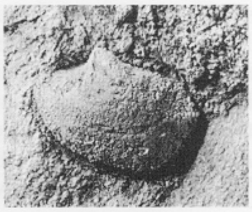

13

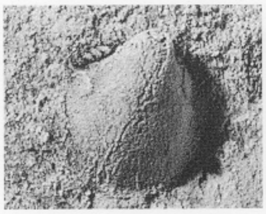

14


15


16


17


18

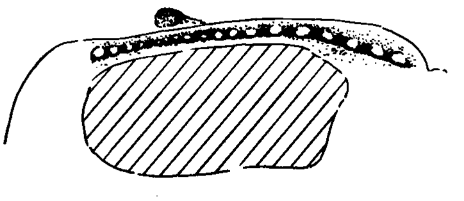

19


20


21


22

COPE, *Pensarnia*, *Paulinea*



TEXT-FIG. 3. *Paulinea parva*; NMW 78. 17G. 1161; *camera lucida* drawing of hinge region of left valve, internal mould. Shaded area is matrix exposed after removal of umbo. Impression of umbo is seen above the hinge line; × 10. Compare with Plate 1, figures 16–17 which are internal mould and latex cast of same specimen before removal of umbo.

Subclass LIPODONTA Cope, 1995

Remarks. The term Lipodonta was originally used by Iredale (1939) at ordinal level. Cope (1995) elevated it to the level of a subclass. Because modern solemyoid and nucinellid forms are protobranch, they have frequently been allied to the other protobranch bivalves, namely the Nuculoida, in the subclass Palaeotaxodonta. However, there are important differences between the two groups including: their shell structure (Taylor *et al.* 1969, 1973), which is unique; a reduced gut in the Lipodonta; a different protobranch gill structure in each group; the Lipodonta also have non-ridged palps and lack the palp proboscides of the Nuculoida. In contrast to the taxodont dentition of the palaeotaxodonts, the majority of lipodontids in which the hinge is known are edentulous. Indeed little seems to unite the two groups except the protobranch gill (as noted by Newell *in* Cox *et al.* 1969, pp. N212–N213). However, as Cope (1995, p. 363) suggested, there now appears good reason to believe that some fossil palaeotaxodonts could have had filibranch gills and so the protobranch condition may not be the diagnostic feature hitherto accepted. Pojeta (1978, 1988) and Pojeta and Runnegar (1985) argued that solemyoids are derived from palaeotaxodonts, and figured anteriorly elongated palaeotaxodonts which are claimed to show the derivation of solemyoids from palaeotaxodonts in the Whiterockian (= Llandeilo). Thus, they claim, both groups should be united in the Palaeotaxodonta. This was also the view of Boss (1982).

The typical solemyoid described below demonstrates that this group was already a separate, fully evolved stock by the early Arenig. Even if they were derived originally from the palaeotaxodonts (a quite reasonable hypothesis) their origins must be pre-Arenig; thus the forms figured and described by Pojeta (1988) must be viewed either as persisting intermediate forms, or as a parallel evolution by palaeotaxodonts during the late mid Ordovician.

Since there are major morphological differences in the soft part anatomy and shell structure and form in these two predominantly protobranch groups, and it is clear that they have been separate since, at latest, earliest Ordovician times, it seems logical to place them in separate subclasses. It seems probable that the separation of the Lipodonta from the Palaeotaxodonta occurred very early in the history of the Bivalvia, but we lack the necessary fossils to link the subclasses. In the *Treatise* (Cox 1969), the solemyoids were placed within the subclass Cryptodonta Neumayr, 1884. However, that subclass has now been discredited as a medley of unrelated forms including pteriomorphians and rostroconchs, amongst others. For this reason, Cope (1995) revived Lipodonta, but as a subclass, which comprises (Cope 1995) one order (Solemyoida Dall, 1889) and two superfamilies. The Solemyoidea Adams and Adams, 1857 includes one family, Solemyidae Adams and Adams, 1857. The Nucinelloidea Vokes, 1956 includes two families: the Nucinellidae Vokes, 1956 and the Manzanellidae Chronic, 1952 (see Pojeta 1988).

Order SOLEMYOIDA Dall, 1889

Superfamily SOLEMYOIDEA Adams and Adams, 1857

Family SOLEMYIDAE Adams and Adams, 1857

Genus OVATOCONCHA gen. nov.

Derivation of name. From the ovoid shape of the shell.

Type species. *Ovatoconcha fragilis* sp. nov.

Diagnosis. Anteriorly elongated bivalve with subdued umbones near posterior end. Straight hingeline three-quarters length of shell. Shell thin. Large anterior and small posterior muscle impressions. Hinge unknown.

Remarks. The assignation of this rather featureless shell to the Solemyoida is based on its general overall shape, its muscle scars and the fact that all the specimens seem to be of conjoined valves displaying an anterior and possibly a posterior gape. This suggests that this species may have lived deeply buried in the sediment, away from post-mortem reworking; this is the mode of life of modern solemyoids. The fracturing of the shell appears to be a product of compression, and the pattern of fractures is quite similar to some of those shown by Carboniferous forms figured by Pojeta (1988, pl. 22). Some specimens also show the tracks of radial mantle muscle scars. All solemyoids are of similar shape and form (see illustrations in Pojeta 1988). *Ovatoconcha* appears closest to *Psiloconcha* Ulrich, 1894, but differs in that the umbones are more subdued and the dorsal and ventral margins of the shell are more parallel. Although the specimens are compressed, they appear to have been originally considerably less inflated than *Psiloconcha* (see Pojeta 1988, figures on pls 17–20) and much less so than in *Dystactella* Hall and Whitfield, 1872 (Pojeta 1988, figures on pls 6–10).

The silicification of shells of this species suggests that they originally had a high organic content, as the lingulate brachiopods and the conulariids (which had a high organic content in their shell) are similarly preserved. Modern solemyoids have a thick periostracum and a thin brittle shell with a high organic content to the calcareous parts of the shell (Taylor *et al.* 1969, 1973).

The early Arenig age of *Ovatoconcha* is earlier than the Upper Whiterock age (Llandeilo), for the earliest known species of *Psiloconcha* (*P. senecta* Sardeson, 1896 from the St Peter Sandstone of Minnesota), and it is thus the earliest solemyoid.

Ovatoconcha fragilis sp. nov.

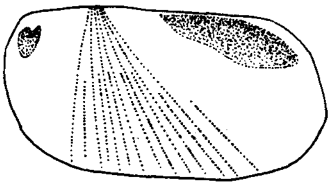
Plate 4, figures 1–2

Derivation of name. From the originally brittle shell.

Material. Five specimens. Holotype: NMW 78. 17G. 1174. Paratypes. NMW 78. 17G. 1175–1178.

Diagnosis. As for genus.

Description. It is assumed that the shell is elongated anteriorly, as in other solemyoids; the umbones thus lie close to the posterior end. The holotype (Pl. 4, fig. 1) is a silicified right valve 17·5 mm long; its height beneath the umbo is 8·7 mm, but the maximum height of 9·6 mm is achieved some 7–8 mm anterior to this point. The umbo is very subdued and appears to be slightly opisthogyral. The surface of the valve is ornamented with fine concentric growth lines; this appears to be the only ornament. Wrinkling of the shell material is believed to be a post-mortem feature. A granulose texture displayed on this specimen is believed to indicate the positions of adductor muscle impressions made visible through compression of the very thin film of silica replacing the shell; these are present as two discrete scars, a small posterior scar and a greatly enlarged anterior scar which extends along the dorsal margin of the valve. Paratype NMW 78. 17G. 1175 (Pl. 4, fig. 2) is somewhat larger (length estimated at 21·5 mm; height below umbones *c.* 9 mm; maximum height 10·5 mm) and both valves are present. The largely hidden left valve is visible at its anterior extremity and shows clearly that the valves gaped anteriorly. From the umbo and directed obliquely forwards are some ill-defined weak radial ridges; these number eight or nine in the umbonal region, probably twice that number towards the ventral margin of the valve. These radial lines appear to be mantle muscle scars (cf. Pojeta 1988, pl. 22) and are also shown, but not so clearly, by paratype NMW 78. 17G. 1176 (not figured). The intersection of the radial mantle tracks with the growth incremental lines produces an irregular reticulation to the shell which is enhanced by secondary wrinkling of the shell and its subsequent cracking. Paratype NMW 78. 17G. 1175 also shows the muscle impressions well; again a small posterior scar and a much larger anterior scar. None of the material shows the hinge which is presumed to be edentulous.



TEXT-FIG. 4. *Ovatoconcha fragilis*; diagrammatic representation of right valve to show position and shape of adductor muscle scars and tracks of radial mantle muscles. Figure is composite of several specimens; ×2.

Remarks. Since at least three of the five specimens of this species consist of conjoined valves, it appears probable that it may have been deeply infaunal (as are modern solemyoids). The fact that the shells were originally clearly so thin and delicate also lends support to the belief that these forms had a mode of life very similar to that of the modern solemyoids. This material is considerably smaller than that figured by Pojeta (1988).

Subclass PALAEOHETERODONTA Newell, 1965
Order ACTINODONTOIDA Douvillé, 1912
Superfamily GLYPTARCOIDEA superfam. nov.

Diagnosis. Actinodontoids in which the cardinal teeth, instead of radiating out from beneath the umbo, as in the Actinodontoidea, radiate out from a point whose origin is beneath the umbo, but well ventral of the hinge plate and towards the centre of the valves; i.e. the teeth fan out in the opposite direction to that which obtains in the Actinodontoidea.

Remarks. The direction of radiation of the teeth appears to be a fundamental point of distinction between the Glyptarcoidea and the Actinodontoidea. Its significance is that the glyptarcoidean is the type of dentition from which it is easy to derive cyrtodontoid dentition; thus the Glyptarcoidea can be seen as the ultimate origin of the subclasses Pteriomorphia and Neotaxodonta (Cope 1995). Glyptarcoideans could also be derived quite readily from a palaeotaxodont ancestor; the anterior teeth being developed from individual palaeotaxodont teeth and the posterior tooth developing a pseudotaxodont form from an initial single blade-like tooth.

Tironucula Morris and Fortey, 1976 was shown by those authors to develop its taxodont dentition from a juvenile pair of blade-like teeth; they suggested that this developmental pattern implied that palaeotaxodonts could have been derived from actinodontoid ancestors. Pojeta (1978) discussed this feature and the opposite pattern discovered in some Recent palaeotaxodonts by Allen and Sanders (1973), where genera such as *Silicula*, which are clearly of palaeotaxodont origin, develop actinodontoid dentition. The opposing views generated by these forms have fuelled speculation on the nature of the ancestral bivalve dentition.

The early Cambrian *Pojetaia*, with its undoubted palaeotaxodont teeth provides evidence of the antiquity of this type of dentition. Runnegar and Bentley (1983) showed that the mean adult size of *Pojetaia* was only 1·2 mm, and that its hinge was basically similar to that of juvenile specimens of *Tironucula* of the same size. In other words, at extremely small sizes it becomes very difficult to distinguish between actinodont and taxodont dentitions. It is possible that *Tironucula* could be the rule rather than the exception – that early Palaeozoic palaeotaxodont teeth developed ontogenetically from blade-like juvenile teeth – but that this has no implications for the greater antiquity of actinodontoid teeth. Indeed, actinodontoid dentition could be readily derived by paedomorphosis of palaeotaxodont dentition of the *Tironucula* type, so that early actinodontoids could be expected to have two simple blade-like teeth, one anterior and one posterior, and that more complex actinodontoid patterns developed from those. I believe the comparison with the modern protobranchs described by Allen and Sanders (1973) and Sanders and Allen (1973) is wholly inappropriate. Those authors agree that a considerable evolution of the protobranchs has taken place in the deep sea; presumably protobranchs have survived in such variety there because of the ready availability of food for deposit feeders, and reduced competition from other bivalves. Appraisal of the dentition of these forms shows that when they are pseudo-actinodontoid, the ligament is still to be found centrally on the hinge plate beneath the umbo. This I believe is of high significance, because palaeotaxodont bivalves had external ligaments until the Silurian (Pojeta and Runnegar 1985) and it is not until then that the ligament becomes internal and housed centrally on the hinge-plate. This differs considerably from actinodonts, which had an external opisthodetic ligament. Thus the dentition of these modern deep-sea non-taxodont protobranchs can logically be interpreted as being secondarily derived from a palaeotaxodont dentition which has a central resilifer; this means that the derivation could not date from further back than early Silurian (in fact it appears likely to be of much later origin and to date from the major deep-sea radiation of the protobranchs in the Mesozoic and Cenozoic).

It could be argued that the glyptarcoideans, with their teeth radiating in the opposite direction to those of the actinodontoideans, are more remotely related to them than at superfamilial level. However, both actinodontoideans and glyptarcoideans have types of dentition which could be readily derived from palaeotaxodont ancestors and both these groups gave rise to forms which have filibranch gills. It therefore seems probable that the Actinodontoida had filibranch gills, as the development of a feeding gill from the protobranch condition is unlikely to have arisen more than once; I therefore draw the parsimonious conclusion that the Actinodontoida is monophyletic and that both its superfamilies had filibranch gills. Allen and Sanders (1969) suggested that the Actinodontoida were probably protobranchs; this was based on their view that the solemyoid *Nucinella* was a living actinodont. However, Pojeta (1988) has shown that *Nucinella* has its umbones at the posterior and is elongated anteriorly; the lateral teeth are entirely anterior and they are separated by an edentulous space from the subumbonal taxodont teeth. In all these features it differs fundamentally from the actinodontoids.

Family GLYPTARCIDAE nov.

Diagnosis. As for superfamily, as this is the only family yet recognized.

Remarks. This new family is proposed to include *Glyptarca* Hicks, 1873 and the species described as ?*Dolabra lusitanica* Sharpe, 1853, and revised by Babin and Gutiérrez-Marco (1991) who referred it with question to *Glyptarca*, which they pointed out was poorly defined. However, it is now possible to define *Glyptarca* precisely with a formal full diagnosis, and it is clear that '?*Dolabra lusitanica*' requires a new generic assignation, for which *Hemiprionodonta* is proposed, with '?*D. lusitanica*' as type species. I agree with Babin and Gutiérrez-Marco (1991) in assigning *Arca naranjoana* Verneuil and Barrande, 1856 to this species. Another species, brought to my attention by Mr S. P. Tunnicliff, which clearly belongs to *Hemiprionodonta* is *Palaearca* (*Matheria*?) *quadrata* Salter, 1866 (p. 343, woodcut 12, fig. 3) from the Caradoc of North Wales. *Hemiprionodonta lusitanica* was fully described and illustrated by Babin and Gutiérrez-Marco (1991, text-figs 6–7). It differs from *Glyptarca* species in having a somewhat different dentition in which the anterior teeth are not a continuous group, which Babin and Gutiérrez-Marco separated into two anterior pseudolaterals and two pseudocardinals; the latter do not overlap the posterior lateral tooth to any significant degree. *H. lusitanica* also has rounder and generally more deeply impressed adductor scars than *Glyptarca* species, and is significantly larger. *Hemiprionodonta* is clearly related to *Glyptarca*, and belongs to the same family; it may even be a direct descendant of *Glyptarca*, being somewhat younger stratigraphically.

Genus GLYPTARCA Hicks, 1873

Type species. Subsequently designated by Newell 1969: *Glyptarca primaeva* Hicks, 1873.

Diagnosis. Carinate bivalve with anterior set of at least four teeth overlapping posterior teeth subumbonally. Posterior teeth anteriorly separate or pseudotaxodont, posteriorly pseudotaxodont or lamellar.

Remarks. Glyptarca was founded by Hicks (1873, p. 48) for *G. primaeva*, which occurs abundantly on Ramsey Island and at Tremanhir in Pembrokeshire (south-west Dyfed). I have examined all the syntype and topotype material in the collections of the British Geological Survey, the Sedgwick Museum and the Manchester Museum. Hicks' description mentions three teeth anterior to the umbo; this is shown unequivocally only by one syntype, a somewhat distorted specimen (BGS GSM 24200) figured by Hicks (1873, pl. 5, fig. 2) and by Carter (1971, pl. 38, fig. 14). The lectotype, (Carter 1971, pl. 38, fig. 8) appears to me to be an unfortunate choice, as it is an external mould and does not show the dentition. Some syntypes show the single posterior tooth, but the majority show no trace of dentition; this is probably a vagary of preservation – much of the Ramsey Island material is badly distorted by cleavage and it is likely that the valve has been sheared over the hinge plate, thus making it invisible. This seems to have occurred regularly with specimens of *Glyptarca*, but often on the same slabs there are occasional palaeotaxodont bivalves with dentition preserved, though distorted. This difference in preservation seems due to the hinge plate being well beneath the dorsal margins of the valves in *Glyptarca* whilst it is not so far beneath them in the palaeotaxodonts. I prefer this interpretation to the alternative, that there are two genera represented by Hicks' syntypes of *G. primaeva*, a toothed form and an edentulous form. I thus interpret the lectotype as a form with a hinge plate which has been effectively obliterated by crushing/shearing of the valve over it. It forms far from ideal material on which to found a genus and some further action is needed if the name is to be preserved as a useful taxonomic entity. No Ramsey Island material of *Glyptarca* appears to exist which has completely preserved dentition. In an attempt to stabilize the nomenclature, I have assumed that the lectotype belongs to the same species as the paralectotype figured by Carter (1971, pl. 38, fig. 14). In order to allow a better interpretation of the genus, a new species of *Glyptarca* is described below which has perfectly preserved dentition. The poor preservation of the Ramsey Island material allowed Hicks only to give an inadequate description of *G. primaeva*.

Carter (1971, p. 259) believed that *Glyptarca* was not included in the *Treatise* (Cox *et al.* 1969), but it is included on p. N256 as a synonym of *Parallelodon*, where Newell designated the type species (by monotypy), making Carter's (1971, p. 258) designation invalid. Newell's designation was also overlooked by Babin and Gutiérrez-Marco (1991). The reference in the *Treatise* may have been inserted at a late stage, as it follows the description and figure references, and it is omitted from the index. The dentition, described fully below (under *G. serrata* sp. nov.) shows that *Glyptarca* is not a *Parallelodon*, but is a palaeoheterodont, and is clearly not related to the modiomorphoid genera *Byssoderma* Isberg, 1934 or *Colpomya* Ulrich, 1894 as Carter (1971, p. 259) suggested it might be.

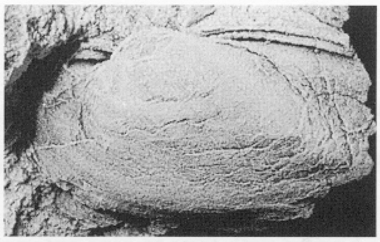
EXPLANATION OF PLATE 2

Figs 1–11. *Glyptarca serrata* sp. nov. 1, NMW 78. 17G. 801, holotype; left valve, internal mould. 2, NMW 78. 17G. 691; left valve, internal mould of small shortened form. 3, NMW 78. 17G. 519; left valve, composite mould. 4, NMW 78. 17G. 550; left valve internal mould, showing non-crenulated posterior end of posterior tooth. 5, NMW 78. 17G. 701; small left valve, internal mould, with posterior tooth entirely fused, but showing crenulations. 6, NMW 78. 17G. 795; internal mould of right valve showing carinate posterior shoulder. 7, NMW 78. 17G. 821; left valve, internal mould showing fused posterior portion of tooth. 8, NMW 78. 17G. 685; latex cast of external mould. 9, NMW 78. 17G. 606; right valve, internal mould. 10, NMW 78. 17G. 490; enlarged view of right valve internal mould with umbo removed, to show overlap of anterior and posterior dentition in subumbonal region. 11, NMW 78. 17G. 540; enlarged view of right valve as in fig. 10. 1–9, ×4; 10–11, ×6·5.

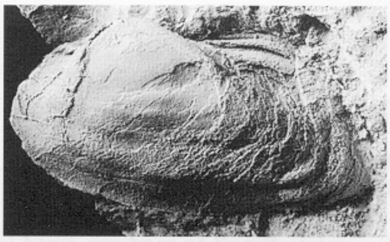
Fig. 12. *Fortowensia grandis* gen. et sp. nov.; NMW 78. 17G. 1192; latex cast of holotype; left valve, internal mould. cf. Pl. 6, fig. 4; ×2·8.

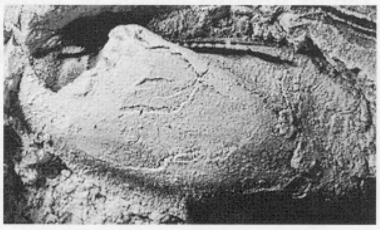
Fig. 13. *Celtoconcha foveata* gen. et sp. nov.; NMW 78. 17G. 1218; poorly preserved internal mould of right valve showing muscle scars and vertical muscle tracks; ×4.

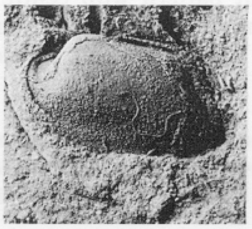
PLATE 2


1

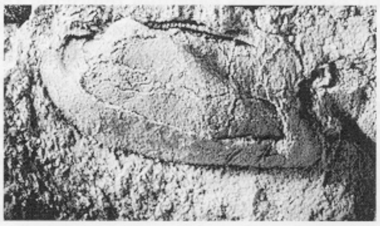

2

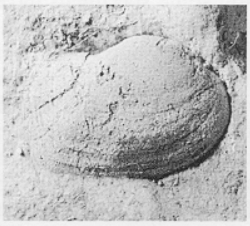

3

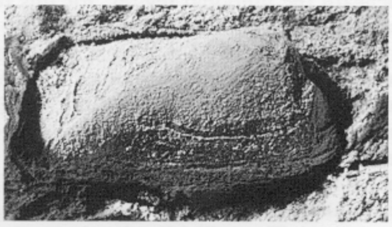

4

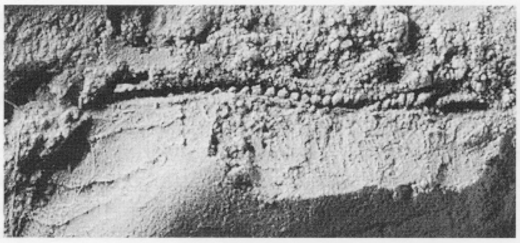

5

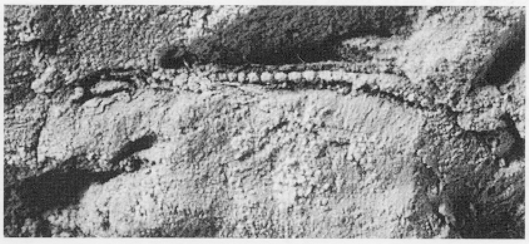

6

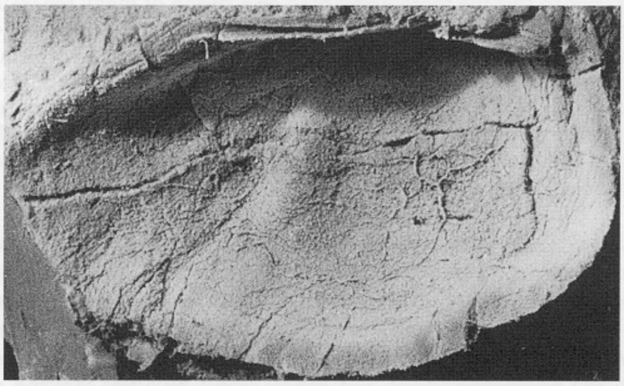

7

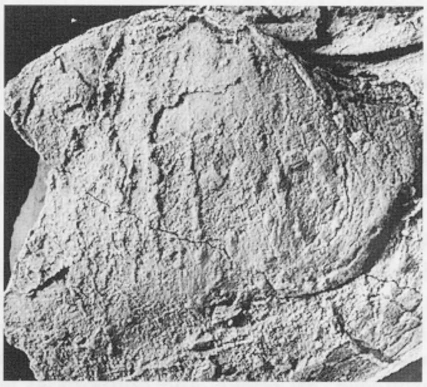

8


9


10


11


12


13

COPE, *Glyptarca*, *Fortowensia*, *Celtoconcha*

Glyptarca serrata sp. nov.

Plate 2, figures 1–11

Derivation of name. From the serrated appearance of the posterior lateral tooth.

Material. 484 specimens (218 LV, 201 RV, 65 CV). Holotype: NMW 78. 17G. 801. Paratypes: NMW 78. 17G. 448–800; 78. 17G. 802–931.

Diagnosis. Small to medium-sized (up to 14·4 mm long) elongate bivalve with four to nine anterior teeth arranged in a radially divergent pattern with centre of radius towards middle of valves. Anterior teeth overlap posterior tooth in central region of hinge-plate; posterior tooth in juveniles single and blade-like in each valve, but developing division into separate peg-like teeth as in palaeotaxodonts in mature forms.

Description. The specimens are 3·4–14·4 mm long and 2·2–7·7 mm high. A plot of length against height for the material shows a fairly continuous spread of points and it seems probable that various growth stages are represented. As the larger specimens show the dentition far better, specimens predominantly towards the larger end of the size range are figured herein.

The holotype shows the dentition well, although it is impossible to see the complex dental arrangement beneath the umbonal region; for this reason some specimens have been prepared by carefully removing the umbonal areas of the internal moulds so that details of the dentition become visible. The holotype is a left valve 11·6 mm long and 7·5 mm high. The external mould shows the exterior to be ornamented solely by growth lines which become most pronounced at the ventral part of the carina-like ridge which extends posteriorly from the umbo. The internal mould is not complete as the posterior end is broken away, but it shows most of the characteristic features of the species. The anterior adductor muscle impression is impressed very shallowly and is heart-shaped; lying adjacent to it in a dorsal position is a narrow triangular impression, presumably of a pedal retractor muscle. The posterior adductor is approximately the same size as the anterior, but is of roughly circular shape. The paratypes commonly show neither adductor scar, and both are, at best, only very shallowly impressed. The pallial line is not deeply impressed either; it is invisible on the holotype, but several paratypes show it to have been entire.

Impressions corresponding to five anterior teeth are visible on the holotype; others may be present beneath the umbo. The most anterior tooth reaches almost to the anterior margin of the valve and is slightly curved. In some paratypes (e.g. Pl. 2, fig. 11) there is pronounced curvature of this tooth. The remainder of the anterior teeth are radially disposed, with the centre of the radius lying towards the centre of the valve. Paratype NMW 78. 17G. 540 (Pl. 2, fig. 10) has had its umbo removed to show the dentition which includes a row of eight anterior teeth, rapidly diminishing in size posteriorly. On the holotype the second most anterior tooth bears fine longitudinal grooves, whilst paratype NMW 78. 17G. 550 (Pl. 2, fig. 4) has horizontal striations on its most anterior tooth; these exceptions apart, the teeth appear entirely smooth. The long posterior lateral tooth is arched to follow closely parallel to the dorsal margin of the valve. The anterior end of this is subdivided into several discrete teeth, and at least three of these are entirely free on the holotype. Paratype NMW 78. 17G. 550 appears to show about nine discrete teeth. Posterior to this the tooth appears to be a fusion of many separate peg-like teeth; in some the anterior end of the posterior lateral tooth may be divided into as many as 14 separate teeth, whilst others have the entire row fused. In this latter case, however, a crenulation is visible at the anterior end, showing a pseudo-separation. The subdivision of this tooth may largely be a function of size or maturity, as the smaller specimens show little or no such separation, merely a single tooth. One of the most distinctive features about the dentition of *Glyptarca serrata* is that the anterior and posterior rows of teeth overlap significantly beneath the umbones, the anterior teeth lying below the posterior. This feature is, however, not visible unless the umbones are removed from the internal moulds.

Remarks. This species is clearly closely related to *Glyptarca primaeva* Hicks, from which it may be distinguished readily by its lack of a median sinus. This feature appears to be real and not just a vagary of distortion. Within Hicks' type material of *G. primaeva* there is at least one specimen (BGS GSM 24199) which may be referred to *G. serrata*; it is on a small slab measuring some 35 mm square, with over 40 small bivalves, most of which are featureless. The slab was labelled '*Glyptarca primaeva*' by Hicks, and contains at least one palaeotaxodont and many small bivalves lacking a

TEXT-FIG. 5. *Glyptarca serrata*; *camera lucida* drawing of hinge region of internal moulds to show details of subumbonal overlap of the two sets of teeth. Shaded areas indicate matrix exposed after removal of umbones. Impressions of umbones may be seen above the hinge line. A, NMW 78. 17G. 490; right valve. B, NMW 78. 17G. 540; left valve. Both ×5.

median sulcus, and one specimen with a crenulated posterior tooth which is referable to *G. serrata*. However, none of Hicks' material of *G. primaeva* is well enough preserved to show the subumbonal dentition, even if the umbones were removed. Many of the characters of the genus are thus best displayed by *G. serrata*, and my intention here is to stabilize the generic name by providing an adequate diagnosis and description of better preserved material.

The overlapping dentition of *Glyptarca* is a rare feature in bivalves, and I have been able to find it in only two other genera: the palaeotaxodonts *Cardiolaria*, from the middle Ordovician, and some Jurassic species of *Palaeoneilo* (see Cox 1937). To find that two of the three genera possessing this distinctive dentition are of very similar age strongly suggests that they could be phylogenetically linked. Cope (1995, p. 363) proposed that such forms could provide a link between palaeotaxodonts and palaeoheterodonts.

Superfamily ACTINODONTOIDEA Douvillé, 1912

Diagnosis. Actinodontids with teeth radiating out ventrally from beneath the umbo.

Remarks. This superfamily includes all the non-glyptarcoidean actinodontians, and ranges from Tremadoc to late Devonian (assuming the families Carydiidae and Babinkidae are actinodontoids). The type species of *Actinodonta*, *A. cuneata* Phillips, 1848, is from the Upper Llandovery of Marloes Bay, Pembrokeshire (Dyfed), but Pojeta (1971) recorded it incorrectly from the middle Ordovician of Britain and designated one of Phillips and Salter's specimens (1848 pl. 21 fig. 2) as the lectotype. A lectotype had, however, been already designated (Stubblefield 1938) making Pojeta's designation invalid. However, both authors chose the same specimen (BGS GSM 59825).

Family CYCLOCONCHIDAE Ulrich, 1894

Remarks. The Cycloconchidae, as here restricted, embraces a group of closely allied genera in which the subumbonal teeth (pseudocardinals of Pojeta and Runnegar 1985) are in general much shorter and at high angles to the hinge when compared with the longer pseudolaterals (Pojeta and Runnegar 1985). However, in some forms there is a gradual lengthening of the posterior pseudocardinals, so that in some cases they merge imperceptibly into the pseudolaterals and it is difficult to separate the two.

The following genera are included: *Cycloconcha* Miller, 1874; *Actinodonta* Phillips, 1848; *Copidens* Pojeta and Gilbert-Tomlinson, 1977; *Ananterodonta* Babin and Gutiérrez-Marco, 1985; *Carminodonta* gen. nov., *Fortowensia* gen. nov. and *Celtoconcha* gen. nov. *Catamarcaia* Sánchez and Babin, 1993 may also belong, although those authors placed it in the Arcoida. However, it has a typical cycloconchid dentition which differs fundamentally from the arcoid type in lacking a subumbonal edentulous area; its one pteriomorph feature is the grooved ligamental area, but, as shown by Waller (1978), this may reflect an entirely lamellar ligament and not indicate a duplivincular condition. It does, however, suggest that the grooved ligamental area may have first arisen in the palaeoheterodonts, and the condition was then acquired by the cyrtodontoids. *Babinka* Barrande, 1881 was regarded by McAlester (1965, 1966) as a lucinoid heterodont; however, as discussed by Cope (1995, p. 366), because of its early appearance (range Tremadoc–Llanvirn) I prefer to regard it as a palaeoheterodont, and it may well be a cycloconchid in which the lateral teeth have been suppressed.

The genera which constitute the Cycloconchidae are a closely related group. *Carminodonta*, *Fortowensia* and *Celtoconcha*, from the lower Arenig, are amongst the earliest known members. *Catamarcaia* is from the upper Arenig, whilst *Copidens* is known from the Nora Formation of Australia which is dated as probably around the early–mid Ordovician boundary (Pojeta and Gilbert-Tomlinson 1977, p. 5). *Ananterodonta* is from the lower Llanvirn, whilst *Cycloconcha* is of mid–late Ordovician age and *Actinodonta* seems restricted to the lower Silurian. However, there are many references to this latter genus from the Ordovician, including one of Hicks' species from Ramsey Island. *Modiolopsis ramseyensis* was quoted by Carter (1971, p. 258) as being 'indistinguishable from *Actinodonta cuneata* Phillips'. I have examined Hicks' holotype of *M. ramseyensis* (Manchester Museum L10041) and found that its length is 22·8 mm as opposed to the 28 mm Carter records; its height is 10·3 mm (not 9 mm) and, although the specimen is quite distorted, the single long posterior tooth is the sole visible dentition and is quite unlike a cycloconchid. As Carter (1971, p. 250) remarked, most of Hicks' material should never have been named and in this case too the name should be restricted to the type material. Other examples of *Actinodonta* from the Ordovician can also now probably be referred to other genera. Pojeta and Gilbert-Tomlinson (1977, p. 4) have suggested that some of the specimens from the Grès Armoricain that Barrois (1891) referred to *Actinodonta* could belong to *Copidens*. Other generic assignations remain to be made, and most of the earlier references to *Actinodonta* seem to have been made by reference to one of the syntypes of *A. cuneata* figured by Phillips (1848), particularly his plate 21, figure 4, which came from the Wenlock (given as Lower Ludlow by Stubblefield 1938) and would now almost certainly be assigned to a separate genus following the stabilization of the nomenclature by the lectotype designation of Stubblefield (1938).

Davidia Hicks, 1873 was included in the Cycloconchidae by Morris (1978). However, as discussed below, Hicks' type material is totally uninterpretable and the figure of its cycloconchid dentition produced by Morris (1978, fig. 25) thus cannot belong to that genus. Regrettably this error was perpetuated by Pojeta and Runnegar (1985, p. 322). Morris' assignation of Barrois' species *Actinodonta carinata* to *Davidia* has been the cause of this confusion.

Genus CARMINODONTA gen. nov.

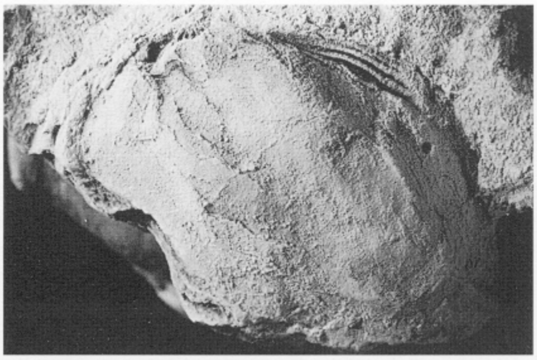
Derivation of name. From the comb-like organization of the hinge teeth.

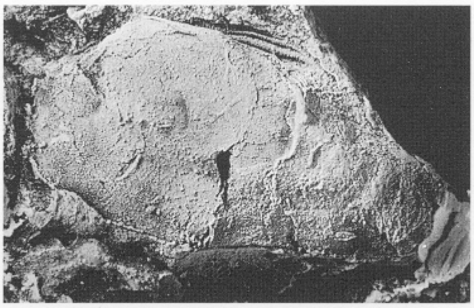
Type species. *Carminodonta crossi* sp. nov.

Diagnosis. Elongate prosogyral cycloconchid, with pronounced shoulder from umbo to posteroventral margin; shell terminated abruptly posteriorly. Radiating sheaf of eight to eleven pseudocardinal teeth elongating posteriorly into four or five pseudolaterals all borne on a hinge plate; one short or no anterior pseudolaterals. Anterior teeth not persisting to anterior end of hinge-line.

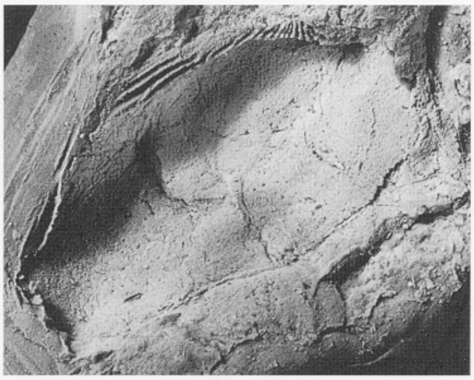
EXPLANATION OF PLATE 3

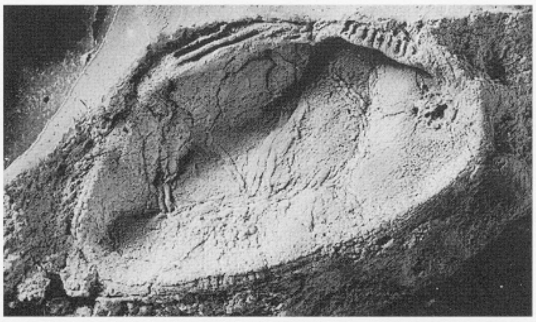
Figs 1–6, 8. *Carminodonta crossi* gen. et sp. nov. 1, NMW 78. 17G. 1185; left valve, internal mould. 2, NMW 78. 17G. 1179, holotype; left valve, internal mould. 3, NMW 78. 17G. 1182; latex cast of external mould of left valve. 4, latex cast of holotype as fig. 2. 5–6, NMW 78. 17G. 1180; latex cast and internal mould of left valve. 8, NMW 78. 17G. 1183; external mould of left valve, showing attached hinge-plate. All ×3.
Fig. 7. *Modiolopsis* sp. B; NMW 78. 17G. 1231; ×2.

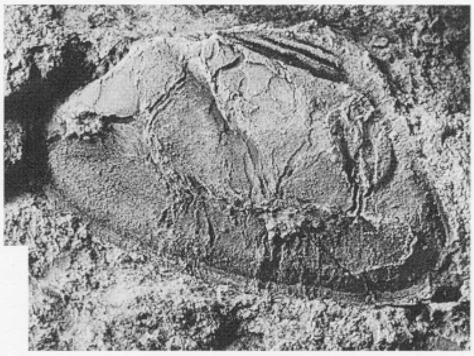

1

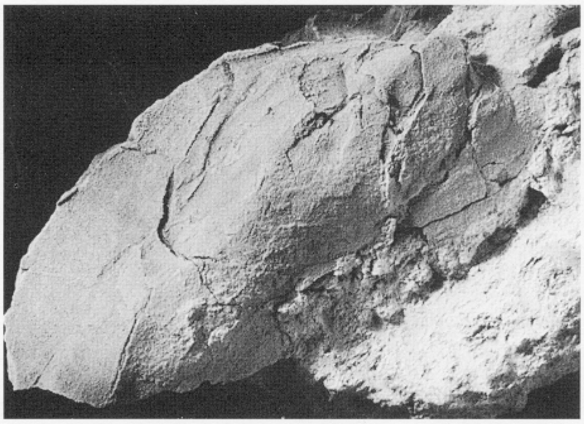

2


3


4


5


6


7


8

COPE, *Carminodonta*, *Modiolopsis*

Remarks. Carminodonta is distinguished from other cycloconchids by its dentition and shape. It is closest to *Actinodonta*, but may be readily distinguished from it by its overall shape, in particular by the posterior end of the shell which is abruptly truncated in *Carminodonta*, and tapers in *Actinodonta*. There are also significant differences in the dentition; the anterior teeth do not reach the anterior end of the hinge-line in *Carminodonta*, whereas in *Actinodonta* the teeth continue right to its anterior end. This was demonstrated best by Pojeta (1978, pl. 4) who figured latex replicas of both the lectotype (a left valve) and a right valve paralectotype (compare with Pl. 3, figs 4–5, 8). *Copidens* is distinguished from *Carminodonta* by its circular outline, the gradual increase in length of the teeth posteriorly, the proximity of its anterior adductor to the hinge-plate, and the lack of any posterior shoulder to the shell.

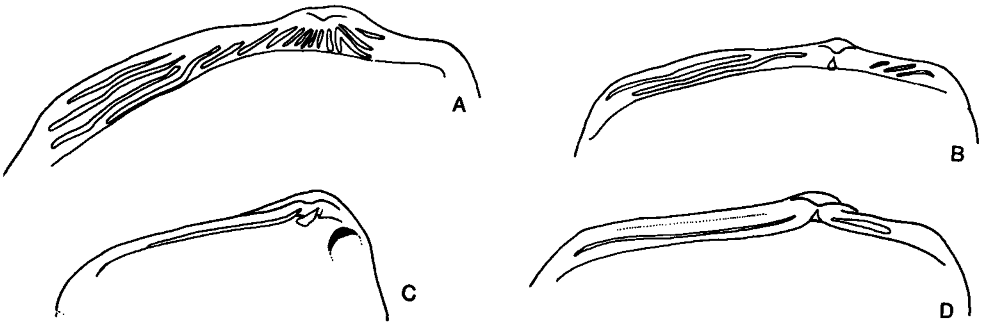
Carminodonta crossi sp. nov.

Plate 3, figures 1–6, 8

Derivation of name. For Mr F. R. B. Cross, formerly Chief Technician, Department of Geology, University College, Swansea, in acknowledgement of his assistance in the field and laboratory for many years.

Material. 13 specimens (8 LV, 4 RV, 1 CV). Holotype: NMW 78. 17G. 1179. Paratypes: NMW 78. 17G. 1180–1191.

Diagnosis. As for genus.



TEXT-FIG. 6. Diagrammatic representation of dentitions of left valves of the new actinodontoidean genera. A, *Carminodonta crossi*; ×4. B, *Celtoconcha foveata*; ×4. C, *Moridunia simplicidens*; ×3. D, *Fortowensia grandis*; ×2.

Description. The holotype is a left valve approximately 17·9 mm long (its posterior extremity is damaged) and 9·8 mm high; the maximum height is achieved slightly posterior of the umbo. Paratype NMW 78. 17G. 1180 (Pl. 3, fig. 6) shows the posterior end of the shell well and it can be seen to be obliquely truncated. Anterior and posterior adductor muscle scars are equally shallowly impressed; the anterior one is circular, the posterior being somewhat the larger and subcircular to scutate in shape. There is a well impressed anterior pedal retractor scar dorsal to the anterior adductor, particularly well shown by paratype NMW 78. 17G. 1181. The same specimen appears to show a faint pallial muscle impression, but this is not visible on any of the other material.

The exterior of the shell is shown by several paratypes, most of which are somewhat distorted. However, NMW 78. 17G. 1182 (Pl. 3, fig. 3), the best preserved, shows that the shell is ornamented by faint growth lines; towards the posterior end some of these are strengthened to form commarginal rugae. There is a marked shoulder running from the umbo to the postero-ventral margin, which is, however, not sharp enough to be termed a carina. One of the less well preserved specimens has a suggestion of a fine radial ornament which appears to be restricted to the posterior extremity of the shell.

The dentition is well shown by the holotype and several of the paratypes. It conforms to the same style in all the material. In the holotype the distinction between pseudocardinal and pseudolateral teeth is difficult to make as the posterior pseudocardinals merge into the anterior pseudolaterals. However, the holotype shows one clear anterior pseudolateral which lies parallel to the hinge; although it arises close to the pseudocardinal cluster it appears to be separated from it. Immediately posterior to this is a sheaf of ten teeth which radiate from the same point and which all appear to be dorsally united; these constitute the pseudocardinal cluster. Lying adjacent to and parallel with the posterior pseudocardinal tooth is the most anterior of the five posterior pseudolateral teeth; the two anteriormost are short, the others longer. The paratypes show a similar style of dentition, although none shows an anterior pseudolateral tooth. The number of pseudocardinal teeth varies from about eight up to eleven.

Dorsal to the posterior pseudocardinal teeth and the anterior two of the posterior pseudolaterals, the holotype bears a shallow impression which may even be a vagary of the preservation, but which may be the site of an external opisthodetic ligament.

Remarks. This is one of the rarer members of the Llangynog fauna, but is so distinctive that it can be recognized even with incomplete material, providing that the dentition is, at least in part, preserved. Similar rarity seems to apply to other genera in this group, *Ananterodonta* being known from only one specimen. In the case of the Llangynog fauna, *Carminodonta* constitutes less than 1 per cent. of the bivalve fauna.

Genus FORTOWENSIA gen. nov.

Derivation of name. After Drs R. A. Fortey and R. M. Owens, in recognition of their work on the Arenig Series.

Type species. Fortowensia grandis sp. nov.

Diagnosis. Elongate cycloconchid with a single pseudocardinal tooth in each valve and with one anterior and one posterior pseudolateral in the left valve; two of each in the right valve.

Stratigraphical range. Known only from the lower Arenig.

Remarks. The dentition and shape of this genus render it readily distinguishable from other palaeoheterodonts in the Llangynog fauna. Superficially it resembles the specimens of *Parallelodus* described below, but this is merely due to their similarity in size, and the two genera differ fundamentally in their shape and dentition. These same characters also serve to distinguish it from other palaeoheterodont genera; the reduced dentition separates it from other cycloconchids, but its shape is quite different from redoniids, and also actinodontoids with reduced dentition. It also differs from redoniids in lacking a deeply inserted anterior adductor with myophoric buttress.

Fortowensia grandis sp. nov.

Plate 2, figure 12; Plate 6, figures 3–4

Derivation of name. From the Latin *grandis* (= large). This is one of the largest bivalves of the fauna.

Material. 20 specimens (8 LV, 6 RV, 6 CV). Holotype: LV NMW 78. 17G. 1192. Paratypes: NMW 78. 17G. 1193–1211.

Diagnosis. Fortowensia c. 30 mm in length. Other characters as for genus.

Description. The holotype is approximately 29 mm long (the posterior extremity is broken) and 18·2 mm high. The anterior adductor muscle is shallowly impressed, but is just visible as a circular scar at the anteriormost part of the shell; the posterior adductor is not visible in most specimens. The umbones, although well-developed, arise gradually from the dorsal part of the valve. There is a single pseudocardinal tooth in each valve; on the holotype this appears to rise from beneath the umbonal region. The hinge-line is straight and there is a single long posterior lateral tooth in the left valve and two posterior lateral teeth in the right valve. There is a single anterior pseudolateral in the left valve and two in the right; both of these are short and closely parallel to the dorsal margin of the valves. The more posterior of the anterior pseudolaterals in the right valve arises close to the pseudocardinal tooth; its course is initially parallel with the pseudocardinal tooth, but then swings forward to be parallel with the dorsal margin.

Paratype 78. 17G. 1193 (Pl. 6, fig. 3) shows the posterior adductor muscle impression; it is considerably larger than the anterior scar, is rounded posteriorly but sharply triangulate towards its anterior origin. This specimen also shows well the posterior end of the shell, which is inclined gently back from the posterior end of the hinge line and rounded. A further feature shown by the same paratype is pallial punctae (extra pallial muscle impressions also found in other members of this fauna, particularly in *Falcatodonta*, described below).

Remarks. The size of *F. grandis* (length 25–*c*. 35 mm; the posterior extremity is missing on the longest specimen) is quite usual amongst Llanvirn or later faunas, but not in the early Arenig, when it was shared only by a few modiomorphoids, from which it is readily distinguished by its dentition and shape.

Genus CELTOCONCHA gen. nov.

Derivation of name. After the former inhabitants of Wales.

Type species. *Celtoconcha foveata* sp. nov.

Diagnosis. Strongly inflated quadrate to subquadrate postero-ventrally extended cycloconchid with single pseudocardinal tooth in left valve, and well-developed anterior and posterior pseudolateral teeth. Multiple pedal muscle insertion scars often prominent sub-umbonally.

Stratigraphical range. Known only from the Moridunian Stage, lower Arenig.

Remarks. This genus has reduced dentition in comparison with other members of the Cycloconchidae, as the pseudocardinal teeth are reduced to one in the left valve and only the single corresponding socket in the right valve. However, both anterior and posterior pseudolaterals are well-developed and there can be no doubt of the familial assignment; the teeth are certainly not reduced sufficiently to merit placement of *Celtoconcha* within the Redoniidae. When compared with other cycloconchids, the closest similarity is with *Cycloconcha*, but the anterior pseudolaterals are longer, and can be separated readily from the single pseudocardinal, whereas in *Cycloconcha* the two are not readily separable (e.g. see Pojeta and Runnegar 1985, fig. 13A). The other point in common with *Cycloconcha* is the multiple pedal muscle scars. The overall shape of the shell contrasts

---

EXPLANATION OF PLATE 4

Figs 1–2. *Ovatoconcha fragilis* gen. et sp. nov.; silicified composite moulds. 1, NMW 78. 17G. 1174, holotype; right valve displaying granulose texture over area of large anterior adductor. 2, NMW 78. 17G. 1175; conjoined valves, displaying right valve showing radial mantle muscle scars and large anterior adductor, much smaller posterior adductor partly visible. Both × 3.

Figs 3, 5. *Goniophorina* (*Cosmogoniophorina*) *extensa* sp. nov. 3, NMW 78. 17G. 1227; latex cast of external mould of left valve. 5, NMW 78. 17G. 1222, holotype; right valve, internal mould. Both × 3·5.

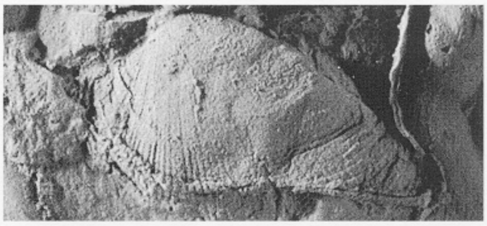
Figs 4, 7–8. *Celtoconcha foveata* gen. et sp. nov. 4, NMW 78. 17G. 1217; badly distorted right valve showing marked discrete pedal muscle scars; × 4·5. 7, NMW 78. 17G. 1215; left valve, internal mould; three pedal muscle scars just visible to posterior of umbo pointing to postero-ventral margin; × 3·5. 8, NMW 78. 17G. 1212, holotype; right valve, internal mould, lit to show pedal muscle scars; × 3·5.

Fig. 6. *Cyrtodontula* cf. *hadzeli* Pojeta and Gilbert-Tomlinson, 1977; NMW 78. 17G. 1234; left valve, internal mould; × 2.

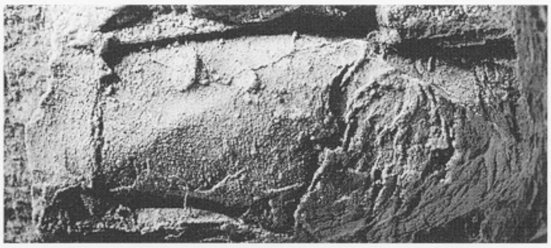
Fig. 9. *Cleionychia* sp.; NMW 78. 17G. 1269; composite mould of left valve; middle Arenig, Whitlandian Stage, Llangynog; × 2.

1

2

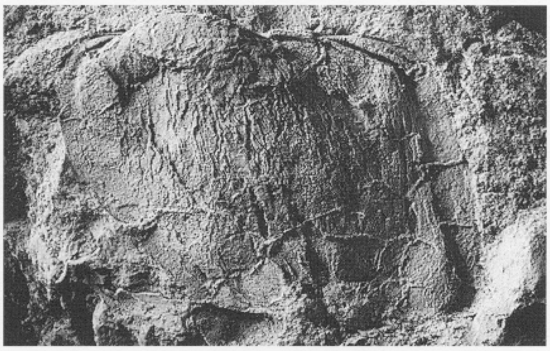


3

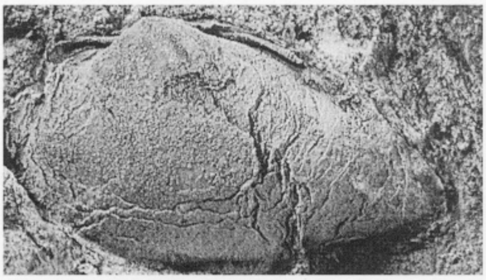


4

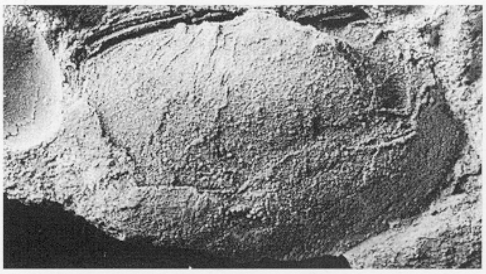
5



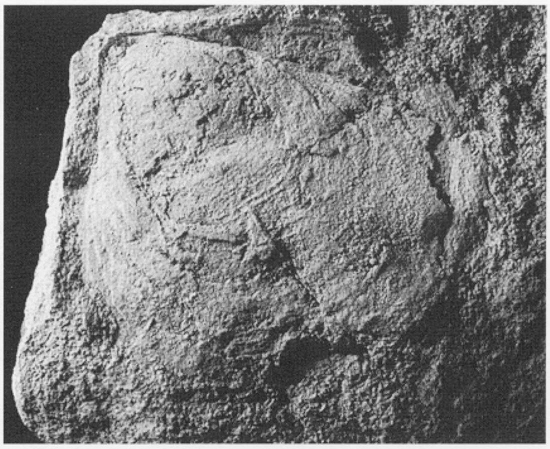
6



7



8



9

COPE, Arenig bivalves

markedly, however, with the circular shape of *Cycloconcha*, as do the very strongly inflated valves of *Celtoconcha*. It is possible that *Celtoconcha* has a common ancestry with *Cycloconcha*, as both share the character of multiple pedal muscle insertions.

Celtoconcha foveata sp. nov.

Plate 2, figure 13; Plate 4, figures 4, 7–8

Derivation of name. From the scars of the multiple pedal muscle insertion points.

Material. Ten specimens (4 LV, 6 RV). Holotype: RV NMW 78. 17G. 1212. Paratypes: NMW 78. 17G. 1213–1221.

Diagnosis. As for genus.

Description. The holotype (Pl. 4, fig. 8) is a well-preserved, largely undistorted, internal mould of a right valve. It is 15·0 mm long and 9·9 mm high, but the postero-ventral margin of the valve (where the height is greatest) is missing. The postero-ventral angle is, however, well displayed by paratype NMW 78. 17G. 1214, in which it is quite acute and posteriorly extended. Left valve features are well shown by paratype NMW 78. 17G. 1215 (Pl. 4, fig. 7), which is 15·2 mm long and 12·2 mm high. The shell is quadrate to subquadrate in outline and is strongly convex. The exterior of the shell is displayed by the three external moulds, none of the which is complete; however, they show that the shell was essentially smooth, the only ornamentation being fine growth increments towards the ventral margin. The umbo is just anterior of central on the hinge-line and is orthogyrate. Beneath the umbo is a narrow single right valve pseudocardinal socket and, immediately anterior to this, one or two anterior pseudolateral teeth arise in the right valve, two or three in the left. There are two posterior pseudolaterals in the left valve, but only one in the right valve. The anterior of the left valve posterior pseudolaterals is the shorter; in addition to being longer, the other more closely parallels the dorsal margin of the valve. The posterior of the shell is abruptly truncated by a sharp angular change at the posterior end of the hinge-line. No specimen shows adductor muscle scars or pallial line, but there is a series of well-defined muscle scars running across the dorsal side of the shell which are presumably pedal retractor muscle impressions. There are five (and possibly a sixth) on the holotype; paratypes NMW 78. 17G. 1215–1217 are all distorted at this area of the shell, but each shows at least two scars. Paratype NMW 78. 17G. 1218 (Pl. 2, fig. 13), which is a poorly preserved internal and external mould, shows vertical tracks associated with some of these accessory muscle scars. The external mould of this specimen is very poorly preserved, but suggests that the only ornament present is fine growth increments.

Remarks. Similar accessory muscle scars to those of *C. foveata* occur in a *Cycloconcha* figured by Pojeta (1971, pl. 2, figs 8–9). A reconstruction by Pojeta and Runnegar (1985, fig. 13) shows seven accessory scars.

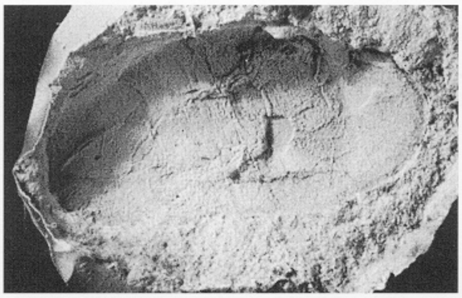
EXPLANATION OF PLATE 5

Fig. 1. *Xestoconcha* sp.; NMW 78. 17G. 1238; latex cast from internal mould of left valve, showing dentition; ×3.

Figs 2–3. *Parallelodus dyfedensis* sp. nov.; NMW 78. 17G. 1233, holotype; latex cast and internal mould; ×2.

Figs 4–11. *Moridunia simplicidens* gen. et sp. nov. 4, NMW 78. 17G. 161, latex cast of holotype; left valve, showing dentition and musculature; note prominent central tooth. 5–6, NMW 78. 17G. 387; internal mould and latex cast of large left valve. 7, NMW 78. 17G. 111; hinge region of latex cast of left valve. 8, NMW 78. 17G. 164; latex cast of right valve, showing apparent gap in hinge-plate, which is a very deep socket corresponding to central left valve cardinal tooth; note how tooth posterior to this socket bends round to posterior lateral attitude. 9, NMW 78. 17G. 359; hinge region of latex cast of a quadrate form showing more acute angle in hinge-plate. 10, NMW 78. 17G. 163; small right valve internal mould. 11, NMW 78. 17G. 170; latex cast of exterior mould of right valve showing commarginal ornamentation. All ×3.

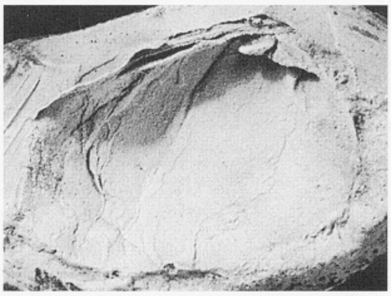
Fig. 12. *Cyrtodonta* cf. *staffordae* Pojeta and Gilbert-Tomlinson, 1977; NMW 78. 17G. 1240; right valve, internal mould; ×2.



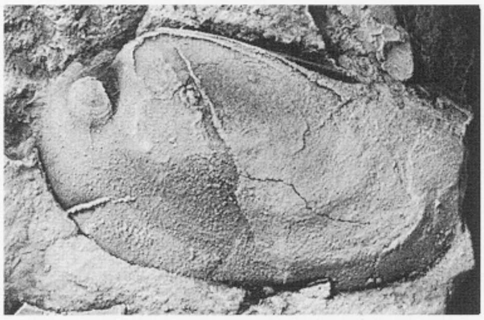
1

2

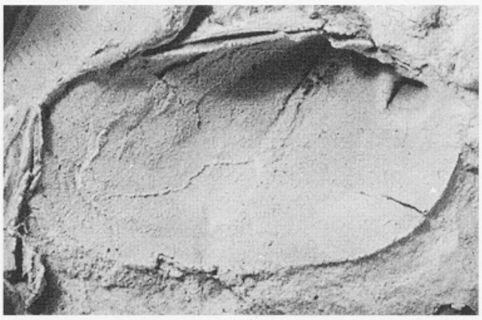
3



4



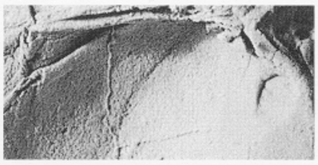
5



6

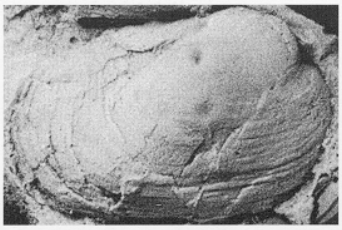
7

8

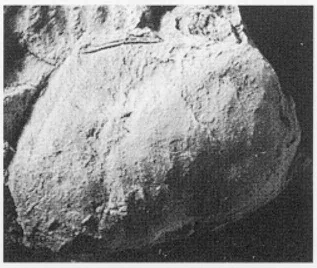


9

10



11



12

COPE, Arenig bivalves

Family REDONIIDAE Babin, 1966

The redoniids are actinodontoideans with a much reduced dentition. The umbo is well to the anterior end of the shell and the hinge-plate has one or two pseudocardinal teeth and one or two posterior pseudolaterals; the teeth may be smooth or microcrenulated. The anterior adductor muscle is very strongly impressed with a variably developed myophoric buttress delimiting its posterior margin. Included are: *Redonia* Roualt, 1851, *Dulcineaia* Babin and Gutiérrez-Marco, 1991, and *Moridunia* gen. nov. Their reduced dentition readily distinguishes them from other actinodontoideans.

Remarks. *Moridunia* is of a similar early Arenig age as the hitherto earliest known redoniid (*Redonia michelae* Babin) from the Montagne Noire and the Moroccan Anti-Atlas, and is interesting in that it shows development of redoniid features, but not to the same extent as in the other genera.

Genus MORIDUNIA gen. nov.

Derivation of name. From the Roman fort of Moridunum, now Carmarthen.

Type species. *Moridunia simplicidens* sp. nov.

Diagnosis. Redoniid with prominent, though not pointed, beak a little back from anterior extremity, anterior adductor well impressed with shallow myophoric buttress to posterior. Single central pseudocardinal tooth in left valve; right valve with blunt anterior pseudocardinal and elongated posterior pseudocardinal. One elongate posterior pseudolateral tooth in each valve. Shells with shallow ligamental nymphs locating opisthodetic ligament.

Range. Known only from the early Arenig.

Remarks. *Moridunia* has dentition most closely resembling that of *Redonia*, with which it shares a well-impressed anterior adductor muscle but with a shallow myophoric buttress. It is also distinguished by the more elongate shape and less prominent umbones. It lacks the ridged teeth of *Dulcineaia*. An apparent similarity in dentition to *Allodesma* Ulrich, 1894 is probably superficial. The figures of that genus in the *Treatise* (Cox *et al*. 1969, p. N400, fig. D8, 3*a*–*b*) are taken directly from Ulrich's figures. Pojeta (1971, pl. 2, figs 1–5) refigured some of these specimens, which are all internal moulds; he remarked (1971, p. 4) that Ulrich's figures are highly interpretative, and certainly the photographs of the material show only faint impressions of the dentition. There is in all probability, therefore, little resemblance between the dentition of the two forms. In any event they differ markedly in shell shape and musculature; *Allodesma* is isomyarian, whilst *Moridunia* is markedly anisomyarian.

Moridunia simplicidens sp. nov.

Plate 5, figures 4–11

Derivation of name. From the Latin *simplex*, (= simple) and *dens*, (= tooth).

Material. 447 specimens (202 LV, 185 RV, 60 CV). Holotype: NMW 78. 17G. 161. Paratypes: NMW 78. 17G. 1–160; NMW 78. 17G. 162–447.

Diagnosis. As for genus.

Description. The holotype is an internal mould of a left valve 16·0 mm long and 12·5 mm high. The anterior adductor muscle scar is rounded and prominent with a myophoric buttress as its posterior; on its dorsal side is a prominent triangular pedal retractor scar. The posterior adductor is far less well defined, roughly triangular, with an area over twice that of the anterior adductor. The upper (apical) region of the triangle could represent a pedal retractor scar, but there is no apparent line of separation between it and the rest of the muscle impression. The hinge-plate shows a single large prominent central pseudocardinal tooth in the left valve (Pl. 5, fig. 4); this has a smaller socket both anterior and posterior to it. The right valve (Pl. 5, fig. 8) displays well the prominent central socket in the hinge-plate corresponding to the left valve pseudocardinal tooth; in most latex casts this appears as a median gap in the right valve hinge-plate, not a socket within it, as the socket is so deep. To both the anterior and posterior of this socket is a pseudocardinal tooth; each arises from behind the hinge-plate and projects forward on it. The posterior pseudocardinal tooth is extended posteriorly so that it is parallel with and below the anterior portion of the right valve pseudolateral socket (Pl. 5, fig. 8). This tooth could thus be interpreted as the most anterior of the pseudolaterals. There is, in addition, one long posterior pseudolateral tooth in each valve. Above the right valve pseudolateral are faintly impressed ligamental nymphs, showing that the ligament was entirely opisthodetic. The pallial line is not well impressed and is not apparent on most specimens.

The shell exterior is essentially smooth; it is ornamented only by fine growth lines.

Remarks. Although *Redonia* is recorded from the upper part of the Arenig Series in Britain, (*R. anglica* occurs in the Mytton Flags of Shropshire) it appears to be absent from South Wales (although shallow water facies are not present in much of the upper Arenig there); it seems probable that *Moridunia* occupied the same ecological niche, as a shallow infaunal filter feeder, and is a major constituent (*c.* 35 per cent.) of the bivalve fauna at Llangynog.

There is some similarity between this species and *Modiolopsis ramseyensis* Hicks (revised by Carter (1971, p. 256, pl. 39, fig. 3) who refigured the holotype and referred it to *Actinodonta*), including the single long posterior pseudolateral tooth and the prominent anterior adductor. It is probable that the proportions of the holotype of *M. ramseyensis* (length 22·8 mm, height 10·3 mm) have been affected by the pervasive cleavage. Reasons are given above for excluding *M. ramseyensis* from *Actinodonta*, and, because of distortion of the type material and lack of preserved pseudocardinal dentition (if any), I propose to restrict Hicks' name to the type material.

Order MODIOMORPHOIDA Newell, 1969
Superfamily MODIOMORPHOIDEA Miller, 1877
Family MODIOLOPSIDAE Fischer, 1887

Genus GONIOPHORA Phillips, 1848
Subgenus COSMOGONIOPHORA McLearn, 1918

Type species. Goniophora bellula Billings, 1874

Goniophora (*Cosmogoniophora*) *extensa* sp. nov.

Plate 4, figures 3, 5

Derivation of name. From the extended postero-ventral margin of the valves.

Material. Seven specimens (1 LV, 2 RV, 3 CV, 1 CVE). Holotype: NMW 78. 17G. 1222. Paratypes: NMW 78. 17G. 1223–1228

Diagnosis. Goniophora (*Cosmogoniophora*) with the posterior part of the ventral margin extended.

Description. The best preserved specimen is the holotype (Pl. 4, fig. 5), a right valve 15·3 mm long and 8·7 mm high. A paratype left valve (NMW 78. 17G. 1223) is not so well preserved and appears to be slightly crushed dorso-ventrally; it is 16·3 mm long and 8·5 mm high (the latter figure probably reduced by distortion). The prosogyrate umbones are well to the anterior; from their posterior, a strong carina runs to the postero-ventral margin, fading in intensity close to the ventral margin. The postero-ventral margin is markedly extended. There are no visible muscle scars and no detail of dentition can be seen. The exterior of the shell is ornamented by a fine radial and concentric ornament (Pl. 4, fig. 3), some elements of which appear to be visible on the internal moulds.

Remarks. The goniophorid shape and fine radial ornament indicate assignment to *Goniophora* (*Cosmogoniophora*) and the extended postero-ventral margin distinguishes this species from others, such as *G.* (*C.*) *bellula* (Billings) from the Silurian of Nova Scotia. The latter also differs in being very much larger (*c.* 40 mm long), but has similar ornament to *G.* (*C.*) *extensa*. The latter shows some similarity to *G.* (*C.*) sp. described and figured by Babin and Gutiérrez-Marco (1991, p. 123, pl. 5, figs 3–4). The Welsh form differs in being further extended at the postero-ventral angle and in having the fine radial costae over the shell surface, whilst in the Spanish examples the radial ornamentation is restricted to the area posterior to the carina.

Genus MODIOLOPSIS Hall, 1847

Type species. Pterinea modiolaris Conrad, 1838, by original designation (Hall 1847, p. 157).

Modiolopsis sp. A

Plate 6, figure 7

Material. Two specimens (2 CV). NMW 78. 17G 1229–1230.

Description. The more complete of the two specimens (NMW 78. 17G. 1229) is 48 mm long and *c.* 29 mm high. It is of elongate modioliform shape with the left valve and part of the conjoined right valve preserved. The umbones of both valves are preserved, and are small and well anterior. Beneath the umbonal area the shell is quite narrow. The width of the shell increases rapidly posteriorly right up to the gently rounded posterior margin of the valve. The anterior adductor muscle scar is small, circular and prominent; the posterior scar is considerably larger, narrow and triangular, the apex of the triangle lying anteriorly. There is no trace of any teeth and it is presumed that this species was edentulous, as moulds from this locality virtually always preserve the dentition.

Remarks. This species appears distinct from any described of this genus, but the poorly preserved material is not satisfactory for the erection of a new species. It is considerably larger than and of a different shape from *Modiolopsis homfrayi* Hicks (lectotype designated and refigured by Carter 1971). I agree with Carter (1971) that Hicks' other species of *Modiolopsis* (*M. ramseyensis* and *M. cambriensis*) are palaeoheterodonts; they may both be distorted specimens of *Moridunia*, but they are so misshapen that I recommend that their respective names should be restricted to the type material. The general shape of the specimens is close to that of *M. modiolaris* Conrad, and differs considerably from that of *M.* sp. B described below.

EXPLANATION OF PLATE 6

Figs 1, 8. *Ribeiria complanata* Salter *in* Murchison, 1859. 1, NMW 92. 28G. 1; right valve, internal mould. 8, BGS GSM 12433, lectotype; left valve internal mould; Mytton Member, Shelve Formation, probably Whitlandian Stage, Arenig, Lord's Hill, Shelve Inlier, Shropshire; ×2.

Fig. 2. *Eurymya* sp.; NMW 78. 17G. 1239; ×3.

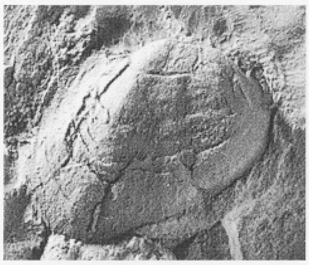
Figs 3–4. *Fortowensia grandis* gen. et sp. nov. 3, NMW 78. 17G. 1193; right valve, internal mould showing pallial punctae. 4, NMW 78. 17G. 1192, holotype; left valve, internal mould. Both ×2·8.

Figs 5–6. *Palaeopteria* sp.; NMW 78. 17G. 1245; latex cast and right valve internal mould; ×3.

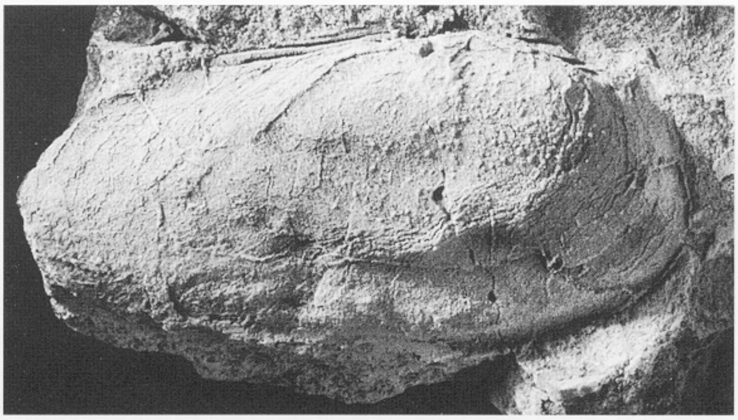
Fig. 7. *Modiolopsis* sp. A; NMW 78. 17G. 1229; left valve which also has part of the conjoined right valve (not figured); ×2.

Fig. 9. *Cyrtodonta* cf. *wattii* (Tate, 1896); NMW 78. 17G. 1241; right valve, internal mould; ×2.

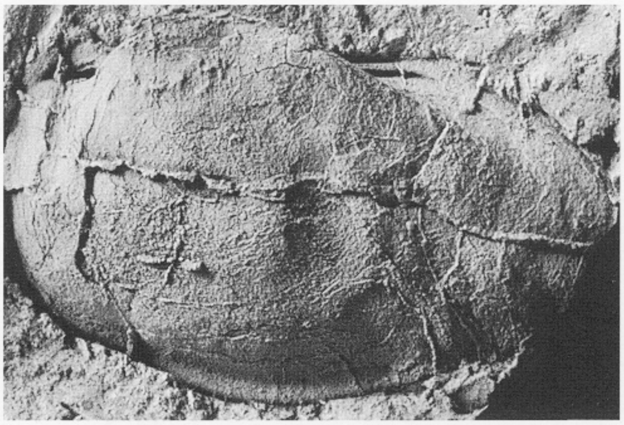
1



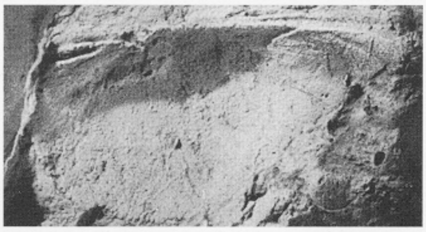
2



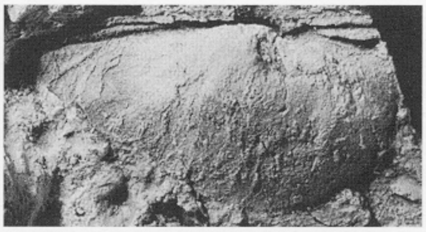
3



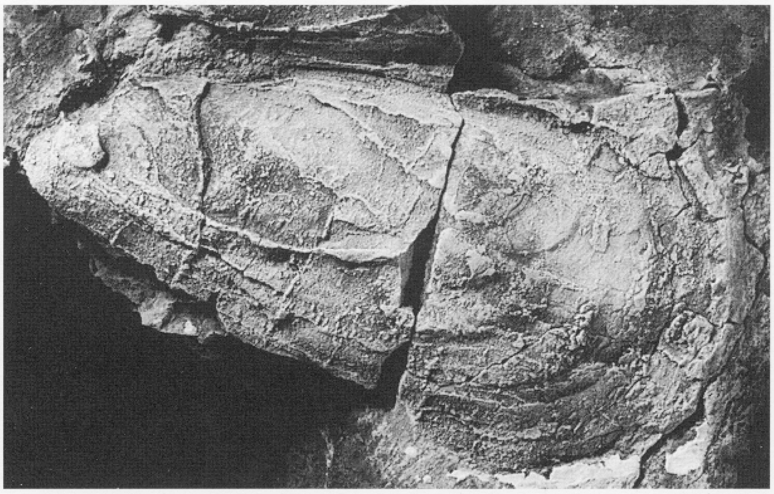
4



5

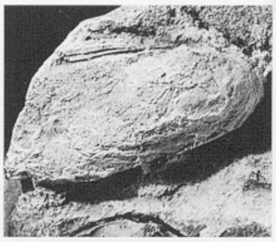


6



7

8



9

Modiolopsis sp. B

Plate 3, figure 7

Material. Two specimens (2 CV). NMW 78. 17G. 1231–1232.

Description. The better preserved of the specimens (NMW 78. 17G. 1231) is that figured, and is 34·2 mm long and 23·8 mm high. It has an oblique modioliform shape with its umbones placed about one-quarter of the length away from the anterior margin. The rounded anterior adductor is well impressed, but there is no obvious posterior adductor impression or any sign of teeth on either specimen. The external mould shows a shallow concentric ornament.

Remarks. The more oblique shape and shorter hinge-line of this specimen serve to distinguish it readily from *M.* sp. A. In general shape this species shows some similarities to *Dipleurodonta* Isberg, 1934 and *Eurymyella* Williams, 1912, but both of these have some teeth and it is thought that some evidence of dentition would have been preserved if *M.* sp. B originally had teeth. A generic assignment to *Modiolopsis* therefore seems preferable.

Genus PARALLELODUS Branson, 1909

Type species. Parallelodus obliquus Branson, 1909.

Parallelodus dyfedensis sp. nov.

Plate 5, figures 2–3

Derivation of name. From the county of Dyfed, South Wales.

Material. Four specimens (3 LV, 1 RV). Holotype: LV, NMW 78. 17G. 1233. Paratypes: NMW 78. 17G. 1234–1236.

Diagnosis. Elongate *Parallelodus*, twice as long as high, with single weak anterior and posterior lateral teeth in each valve. Shell terminated acutely postero-ventrally.

Description. The holotype is 37·8 mm long and is *c.* 18·5 mm high, (the ventral margin is not perfectly preserved). The internal mould is rather featureless; no muscle impressions are visible. The umbo is in the anterior third of the shell and is prosogyrate. A long blunt ridge extends back from the umbo to the acute postero-ventral angle of the shell, and although strong, is not acute enough to form a discrete carina. The left valves show the impression of a long posterior lateral tooth, arising just posterior to the umbo and running the entire length of the hinge; there is a short anterior lateral tooth which does not extend far anterior to the umbo. Although the teeth are well-defined, they are not strong features, and the corresponding sockets are shallow. The partial external moulds show that the exterior was ornamented with fine concentric growth increments, some of them occasionally stronger.

Remarks. There is good agreement in general shape with *Parallelodus obliquus*, although that species attains its maximum height about two-thirds of the way from the anterior end of the shell, whereas in *P. dyfedensis* it is nearer to the umbones. *Parallelodus* was also described by Branson (1909) as having two anterior and two posterior teeth in the right valve; one of each in the left valve. Because modiomorphoid teeth vary so considerably, dentition does not appear to be a good genus-diagnostic feature. Indeed, this variability causes problems with the placement of modiomorphoideans at subclass level. Thus, whilst Pojeta (e.g. 1978, 1987) regarded them as isofilibranchs, Bailey (1983) retained them within the Palaeoheterodonta, as '*Modiomorpha*... has a heterodont arrangement with weak posterior laterals... other modiomorphids... have strong posterior elements as part of a continuous actinodont series' (Bailey 1983, p. 200). This was one of the reasons why the latter author retained the Palaeoheterodonta as a subclass. This apparent dilemma is surely answered by regarding the modiomorphoideans as another example of a bivalve stock which is able to repeat different styles of dentition at different periods of time. In this manner the modern solemyoids can produce pseudo-actinodont dentition (Allen and Sanders 1969) as can modern nuculoids (Allen and Sanders 1973). Similarly the taxodont dentition of some neotaxodontids (see below, and Cope 1995, p. 367) does not imply any phylogenetic relationship to the palaeotaxodonts, as Cox (1959) demonstrated. I thus view the presence of teeth in the modiomorphoid stock as a feature which appears and disappears. It may help to support the hypothesis that the modiomorphoids were derived from an actinodontoid stock by loss of teeth; in this case, early Ordovician forms might well show dentition differently developed from later forms.

P. dyfedensis is also very similar in shape to the specimens of *Whiteavesia* figured by Pojeta (1971, pl. 17) although that genus is essentially edentulous. According to LaRocque and Newell (*in* Cox *et al.* 1969, p. N399) *Whiteavesia* also has an ornamentation of fine radial ridges on the interior of the shell. As the internal moulds of *P. dyfedensis* are smooth, this feature was clearly absent in these specimens.

No species of *Parallelodus* has been described hitherto from the lower Ordovician, the type species coming from the Blackriveran (middle Ordovician) of Missouri. Although there are differences in dentition and of age, neither of these appear to be major obstacles to the generic assignment made here, and a placement in *Parallelodus* is preferred, rather than to erect a new genus for a clearly closely allied form which bears fewer teeth in one valve.

Family COLPOMYIDAE Pojeta and Gilbert-Tomlinson, 1977

Remarks. This family is distinguished from the Modiolopsidae by the presence of a rather blunt 'articulation device' (Pojeta and Gilbert-Tomlinson 1977, p. 27) in the right valve, which articulates with similar or sometimes more lamellar structures in the left valve.

Genus XESTOCONCHA Pojeta and Gilbert-Tomlinson, 1977

Type species. Xestoconcha kraciukae Pojeta and Gilbert-Tomlinson, 1977

Xestoconcha sp.

Plate 5, figure 1

Material. Two specimens (1 LV, 1 RV). NMW 78. 17G. 1237–1238.

Description. The larger of the two specimens, left valve NMW 78. 17G. 1238 is *c.* 17·5 mm long (the posterior extremity is damaged) and 9·2 mm high. The right valve is 15·0 mm long and 9·2 mm high. In each case the maximum height obtains subumbonally. The umbones are prosogyrate and about two-fifths of the way from the anterior of the shell. The anterior adductor scar is moderately impressed and rounded; the posterior adductor is not visible in either specimen. There is a thick blunt tooth beneath the umbo of the left valve (Pl. 5, fig. 1) which also bears a single, rather subdued posterior blade-like tooth. The right valve may have a similar subumbonal tooth, but its preservation does not allow any posterior dentition to be seen. The external of the shell, revealed by the partial external mould, is ornamented by some fine, commarginal growth increments towards the commissural region.

Remarks. The shape of these specimens is very similar to that of the type species, figured by Pojeta and Gilbert-Tomlinson (1977, pl. 25), which is, however, slightly larger. The Welsh form also differs in the presence of the single posterior lateral tooth in the left valve. *Xestoconcha* sp. differs from *Colpomya* species in having the maximum height in the anterior part of the shell (subumbonally) and in that the shell tapers posteriorly. The dentition is, however, remarkably close to that of *Colpomya* species, with a single thick blunt tooth. The Welsh material shows that *Xestoconcha* has a blunt tooth in the right valve, a feature not determinable from the type species. Differences between the Welsh and Australian material warrant specific distinction, but the preservation of the former is too poor to name it formally.

The type material of *X. kraciukae* is from the Pacoota Sandstone of the Amadeus Basin of Australia. This formation was dated as Arenig by Pojeta and Gilbert-Tomlinson (1977, pp. 3–4), and as late Tremadoc by Shergold *et al.* (1991, p. 9). Although South Wales was in a high Gondwanan latitude at this time, as opposed to the equatorial latitude of Australia, both areas are on the margins of the Gondwanan continent and bivalves which were tolerant of temperature differences could presumably have migrated larvally around the shores.

Genus EURYMYA Ulrich, 1894

Type species. Modiolopsis plana Hall, 1861.

Eurymya sp.

Plate 6, figure 2

Material. One right valve, NMW 78. 17G. 1239.

Description. The specimen is 12·0 mm long and 8·5 mm high. Maximum height is at the postero-ventral angle of the shell. The mould is rather featureless and the anterior adductor impression is shallowly impressed, virtually on the anterior margin of the shell; the posterior adductor muscle scar is not visible. There is a faintly impressed pallial line. The umbo is situated approximately one-third of the way back from the anterior end; it has been crushed downwards, thus making it difficult to determine whether there is any subumbonal dentition. There appears to be a single large blunt structure preserved beneath the umbo, but its nature cannot be ascertained without removal of the umbo which would damage the specimen. There are no anterior or posterior teeth preserved. There is an extremely fine radial striation on the posterior two-thirds of the mould which may reflect shell ornamentation, or which could be a preservational feature. There is some concentric ornament present, particularly on the post-umbonal shoulder of the shell.

Remarks. There is close correspondence in shape to the specimens of *Eurymya* figured by Pojeta (1978, particularly pl. 13, fig. 6) and Pojeta and Runnegar (1985), and also some similarity to the specimen figured by Babin and Gutiérrez-Marco (1991, pl. 5, fig. 1) as *Modiolopsis*? *elegantulus* Sharpe; the last appears to be more appropriately placed in *Eurymya* as far as its shape is concerned, but it is apparently edentulous. *Eurymya* was included with question in the Pterioida by Cox *et al.* (1969), but it appears to have only a single subumbonal tooth, and Pojeta (1978) decided that it was probably a modiomorphoid. Later, Pojeta and Runnegar (1985, p. 313, fig. 9) included it in the Colpomyidae.

Subclass PTERIOMORPHIA Beurlen, 1944

Order CYRTODONTIDA ord. nov.

Diagnosis. Ovoid shells with tendency to prominent prosocline umbones, with or without radial or commarginal ornamentation. Isomyarian to anisomyarian. Well-developed teeth divided into anterior group including arcuate teeth separated by edentulous area from posterior group parallel or sub-parallel to hinge margin. Ligament opisthodetic external, lamellar, duplivincular or without grooved ligament area.

Stratigraphical range. Late Tremadoc to Devonian.

Remarks. In this order, which is formed by enlarging the concept of the cyrtodontoids, I recognize two superfamilies: the Cyrtodontoidea Ulrich, 1894 and the Falcatodontoidea superfam. nov. The ligamental area of the Cyrtodontoidea bears fine longitudinal ridges and grooves, characteristic of forms with a duplivincular ligament, although as suggested by Waller (1978) these grooves may be indicative only of an entirely lamellar ligament. The grooves and ridges intersect the dorsal margin at a very low angle, and thus more than one of these was functional at any one time (Pojeta and Runnegar 1985); it was consideration of the way that the growth lines extended onto the ligamental area which led Waller (1978) to suggest that the cyrtodontoidean ligament may have been entirely lamellar. In contrast, the ligamental area of the falcatodontoideans is devoid of grooving and the ligament was probably parivincular.

For the reasons outlined above I prefer to regard *Catamarcaia* Sánchez and Babin, 1993 as a cycloconchid with a grooved ligamental area, rather than a cyrtodontoid lacking an edentulous area on the hinge-plate.

Cope (1995) separated the superfamilies Arcoidea Lamarck, 1809 and Limopsoidea Dall, 1895 from other forms included in the order Arcoida Stoliczka, 1871 by Cox *et al.* (1969), and combined them in the subclass Neotaxodonta, Korobkov, 1954, which is characterized by a unique combination of a duplivincular ligament, a shell with crossed lamellar or complex crossed lamellar structure, and a tendency to develop taxodont dentition. The Neotaxodonta range from ?Devonian to Recent. It should be noted that Cox *et al.* (1969, p. N256) included *Glyptarca* Hicks, 1873 as a synonym of *Parallelodon*, but it is now clear that the latter is a palaeoheterodont (see above), and this removes the early Ordovician age given for the earliest *Parallelodon*. Since a new ordinal level taxon is required for the cyrtodontoids and falcatodontoids, the Cyrtodontida is established here.

Superfamily CYRTODONTOIDEA Ulrich, 1894
Family CYRTODONTIDAE Ulrich, 1894
Genus CYRTODONTA Billings, 1858

Type species. Cyrtodonta rugosa Billings, 1858 (by subsequent designation of Williams and Breger 1916).

Cyrtodonta cf. *staffordae* Pojeta and Gilbert-Tomlinson, 1977

Plate 5, figure 12

Material. One right valve, NMW 78. 17G. 1240.

Description. The specimen is subquadrate, but with the antero-dorsal and postero-ventral margins rounded. It is 19·4 mm long and 16·0 mm high and is strongly convex. There is a single posterior lateral tooth and a socket corresponding to a left valve tooth; no detail is visible of any anterior dentition. An ill-defined anterior circular area may be the site of the anterior adductor muscle, but there is no trace of a posterior adductor scar. The umbo scarcely projects above the dorsal line.

Remarks. There is good agreement with the holotype of *C. staffordae* in shape and general appearance; the Welsh form is, however, slightly smaller. The other point of difference is that the Australian species has a single posterior lateral tooth in the right valve, but apparently not in the left. The type material of the latter is from the Stairway Sandstone of the Amadeus Basin, which is of Llanvirn to Llandeilo age, and thus somewhat younger geologically than the specimen described here.

Cyrtodonta cf. *wattii* (Tate, 1896)

Plate 6, figure 9

Material. One right and one left valve. NMW 78. 17G. 1241–1242.

Description. The left valve is the larger specimen with an estimated length of 22 mm (the posterior extremity is broken) and is 16 mm high. The right valve is the better preserved and is figured herein. The dorsal margin is straight and the shell is obliquely elongated from the antero-dorsal to the postero-ventral margins. The adductor muscles were evidently very shallowly impressed, as no muscle scars are visible. The left valve shows one arched anterior tooth overlying a similarly arched socket and a long posterior lateral tooth. The right valve hinge-plate is broken anteriorly, but posteriorly shows two elongated teeth and one socket. There is a slight commarginal rugation of the shell, but this is not raised strongly as in *Pharcidoconcha* Pojeta and Gilbert-Tomlinson, 1977.

Remarks. In size and shape this species shows marked similarity to *Cyrtodonta wattii* (Tate, 1896), refigured by Pojeta and Gilbert-Tomlinson (1977), from the Llanvirn–Llandeilo Stairway Sandstone of the Amadeus Basin. There is closest similarity with their plate 15, figure 2, which differs in the posterior curvature of the hinge-line. *C. wattii* also has three anterior and posterior teeth in the left valve. Although a new species may be represented by the material described above, the preservation is not good enough to name it.

Genus CYRTODONTULA Tomlin, 1931

Type species. Whitella obliquata Ulrich, 1890.

Cyrtodontula cf. *hadzeli* Pojeta and Gilbert-Tomlinson, 1977

Plate 4, figure 6

Material. Two specimens (LV, NMW 78. 17G. 1243; RV, NMW 78. 17G. 1244).

Description. The left valve is the more complete specimen; it is 35·0 mm long and 27·5 mm high. The dorsal line is curved anteriorly and posteriorly and shows the impressions of two anterior right valve teeth, the lower one thicker and projecting farther forwards and more strongly curved; between them is a single left valve anterior tooth. The right valve confirms this arrangement of teeth. There is an edentulous area around the umbonal region of the hinge-line, behind which is a long curved left valve posterior tooth, and above it and confined to the postero-dorsal angle is a right valve posterior tooth. The elliptical anterior adductor impression is reasonably well impressed; the posterior adductor is not visible. A subdued carina runs from the umbo towards the ventro-posterior angle, but the slight crushing of the specimen makes it difficult to determine its original strength. The partial external mould shows fine concentric ornamentation.

Remarks. There is good agreement with the description and figures of Pojeta and Gilbert-Tomlinson (1977, pl. 17, figs 8–11). The Welsh specimens are somewhat larger and have slightly different dentition, but there is closer agreement with the Australian species than, for instance with the highly tumid form figured from Spain by Babin and Gutiérrez-Marco (1991, pl. 5, figs 6–7). There appear to be no other early or mid Ordovician forms to compare with this species, but later forms, such as the late Ordovician species figured by Isberg (1934, pl. 18, figs 1–2) are also more inflated. *Sphenolium* Miller, 1889 (type species *Orthodesma cuneiforme* Miller, 1881), also from the upper Ordovician has a very similar shape, but hinge details are not known. LaRocque and Newell (*in* Cox *et al.* 1969, p. N397) included *Sphenolium* under synonymy with *Modiolopsis* with a query; however, it appears too tumid to belong to the latter, and its shape suggests cyrtodontid affinities.

Superfamily FALCATODONTOIDEA superfam. nov.

Diagnosis. Ovoid cyrtodontoids with radial ornamentation. Ligament simple, opisthodetic external.

Stratigraphical range. Known only from the lower Arenig.

Remarks. This new superfamily is based upon *Falcatodonta*, described below. Its remarkable, strongly costate shell is totally different from the smooth shells of the Cyrtodontoidea. In their diagnosis of the latter, Pojeta and Gilbert-Tomlinson (1977) mention the absence of radial ornament as a characteristic feature, and this is one immediate point of distinction between the two superfamilies. The only member of the Cyrtodontoidea with ornament other than growth lines, is *Pharcidoconcha* Pojeta and Gilbert-Tomlinson, 1977 which has marked commarginal rugae.

Cyrtodontoideans are believed to have been byssate like other pteriomorphians. In view of their predominantly smooth shells it is most probable that they were infaunal; although the shell does not show obvious characters of retaining a byssus in the adult, they may well have used a weak one in much the same manner as the modern *Anadara*, as a stabilizing organ (Stanley 1972). Thus, if falcatodontoideans were byssate they would have been endobyssate. Their ribbed form, on the other hand, suggests that they may have been epifaunal (epibyssate), and they appear remarkably homeomorphous in external morphology with the late Palaeozoic and Mesozoic epibyssate arcoids figured by Stanley (1972, fig. 15D–E). If *Falcatodonta* was epibyssate (the evidence is purely on shell shape comparison), it would be the earliest epifaunal bivalve; it may be significant that although the Ambonychioidea evolved from the Cyrtodontoidea, the latter were initially infaunal, so that the Falcatodontoidea make a more attractive prospect as the origin of an often strongly ribbed, predominantly epifaunal group, although it should be noted that the ambonychians have a duplivincular ligament. At present, only the Falcatodontidae is assigned to this superfamily.

Family FALCATODONTIDAE fam. nov.

Diagnosis. As for the superfamily Falcatodontoidea.

Genus FALCATODONTA gen. nov.

Derivation of name. From the Latin *falcatus* (= sickle-shaped), referring to the shape of the anterior teeth.

Type species. *Falcatodonta costata* sp. nov.

Diagnosis. Shell with strong radial ribs and dentition of anterior curved teeth separated by edentulous area from posterior teeth which are parallel to dorsal margin of shell. Ligament external opisthodetic. Numerous accessory mantle insertion points. Integripalliate, with pallial line deeply inserted in some.

Remarks. The strongly ribbed shell is unique among early Ordovician bivalves and, apart from the ambonychids, there appears to be only one other Ordovician bivalve genus described which has strong ornamentation, *Paraphtonia* Khalfin, 1958 from the middle Ordovician of the Chu-Ili Mountains, Kazakhstan, which is believed to be a modiomorphoid (Cox *et al.* 1969, p. N398).

Stratigraphical range. Known only from the lower Arenig.

Falcatodonta costata sp. nov.

Plate 7, figures 1–11

Derivation of name. From the Latin *costatus* (= ribbed), referring to the strongly ribbed shell.

Material. 90 specimens (29 LV, 33 RV, 28 CV). Holotype: NMW 78. 17G. 975. Paratypes: NMW 78. 17G. 932–974; NMW 78. 17G. 976–1012.

Diagnosis. As for genus.

Description. The holotype is the internal mould of a right valve 12·6 mm long and 10·7 mm high. These measurements show that it is a rather squarer individual than most of the paratypes, but this specimen displays the most characteristic features of this species well and, in particular, has excellent dentition. Paratypes include smaller specimens (e.g. Pl. 7, figs 2, 5), but one, possibly gerontic individual is 18·3 mm in length.

The umbo, which is prosogyrous, is located towards the anterior end of the shell. The anterior adductor impression tends to be semicircular, with the convex side pointing towards the umbo; there is a well-marked pedal retractor scar dorsal to the anterior adductor impression. Neither of these muscle scars is shown particularly well on the holotype, but both are well-displayed by paratype NMW 78. 17G. 976, which also shows a well impressed pallial line. The pallial line is variably impressed, but is seen on many specimens (Pl. 7). The posterior adductor is considerably larger than the anterior one, and is triangular with the acute angle of the triangle lying close to the dorsal margin of the valve.

The exterior of the shell has strong radial costae, rounded in cross section as are the equally sized intercostal areas. The ribs are crossed by growth lines which only become apparent on some of the larger shells, where there is sometimes a pronounced growth increment (e.g. Pl. 7, fig. 7). This ornament is unusual in Ordovician bivalves and recalls that seen in some Mesozoic and later species. The posterior end of the valves is flattened dorsally to produce a 'wing'.

Within the floor of the valves there is a variable number of small punctuations, which are apparent as small raised stumps on the internal mould. They are arranged in a radial fashion and tend to lie, therefore, parallel to the ribs. The best clue to the function of these punctae lies in their restriction to an area inside the pallial muscle scar (in those specimens which have a pallial line impressed; in others it is restricted to the same area of the shell), and I conclude that they represent auxilliary mantle muscle attachment sites. Similar structures were described by Newell (1942) in mytiloideans and later (1956) in Permian anomalodesmatans; they have also been reported in some lucinid heterodonts (Cox *et al.* 1969), trigonioideans (Newell and Boyd 1965), the pteriniid *Ptychopteria*, the ambonychiid *Gosseletia* and in the cyrtodont *Ptychodesma* by Bailey (1983) who referred to them as pallial punctae.

The right valve has three anterior teeth, the anterior two of which are strongly hooked forwards; the left valve also has three similarly arranged teeth. There is an edentulous area separating these anterior teeth from the posterior teeth. There are three of the latter in the right valve, two in the left. This dentition style is characteristic of cyrtodontoideans.

The preservation of the external moulds of some of the conjoined specimens has allowed the preparation of latex casts which show the hinge-line well (Pl. 7, fig. 10). From these it may be inferred that *Falcatodonta* had a simple external ligament. There is certainly no sign of any grooving in the ligamental area, which would betray a duplivincular ligament, and it is suggested that the ligament in *Falcatodonta* was parivincular.

Remarks. Together with the specimens of *Cyrtodonta* and *Cyrtodontula* described above, *F. costata* is of similar age to the earliest known cyrtodontoids, *Cyrtodontula hadzeli* Pojeta and Gilbert-Tomlinson, 1977 and *Pharcidoconcha raupi* Pojeta and Gilbert-Tomlinson, 1977, both from the upper Tremadoc (see Shergold *et al.* 1991, p. 9) portion of the Pacoota Sandstone of the Amadeus Basin of Australia. Of probably similar age is *Pharcidoconcha parallela* (Hsü *in* Hsü and Ma, 1948) from China. The group is well known from many parts of the world by the early part of the mid Ordovician. *Falcatodonta costata* is also the only cyrtodontide yet described to lack a grooved ligamental area; in fact a duplivincular ligament usually figures in the diagnosis of the Cyrtodontoidea. However, the dentition of *Falcatodonta* leaves no doubt about its taxonomic placing within the Cyrtodontida, but because of the differences in ligament type and ornament,

---

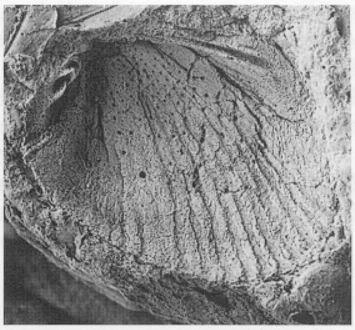
EXPLANATION OF PLATE 7

Figs 1–11. *Falcatodonta costata* gen. et sp. nov. 1, NMW 78. 17G. 975, holotype; right valve, internal mould. 2, NMW 78. 17G. 976; latex cast of right valve external mould of a small individual to show ornament. 3, latex cast of holotype to show dentition and pallial punctae. 4, NMW 78. 17G. 1006; latex cast of internal mould of left valve showing dentition and pallial line. 5, internal mould of right valve as in fig. 2, to show pallial line. 6, internal mould of specimen seen in fig. 4. 7, NMW 78. 17G. 1003; latex cast of right valve, external mould showing commarginal and radial ornament; one of the very few bivalves to show abrasion. 8, NMW 78. 17G. 993; latex cast of external mould of left valve. 9, NMW 78. 17G. 986; right valve internal mould lit to show pallial punctae. 10, NMW 78. 17G. 992; latex cast of hinge region of conjoined valves. 11, NMW 78. 17G. 946; latex cast of internal mould of left valve. All × 3.

Figs 12–14. *Arenigomya carinata* gen. et sp. nov. 12, NMW 78. 17G. 1265; latex cast of external mould of left valve; × 3. 13, NMW 78. 17G. 1246, holotype; internal mould of left valve; × 3. 14, SEM photograph of portion of specimen in fig. 12 enlarged to show pustulose ornament; × 16.

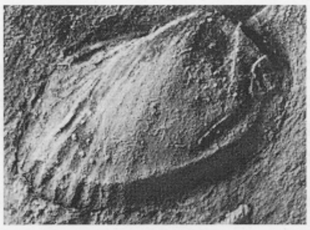
1

2



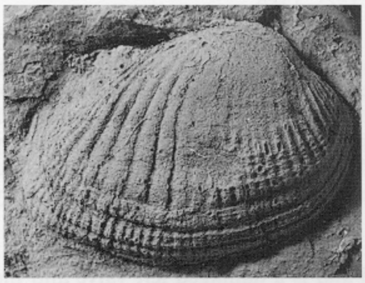
3

4

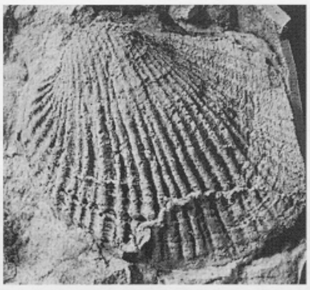


5

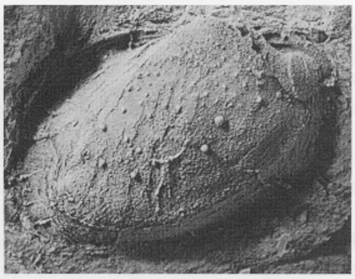
6



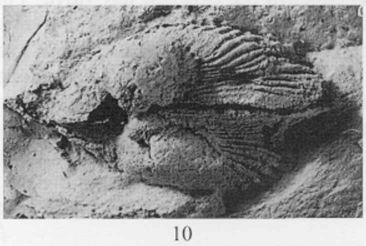
7



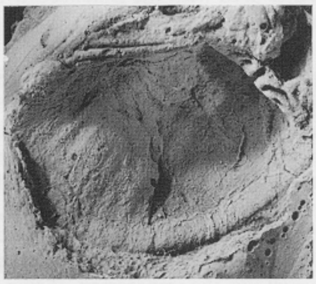
8



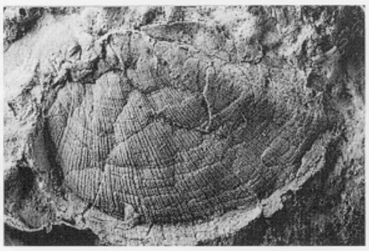
9



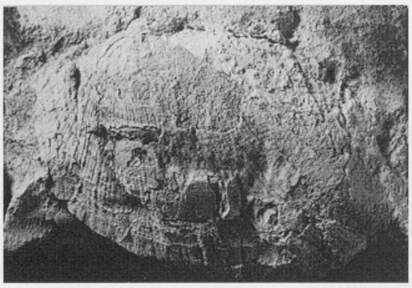
10



11



12



13

14

COPE, *Falcatodonta*, *Arenigomya*

merits separate superfamilial status. The origins of the cyrtodontides are therefore likely to be pre-Arenig and may be sought from the glyptarcoid stock of palaeoheterodonts. These possess dentition from which a cyrtodontide type could be derived quite readily by suppression of the central teeth. Furthermore, the anterior teeth of *Glyptarca* have a configuration remarkably similar to that obtaining in many cyrtodontide genera.

The combination of the type of dentition and lack of a grooved ligamental area in the falcatodontoideans is another example of the mosaic evolution that occurred in the plexus of early Ordovician palaeoheterodonts and their descendants.

The strongly ribbed nature of *F. costata* is a distinctive character that renders it immediately identifiable. It also appears to be the earliest bivalve which has (or sometimes has) a deeply impressed pallial line.

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

Genus CLEIONYCHIA Ulrich, 1892

Type species. Ambonychia lamellosa Whitfield, 1882. By original designation.

Cleionychia sp.

Plate 4, figure 9

Material. A composite mould of left valve and counterpart. NMW 78. 17G. 1269.

Horizon and locality. Middle Arenig, Whitlandian Stage, from old quarry on east side of road, Llangynog, Dyfed [SN 3385 1596]; the lowest beds exposed here, on Pen-y-Moelfre Hill, have yielded a small species of *Paralenorthis* and ellesmerocerid nautiloids. *Paralenorthis proava* (Salter) and *Hesperonomiella carmelensis* Bates occur 150 m higher in the succession, a fauna also recorded from the Carmel Formation of Anglesey (Bates 1968), and there of highest Whitlandian or earliest Fennian age. The sandstones of Pen-y-Moelfre find their closest equivalents in the South Wales area with the Blaencediw Formation of the Whitland area (Fortey and Owens 1987), of early Whitlandian age.

Description. The limonite-coated composite mould is somewhat crushed and is a damaged left valve and the dorsal region of the right valve; the whole of the latter may be preserved beneath the exposed left valve. The specimen is *c.* 25 mm long (the posterior extremity is damaged) and is 26 mm high. The surface of the valve is ornamented by concentric growth lines; there are well-marked commarginal rugae both on the anterior and posterior parts of the valve, although these are not apparent around the middle. There is no radial ornament.

The posterior adductor muscle impression is a large rounded scar, possibly with a smaller accessory scar anterior and dorsal to this (?pedal retractor scar). Impression of the dorsal region of the right valve suggests that there may have been an anterior (pseudocardinal) tooth, almost parallel with the hinge line. In addition, the posterior extremity of the right valve shows the impression of two short ridges beneath the dorsal margin; these appear to be poorly preserved posterior teeth, but could be structures associated with the ligamental insertion.

Remarks. The strongly reduced anterior, together with the long hinge line, apparently monomyarian musculature and reduced dentition clearly identify this bivalve as an ambonychiid. Species of *Cleionychia* are very similar in lacking radial ornament, possessing rugae and having a single pseudocardinal tooth, but lack posterior lateral teeth (*fide* Newell and LaRocque *in* Cox *et al.* 1969) and if the Llangynog specimen does have these, a new generic assignment may be required. The earliest ambonychiids recorded are from the Chazyan (= upper Llanvirn; Pojeta 1978), and this specimen predates these by a considerable margin. Because of poor preservation, this specimen is described under open nomenclature.

Superfamily PTERIOIDEA Gray, 1847
Family PTERINIIDAE Miller, 1877

Genus PALAEOPTERIA Whiteaves, 1897

Type species. Palaeopteria parvula Whiteaves, 1897 (by monotypy).

Palaeopteria sp.

Plate 6, figures 5–6

Material. One right valve, NMW 78. 17G. 1245.

Description. The specimen is 17·2 mm long and 9·2 mm high, but it appears probable that the anterior extremity of the dorsal margin is missing. The valve appears to be essentially undistorted and is moderately convex, but without the left valve it is not possible to compare the convexity of the two valves; in Whiteaves' (1897) type material both valves of *P. parvula* are convex, but the left valve more so. The hinge-line of the Llangynog example is straight and the anterior and posterior lateral teeth closely parallel the dorsal margin of the valves; there are no cardinal teeth. Two anterior and two posterior teeth are present, the latter being rather shallow; none cuts the dorsal valve margin. The posterior end of the shell is extended, but not truly auriculate. The anterior extremity of the hinge-line is missing and it is therefore not possible to judge whether there was an anterior auriculation. The umbo appears to be orthogyrate and is anterior of the centre. There is no visible impression of a posterior adductor, but there is a large scutate smooth area at the anterior extremity of the shell which could be an adductor impression.

Remarks. This specimen is kept in open nomenclature, as it is imperfectly preserved, and the left valve is unknown. The latter is considered important in a group where asymmetry of the two valves is the norm. As this is the earliest known example of a pterineid, it is quite possible, however, that the two valves were of equal convexity, since the group was presumably descended form equivalved ancestors.

Much of Whiteaves' type series consists of smaller material than the Llangynog example. He (1897, p. 182) quotes an 'average' specimen as being 5·8 mm long but also figures a much larger one, *c.* 15 mm long. It is clear that the Welsh specimen does not belong to *P. parvula*, as there are important differences in the ventral shape of the shell, but the straight hinge-line with its anterior and posterior laterals parallel to the dorsal margin make assignation to the Pteriniidae certain. It is believed that there are enough similarities with the Canadian material and with that figured from the Lexington Limestone of Kentucky by Pojeta (1971, pl. 11, fig. 9) to assign it to *Palaeopteria.*

This specimen of *Palaeopteria* predates the hitherto earliest known pterineid, *Denticelox turtuosa* (Tate) from the Stairway Sandstone (Llanvirn–Llandeilo) of the Amadeus Basin of Australia described by Pojeta and Gilbert-Tomlinson (1977), who also designated and refigured the lectotype. It is noteworthy that this latter species is biconvex, with the left valve showing the greater convexity.

Subclass ANOMALODESMATA Dall, 1889
Order PHOLADOMYOIDA Newell, 1965
Superfamily PHOLADOMYOIDEA Gray, 1847
Family GRAMMYSIIDAE Miller, 1877

Genus ARENIGOMYA gen. nov.

Derivation of name. Combination of Arenig with the Latin *mya* (= bivalve).

Type species. Arenigomya carinata sp. nov.

Diagnosis. Equivalve, edentulous, trapezoidal bivalve with length one-and-a-half times greater than height. Surface with fine concentric undulose ornament, radial striae and anteriorly prominent commarginal rugae. Surface detail of finely granulose ornament. Strong carina runs from posterior side of umbo to postero-ventral margin of valves. Each valve with subumbonal articulation device.

Remarks. The oldest known anomalodesmatans described hitherto are of late mid Ordovician age (Pojeta and Runnegar 1985; Pojeta 1987); thus this record from the early Arenig extends the origin of this subclass further back into the Ordovician. Cox *et al.* (1969) listed *Davidia* Hicks, 1873 (wrongly ascribed therein to the Tremadoc rather than the Arenig) as a possible anomalodesmatan, but Carter (1971) demonstrated that the type material is uninterpretable, and refigured (1971, pl. 39, fig. 5) the type specimen of the type species (*Davidia ornata* Hicks). I have examined this specimen (BGS GSM 24197) and concur with Carter, and agree that the radiating ribs figured by Hicks (1873, pl. 5, fig. 12) and refigured by Newell (1969, fig. F3, 4) are an overoptimistic interpretation of a poorly preserved specimen. The other species of *Davidia* described by Hicks, *D. plana* (1873, pl. 5, fig. 14; Manchester Museum L10021), is also uninterpretable. Carter considered that both species could be placed in synonymy with '*Modiolopsis ramseyensis*' Hicks (which may be a redoniid palaeoheterodont), and it can be confidently concluded that *Davidia* is not an anomalodesmatan bivalve; nor is it a cycloconchid palaeoheterodont as Morris (1978) suggested (see above). The name should be restricted to that type material as Carter (1971, p. 251) recommended.

Arenigomya possesses the commarginal and beaded radial ornament with a fine scale granulose texture which is considered typical of the other Ordovician members of the group, such as *Cuneamya* Hall and Whitfield, 1875 and *Rhytimya* Ulrich, 1894, the latter overlooked by Cox *et al.* (1969). Unlike some of the other Ordovician members of this subclass, details of the hinge of *Arenigomya* are well-preserved in some specimens (Text-fig. 7). The hinge structure shows that *Arenigomya* was edentulous, but had a well-developed articulation device in each valve. Chondrophores are quite characteristic features of many Recent anomalodesmatans, but this appears to be the earliest record of a possibly analogous structure not only in the Anomalodesmata, but in any bivalve.

Stratigraphical range. Known only from the lower Arenig.

Arenigomya carinata sp. nov.

Plate 7, figures 12–14

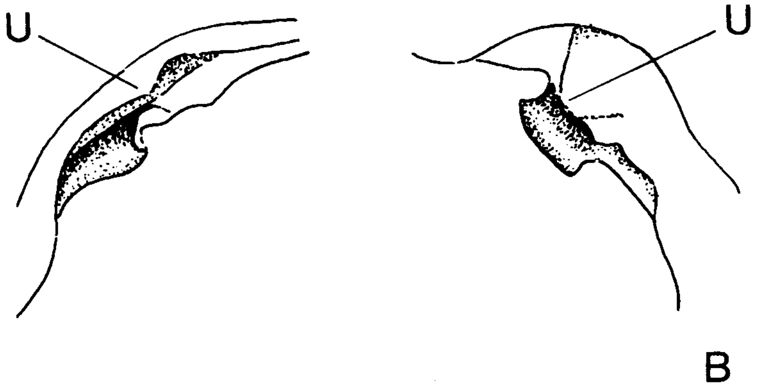
Derivation of name. From the Latin *carinata* (= carinate).

Material. 23 specimens (6 LV, 9 RV, 5 CV, 3E). Holotype: NMW 78. 17G. 1246. Paratypes: NMW 78. 17G. 1247–1268.

Diagnosis. As for genus.

Description. The holotype is a left valve composite mould 24·8 mm long with a subumbonal height of 15·5 mm. The surface is ornamented with fine radial grooves, about 4 per mm half-way down the shell; these are intersected by concentric undulose ornament of about the same spacing, giving a fine reticulate pattern. At the anterior end there is a series of strong rugae, fading posteriorly. The hinge-line is well shown by paratypes NMW 78. 17G. 1247–1248. The species is edentulous but bears a single curved plate in each valve. This is developed from the underside of the umbones (see Text-fig. 7) and is strongly concave upwards; it seems probable that this structure housed an internal ligament and can therefore be identified as a chondrophore. The well-preserved hinge area on several specimens shows that this species is edentulous.

Paratype NMW 78. 17G. 1248 shows a small, shallowly impressed anterior adductor muscle scar, but neither the posterior adductor nor the pallial line are shown by any specimens; both presumably had shallow insertion. A strong carina runs from the posterior side of the umbo to the postero-ventral margin of the valves; it



TEXT-FIG. 7. *Arenigomya carinata*; *camera lucida* drawings of the hinge-line of two specimens to show spoon-shaped subumbonal structures in each valve, viewed from the anterior. U = umbo. A, NMW 78. 17G. 1247; right valve. B, NMW 78. 17G. 1248; left valve. Both ×4.

becomes a discrete ridge projecting for up to 1 mm above the adjacent surface of the valves. Dorsally and posteriorly to the carina the ornament is somewhat subdued.

Remarks. A carina characterizes some other Palaeozoic anomalodesmatan genera, including *Alula* Girty, 1912 (Permian) and *Sanguinolites* McCoy, 1844 (late Devonian–Permian), as well as a large number of Mesozoic and later forms; it seems to be a character of generic rather than specific distinction. The silica replacement of parts of the shell in some specimens suggests that *Arenigomya carinata* may have had a shell with a thick periostracum or high organic content of the calcareous parts of the valves, as in *Ovatoconcha*, described above.

Class ROSTROCONCHIA Pojeta, Morris and Newell, 1972
Order RIBEIRIOIDA Kobayashi, 1933
Family RIBEIRIIDAE Kobayashi, 1933

Genus RIBEIRIA Sharpe, 1853

Type species. Ribeiria pholadiformis Sharpe, 1853.

Ribeiria complanata Salter *in* Murchison, 1859

Plate 6, figures 1, 8

1859	*Ribeiria complanata* Salter *in* Murchison, p. 50, Fossils 8, fig. 3 [listed on p. 50 as *Redonia*? *complanata*, but corrected in Errata and Corrigenda, p. xx, to *Ribeiria*.]
1866	*Ribeiria complanata* Salter, p. 346, pl. 11B, fig. 16.
1976	*Ribeiria complanata* Salter; Pojeta and Runnegar, p. 51, pl. 9, fig. 10.

Material. NMW 92. 28G.1*a*–1*b*, internal and external moulds.

Description. The specimen has separated from the matrix exposing the right side of the crushed internal mould, but it is clear that this is of the whole of the interior of the shell. The specimen is just over 20 mm long (the posterior extremity is damaged so that the exact length is unknown) and is 9·5 mm high. There is a well-marked slit in the internal mould marking the position of the pegma. There is a possible muscle insertion point of the primary pedal retractor visible on the specimen, which is, however, rather distorted at this point (see Pojeta and Runnegar 1976, fig. 3). The dorsal margin of the mould is virtually straight and this impression is confirmed by the external mould, although the internal mould shows a raised area on the dorsum which may be a crushed impression of the posterior median muscle. As far as can be seen the posterior of the shell is rounded.

Remarks. There is reasonably good agreement between this specimen and the specimen figured by Salter and re-figured by Pojeta and Runnegar (1976, pl. 9, fig. 10) and herein (Pl. 6, fig. 8). The latter authors (p. 51) quoted their figured specimen as the holotype and only known specimen but two of Salter's specimens are in the collections of the Geological Survey (BGS GSM 12433–12434). They gave the horizon and locality of the figured specimen as 'Lower Llandeilian [*sic*], Lord's Hill, Shelve, North Wales'. This is properly the Mytton Member of the Shelve Formation, of Arenig age (probably Whitlandian Stage) of Lord's Hill, Shelve Inlier, Shropshire (Whittard 1979, pp. 16–24). Pojeta and Runnegar erroneously believed that the species dated from 1866 (Salter *in* Ramsay). In order to stabilize the nomenclature I designate BGS GSM 12434 (the figured specimen) as the lectotype. The other, rather incomplete, specimen (BGS GSM 12433) therefore becomes a paralectotype. *R. complanata* is similar to *R. pholadiformis* Sharpe from the middle Ordovician of Portugal, which is somewhat younger geologically. The main point of difference appears to be the shell thickening dorsal to the posterior pedal retractor muscle in the latter species, which produces a shallow notch in the dorsal margin of internal moulds. *R. complanata* and *R. pholadiformis* were noted by Pojeta (1979) as being two of the few species of rostroconchs to be found in clastic sediments. The Welsh specimen is a little larger than the lectotype of *R. complanata* and is somewhat crushed, but the two are clearly conspecific.

PHYLOGENY

The fauna described herein has major implications for the early radiations of the class Bivalvia, and emphasizes the key role of the western Gondwanan shelves in this (Babin 1995). Space considerations preclude a phylogenetic analysis of this fauna herein, but some of the principal conclusions have already been outlined (Cope 1995); a more thorough appraisal of the Ordovician radiation of the Bivalvia will be published elsewhere.

Acknowledgements. I am indebted to Dr John Pojeta Jr for many helpful discussions and advice; to Mr F. R. B. Cross for his skilled assistance in the field and with preparation of latex moulds in the laboratory, and to many colleagues and friends for their encouragement. Members of my former Extra Mural class in Swansea helped with collection of material in bulk. Drs R. M. C. Eagar, J. R. Nudds, R. B. Rickards and Mr S. P. Tunnicliff assisted with the loan of materials in their care. Mrs D. G. Evans (National Museum of Wales) drafted the text-figures, by courtesy of Professor M. G. Bassett.

REFERENCES

ADAMS, H. and ADAMS, A. 1854–58. *The genera of Recent Mollusca arranged according to their organization*, Vol. 2. J. van Voorst, London, 661 pp.

ALLEN, J. A. and SANDERS, H. L. 1969. *Nucinella serrei* Lamy (Bivalvia: Protobranchia), a monomyarian solemyid and possible living actinodont. *Malacologia*, **7**, 381–396.

—— —— 1973. Studies on deep-sea protobranchia (Bivalvia); the families Siliculidae and Lametilidae. *Bulletin of the Museum of Comparative Zoology, Harvard University*, **145**, 263–309.

BABIN, C. 1966. *Mollusques bivalves et céphalopodes du Paléozoïque armoricain*. Imprimerie Commerciale et Administrative, Brest, 470 pp., 18 pls.

—— 1982. Mollusques bivalves et rostroconches. 37–49, pls 8–12. *In* BABIN, C., COURTESSOLE, R., MELOU, M., PILLET, J., VIZCAÏNO, D. and YOCHELSON, E. L. Brachiopodes (articulés) et mollusques (bivalves, rostroconches, monoplacophores, gastropodes) de l'Ordovicien inférieur Trémadocien–Arenigien) de la Montagne Noire (France méridionale). *Mémoire de la Société des Études Scientifiques de l'Aude*. Sival, Carcassone, 63 pp., 15 pls.

—— 1995. The initial Ordovician bivalve mollusc radiations on the western Gondwanan shelves. 491–498. *In* COOPER, J. D., DROSER, M. L. and FINNEY, S. C. (eds). *Ordovician odyssey: short papers for the Seventh International Symposium on the Ordovician System*. Pacific Section Society for Sedimentary Geology (SEPM), Fullerton, 498 pp.

—— and DESTOMBES, J. 1992. Les mollusques bivalves et rostroconches ordoviciens de l'Anti-Atlas marocain: intérêt paléogéographique de leur inventaire. *Géologie Méditerranéene*, **17**, 243–261. [Dated 1990].

—— and GUTIÉRREZ-MARCO, J. C. 1985. Un nouveau cycloconchide (Mollusca, Bivalvia) du Llanvirn inférieur (Ordovicien) des Monts de Tolède (Espagne). *Geobios*, **18**, 609–614.

—— —— 1991. Middle Ordovician bivalves from Spain and their phyletic and palaeogeographic significance. *Palaeontology*, **34**, 109–147.

—— and MELOU, M. 1972. Mollusques bivalves et brachiopodes des 'Schistes de Raguenez' (Ordovicien supérieur de Finistère); conséquences stratigraphiques et paléobiogéographiques. *Annales de la Société Géologique du Nord*, **92**, 79–94.

BAILEY, J. B. 1983. Middle Devonian Bivalvia from the Solsville Member (Marcellus Formation), central New York State. *Bulletin of the American Museum of Natural History*, **174**, 193–326.

BARRANDE, J. 1881. *Système silurien du centre de la Bohême. Vol. VI: Classe des Mollusques. Ordre des Acéphalés.* Prague and Paris, xxiv + 342 pp., 361 pls.

BARROIS, C. 1891. Mémoire sur la faune du Grès armoricain. *Annales de la Société Géologique du Nord*, **19**, 134–237, pls 1–5.

BATES, D. E. B. 1968. The Lower Palaeozoic brachiopod and trilobite faunas of Anglesey. *Bulletin of the British Museum (Natural History), Geology Series*, **16**, 127–199, pls 1–14.

BEURLEN, K. 1944. Beiträge zur Stammesgeschichte der Muscheln. *Bayerische Akademie der Wissenschaften*, **1–2**, 133–145.

BILLINGS, E. 1858. Black River fauna. *Canadian Geological Survey Report of Progress*, **1857**, 147–192.

—— 1861–65. *Palaeozoic fossils: containing description and figures of new or little known species of organic remains from the Silurian rocks.* Vol. 1. Geological Survey of Canada, Montreal, 426 pp.

—— 1874. Palaeozoic fossils. *Canadian Naturalist and Geologist*, **2**, 144 pp.

BLAKE, J. F. 1902. *List of the types and figured specimens in the collections of the Geological Society of London.* Geological Society, London, 100 + xxxi pp.

BOSS, K. J. 1982. Mollusca. 945–1166 of Vol. 1. *In* PARKER, S. P. (ed.). *Synopsis and classification of living organisms.* McGraw Hill, New York, Vol. 1, 1166 pp.; Vol. 2, 1232 pp.

BRADSHAW, J. D. and BRADSHAW, M. A. 1971. Functional morphology of some palaeotaxodont bivalve hinges as a guide to orientation. *Palaeontology*, **14**, 242–249.

BRADSHAW, M. A. 1970. The dentition and musculature of some Middle Ordovician (Llandeilo) bivalves from Finistère, France. *Palaeontology*, **13**, 623–645.

BRANSON, E. E. 1909. The fauna of the residuary Auburn Chert of Lincoln County, Missouri. *Transactions of the Academy of Science of St Louis*, **18**, 39–52, pl. 7.

BUTTS, C. 1941. Geology of the Appalachian Valley in Virginia. Part 2. Fossil plates and explanation. *Bulletin of the Geological Survey of Virginia*, **52**, 1–271, pls 64–135.

CARTER, R. M. 1971. Revision of Arenig Bivalvia from Ramsey Island, Pembrokeshire. *Palaeontology*, **14**, 250–261, pls 38–39.

CHRONIC, H. 1952. Molluscan fauna from the Permian Kaibab Formation, Walnut Canyon, Arizona. *Bulletin of the Geological Society of America*, **63**, 96–166, pls 1–11.

CLOUD, P. E. and BARNES, V. E. 1948. The Ellenburger Group of central Texas. *University of Texas Publication*, **4621**, [for 1946], 473 pp, 44 pls.

CONRAD, T. A. 1838. Report on the palaeontological department of the survey [of New York]. *Annual Report of the New York Geological Survey*, **2**, 107–119.

COPE, J. C. W. 1980. The early history of the southern margin of the Tywi Anticline in the Carmarthen area, South Wales. 527–532. *In* HARRIS, A. L., HOLLAND, C. H. and LEAKE, B. E. (eds). *The Caledonides of the British Isles – reviewed.* Special Publication, 8, Geological Society, London, xii + 768 pp.

—— 1982. The geology of the Llanstephan peninsula. 259–269. *In* BASSETT, M. G. (ed.). *Geological excursions in Dyfed, south-west Wales.* National Museum of Wales, Cardiff, 327 pp.

—— 1995. The early evolution of the Bivalvia. 361–370. *In* TAYLOR, J. D. (ed.). *Origin and evolutionary radiation of the Mollusca.* Oxford University Press, Oxford, xiv + 392 pp. [Dated 1996]

COX, L. R. 1937. Notes on Jurassic Lamellibranchs. I. On the occurrence of the genus *Palaeoneilo* in the Jurassic of Great Britain. *Proceedings of the Malacological Society, London*, **22**, 190–193, pl. 15, figs 1–7.

—— 1959. The geological history of the Protobranchia and the dual origin of the taxodont Lamellibranchia. *Proceedings of the Malacological Society, London*, **33**, 200–209.

—— and 24 others. 1969–1971. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part N. Mollusca 6, Bivalvia, Vol. 1*, xxxviii + N1–N489; Vol. 2, ii + N491–N952; Vol. 3, iv + N953–N1124. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas.

DALL, W. H. 1889. On the hinge of pelecypods and its development, with an attempt towards a better subdivision of the group. *American Journal of Science*, **38**, 445–462.

DALL, W. H. 1895. *Contributions to the Tertiary fauna of Florida with especial reference to the Miocene Silex beds of Tampa and the Pliocene Beds of Caloosahatchie river.* 483–570. *In* Volume 3, Part 3. *A new classification of the Pelecypoda.* Wagner Free Institute of Science, Philadelphia, 1654 pp., 60 pls.

DESPARMET, R., TERMIER, G. and TERMIER, H. 1971. Sur un bivalve protobranche anté-arénigien trouvé au nord de Wardak (Afghanistan). *Geobios*, **4**, 143–150.

DOUVILLÉ, H. 1912. Classification des lamellibranches. *Bulletin de la Société Géologique de France, 4ème Série*, **12**, 419–467.

FISCHER, P. H. 1880–87. *Manuel de conchyliologie et de paléontologie conchyliologique.* F. Savy, Paris, xxv + 1369 pp., 23 pls.

FORTEY, R. A. and OWENS, R. M. 1978. Early Ordovician (Arenig) stratigraphy and faunas of the Carmarthen district, south-west Wales. *Bulletin of the British Museum (Natural History), Geology Series*, **30**, 225–294, 11 pls.

—— —— 1987. The Arenig Series in South Wales: stratigraphy and palaeontology. *Bulletin of the British Museum (Natural History), Geology Series*, **41**, 69–307.

GIRTY, G. H. 1912. On some invertebrate fossils from the Lykins Formation of eastern Colorado. *Annals of the New York Academy of Sciences*, **22**, 1–8, pl. 1.

GRAY, J. E. 1824. A natural arrangement of Mollusca, according to internal structure. *Repository*, **15**, 229–239.

—— 1847. A list of the genera of Recent Mollusca, their synonyms and types. *Proceedings of the Zoological Society of London*, **15**, 129–219.

HALL, J. 1847. Palaeontology. *Geological Survey of New York*, **1**, 1–338.

—— 1861. Containing descriptions and figures of the organic remains of the lower Helderberg group and the Oriskany sandstone. *Geological Survey of New York*, **3**, 1855–1859, (2), 120 pls.

—— and WHITFIELD, R. P. 1872. Descriptions of new species of fossils from the vicinity of Louisville, Kentucky, and the falls of the Ohio. *Annual Report of the New York State Museum of Natural History*, **24**, 181–200a.

—— —— 1875. Fossils of the Hudson River Group (Cincinnati formations). *Report of the Geological Survey of Ohio*, **2**, (2), 67–161, pls 1–13.

HARRINGTON, H. J. 1938. Sobre las faunas del Ordoviciano inferior del Norte Argentino. *Revista del Museo de La Plata, Nueva Serie*, **1**, 109–289, 14 pls.

HAVLÍČEK, V. and KŘÍŽ, J. 1978. Middle Cambrian *Lamellodonta simplex* Vogel: 'bivalve' turned brachiopod *Trematobolus simplex* (Vogel). *Journal of Paleontology*, **52**, 972–975.

HERTWIG, C. W. T. R. 1895. *Lehrbuch der Zoologie.* Gustav Fischer, Jena, 599 pp.

HICKS, H. 1873. On the Tremadoc rocks in the neighbourhood of St. David's, South Wales and their fossil contents. *Quarterly Journal of the Geological Society, London*, **29**, 39–52.

HSÜ, S. C. and MA, C. T. 1948. The I-Chang Formation and the Ichangian fauna. *Contributions to the National Research Institute of Geology, Academia Sinica*, **8**, 51 pp., 9 pls.

IREDALE, T. 1939. Great Barrier Reef expedition 1928–1929. *Scientific Reports, British Museum (Natural History)*, **5**, [Mollusca, Part 1], 209–425.

ISBERG, O. 1934. *Studien über Lamellibranchiaten des Leptaenakalkes in Dalarna.* Håkan Ohlssons Buchdruckerei, Lund, 496 pp., 32 pls.

JELL, P. A. 1980. Earliest known pelecypod on Earth. A new Early Cambrian genus from South Australia. *Alcheringa*, **4**, 233–239.

KHALFIN, L. L. 1958. Plastinchatozhabernye mollyuski ordovika Chu Iliyskikh gor. *Transactions of the Geological Institute of the USSR*, **9**, 130–136, pls 1–7. [In Russian].

KOBAYASHI, T. 1933. Faunal study of the Wanwanian (basal Ordovician) series with special notes on the Ribeiridae and the ellesmeroceroids. *Faculty of Science Journal of Tokyo Imperial University*, 2, **3**, 249–328, pls 1–10.

KOROBKOV, I. A. 1954. *Spravochnik i metodicheskoe rukovodstvo po tetrichnūm mollyuskam Plastinchatozhabernye.* Nauchno-tecnoï Isledov, Leningradskoi Otdelenie, 444 pp., 96 pls. [In Russian].

LAMARCK, J. B. P. A. de M. de 1809. *Philosophie zoologique, ou exposition des considérations relatives à l'histoire naturelle des animaux, la diversité de leur organisation et des facultés qu'ils en obtiennent, aux causes physiques qui maintiennent en eux la vie, et donnent lieu aux mouvement qu'ils exécutent; enfin, à celles qui produisent les unes des sentiments, et les autres l'intelligence de ceux qui en sont doués.* Dentu, Paris. Vol. 1, 422 pp; Vol. 2, 473 pp.

LINNAEUS, K. 1758. *Systema naturae per tria regna naturae*... Edit. decima, 1, Laurentii Salvii, Stockholm, 824 pp.

McALESTER, A. L. 1962. Mode of preservation in early Paleozoic pelecypods and its morphological and ecological significance. *Journal of Paleontology*, **36**, 69–73.

—— 1965. Systematics, affinities, and life habits of *Babinka*, a transitional Ordovician lucinoid bivalve. *Palaeontology*, **8**, 231–246.

—— 1966. Evolutionary and systematic implications of a transitional Ordovician lucinoid bivalve. *Malacologia*, **3**, 433–439.

—— 1968. Type species of Paleozoic nuculoid bivalve genera. *Memoir of the Geological Society of America*, **105**, ix + 143 pp., 36 pls.

McCOY, F. 1844. *A synopsis of the characters of the Carboniferous limestone fossils of Ireland.* Privately printed. Re-issued 1862, Williams and Norgate, London, 274 pp., 29 pls.

McLEARN, F. H. 1918. The Silurian Arisaig Series of Arisaig, Nova Scotia. *American Journal of Science*, **45**, 126–140.

MILLER, S. A. 1874. Monograph of the Lamellibranchiata of the Cincinnati group. *Cincinnati Quarterly Journal of Science*, **1**, 211–231.

—— 1877. *The American Palaeozoic fossils, a catalogue of the genera and species.* Published by the author, Cincinnati, 253 pp.

—— 1881. Description of five new species of Silurian fossils, and remarks upon an undetermined form. *Journal of the Cincinnati Society of Natural History*, **3**, 314–317, pl. 8.

—— 1889. *North American geology and palaeontology for the use of amateurs, students, and scientists.* Western Methodist Book Concern, Cincinnati, 664 pp.

MORRIS, N. J. 1978. The infaunal descendants of the Cycloconchidae: an outline of the evolutionary history and taxonomy of the Heteroconchia, Superfamilies Cycloconchacea to Chamacea. *Philosophical Transactions of the Royal Society of London, Series B*, **284**, 259–275.

—— and FORTEY, R. A. 1976. The significance of *Tironucula* gen. nov. to the study of bivalve evolution. *Journal of Paleontology*, **50**, 701–709.

MURCHISON, R. I. 1839. *The Silurian system, founded on geological researches in the counties of Salop, Hereford, Radnor, Montgomery, Caermarthen, Brecon, Pembroke, Monmouth, Gloucester, Worcester and Stafford: with descriptions of the coalfields and overlying formations.* John Murray, London, 2 vols, 768 pp.

—— 1859. *Siluria. The history of the oldest fossiliferous rocks and their foundations, with a brief sketch of the distribution of gold over the earth.* 3rd [2nd] Edition, John Murray, London, xx + 592 pp., 41 pls.

NEUMAYR, R. M. 1884. Zur Morphologie des Bivalvenschlosses. *Kaiser-Königlichen Akademie der Wissenschaften, Wien, Abteilung 1*, **88**, 385–418.

NEWELL, N. D. 1942. Late Paleozoic polecypods: Mytilacea. *Report of the Geological Survey of Kansas*, **10**, (2), 1–115, 15 pls.

—— 1956. Primitive desmodont pelecypods of the Australian Permian. *American Museum Novitates*, **1799**, 13 pp.

—— 1965. Classification of the Bivalvia. *American Museum Novitates*, **2206**, 25 pp.

—— 1969. Order Modiomorphoida. N393–N401. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part N. Mollusca 6, Bivalvia.* Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, 1124 pp.

—— and BOYD, D. W. 1965. Parallel evolution in early trigoniacean bivalves. *Bulletin of American Natural History*, **154**, 53–162.

PAUL, C. R. C. 1985. The adequacy of the fossil record reconsidered. *In* COPE, J. C. W. and SKELTON, P. W. (eds). Evolutionary case histories from the fossil record. *Special Papers in Palaeontology*, **33**, 7–15.

—— and COPE, J. C. W. 1982. A parablastoid from the Arenig of South Wales. *Palaeontology*, **25**, 499–507.

PFAB, L. 1934. Revision der Taxodonta des böhmischen Silurs. *Palaeontographica, Abteilung A*, **80**, 195–253, pls 2–4.

PHILLIPS, J. 1848. *In* PHILLIPS, J. and SALTER, J. W. Palaeontological appendix to Professor John Phillips' memoir on the Malvern Hills compared with the Palaeozoic districts of Abberley etc. *Memoir of the Geological Survey of Great Britain*, **2**, (1), viii–xiv + 331–386, pls 4–30.

POJETA, J. 1971. Review of Ordovician Pelecypods. *Professional Paper of the United States Geological Survey*, **695**, 46 pp., 20 pls.

—— 1978. The origin and early taxonomic diversification of pelecypods. *Philosophical Transactions of the Royal Society of London, Series B*, **284**, 225–246, 15 pls.

—— 1979. Geographic distribution of Cambrian and Ordovician rostroconch molluscs. 27–36. *In* GRAY, J. and BOUCOT, A. J. (eds). *Historical biogeography, plate tectonics, and the changing environment.* Oregon State University Press, Corvallis, xii + 500 pp.

—— 1987. Class Pelecypoda. 386–435. *In* BOARDMAN, R. S., CHEETHAM, A. H. and ROWELL, A. J. (eds). *Fossil* *invertebrates*. Blackwell Scientific Press, Palo Alto, Oxford, London, Edinburgh, Boston, Melbourne, xi + 713 pp.

POJETA, J. 1988. The origin and Paleozoic diversification of solemyoid pelecypods. *Memoir of the New Mexico Bureau of Mines and Mineral Resources*, **44**, 201–71, pls 1–24.

—— and GILBERT-TOMLINSON, J. 1977. Australian Ordovician pelecypod molluscs. *Bulletin of Mineral Resources, Geology and Geophysics, Canberra*, **174**, i–vi + 1–64, pls 1–29.

—— and RUNNEGAR, B. 1976. The paleontology of rostroconch molluscs and the early history of the Phylum Mollusca. *Professional Paper of the United States Geological Survey*, **968**, iv + 88 pp., 54 pls.

—— —— 1985. The early evolution of diasome molluscs. 295–336. *In* TRUEMAN, E. R. and CLARKE, M. R. (eds). *The Mollusca, 10, Evolution*, Academic Press, Orlando, San Diego, New York, Austin, London, Montreal, Sydney, Tokyo, Toronto, 491 pp.

—— —— MORRIS, N. J. and NEWELL, N. D. 1972. Rostroconchia: a new class of bivalved mollusks. *Science*, **177**, 264–267.

RIDEWOOD, W. G. 1903. On the structure of the gills of lamellibranchs. *Philosophical Transactions of the Royal Society of London, Series B*, **194**, 147–284.

ROUALT, M. 1850–51. Mémoires sur le terrain paléozoïque des environs de Rennes. *Bulletin de la Société Géologique de France, 2ème Série*, **8**, 358–399.

RUNNEGAR, B. and BENTLEY, C. 1983. Anatomy, ecology and affinities of the Australian early Cambrian bivalve *Pojetaia runnegari* Jell. *Journal of Paleontology*, **57**, 73–92.

—— and POJETA, J. 1992. The earliest bivalves and their Ordovician descendants. *American Malacological Bulletin*, **9**, 117–122.

SALTER, J. W. 1859. *In* MURCHISON, R. I., *Siluria*. 3rd [2nd] Edition, John Murray, London, xx + 592 pp., 41 pls.

—— 1866. On the fossils of North Wales. Appendix, 240–381, pls 1–26. *In* RAMSAY, A. C. The geology of North Wales. *Memoir of the Geological Survey of Great Britain*, **3**, vii + 381 pp., 28 pls.

SÁNCHEZ, T. M. and BABIN, C. 1993. Un insolite mollusque bivalve, *Catamarcaia* n. g., de l'Arenig (Ordovicien inférieur) d'Argentine. *Comptes Rendus de l'Académie des Sciences, Paris, Série II*, **316**, 265–271.

SANDERS, H. L. and ALLEN, J. A. 1973. Studies on deep-sea Protobranchia (Bivalvia); prologue and the Pristiglomidae. *Bulletin of the Museum of Comparative Zoology, Harvard University*, **145**, 237–262.

SARDESON, F. W. 1896. The Saint Peter Sandstone. *Bulletin of the Minnesota Academy of Natural Sciences*, **4**, 64–88, pls 2–4.

SAY, T. 1824. An account of the fossil shells of Maryland. *Journal of the Academy of Natural Sciences of Philadelphia*, **4**, 124–155, pls 7–13.

SEPKOSKI, J. J. 1981. A factor analytic description of the marine fossil record. *Paleobiology*, **9**, 36–53.

—— and MILLER, A. I. 1985. Evolutionary faunas and the distribution of Paleozoic marine communities in space and time. 153–190. *In* VALENTINE, J. W. (ed.). *Phanerozoic diversity patterns. Profiles in Macroevolution.* Princeton University Press, Princeton and San Francisco, 441 pp.

SHARPE, D. 1853. Description of the new species of Zoophyta and Mollusca (Appendix B *In* RIBEIRO, C. Carboniferous and Silurian formations of the neighbourhood of Bussaco in Portugal). *Quarterly Journal of the Geological Society, London*, **9**, 146–158, pls 7–9.

SHERGOLD, J. H., GORTER, J. D., NICOLL, R. S. and HAINES, P. W. 1991. Stratigraphy of the Pacoota Sandstone (Cambrian–Ordovician), Amadeus Basin, N.T. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics*, **237**, 1–14.

SOOT-RYEN, H. 1969. A new species of *Babinka* (Bivalvia) from the Lower Ordovician of Öland, Sweden. *Palaeontology*, **12**, 173–177, pl. 34.

STANLEY, S. M. 1972. Functional morphology and evolution of byssally attached bivalve mollusks. *Journal of Paleontology*, **46**, 165–212.

STOLICZKA, F. 1870–71. Cretaceous fauna of southern India. 3. The Pelecypoda, with a review of all known genera of this class, fossil and Recent. *Geological Survey of India, Palaeontologica Indica, Series 6*, **3**, 537 pp.

STRAHAN, A., CANTRILL, T. C., DIXON, E. E. L. and THOMAS, H. H. 1909. The geology of the South Wales Coalfield. X, The country around Carmarthen. *Memoir of the Geological Survey of Great Britain*, vii + 262 pp.

STUBBLEFIELD, C. J. 1938. The types and figured specimens in Phillips and Salter's palaeontological appendix to John Phillips' memoir on 'The Malvern Hills compared with the Palaeozoic districts of Abberley, etc.' *Summary of Progress of the Geological Survey of Great Britain and the Museum of Practical Geology for the Year 1936*, 27–51.

TATE, R. 1896. Palaeontology. 97–116, pls 1–3. *In* SPENCER, B. (ed.). *Report on the work of the Horn Scientific Expedition to central Australia. Part III. Geology and Botany.* Dulau and Co., London; Melville, Mullen and Slade, Melbourne, 204 pp.

TAYLOR, J. D., KENNEDY, W. J. and HALL, A. 1969. The shell structure and mineralogy of the Bivalvia. Introduction. Nuculacea–Trigonacea. *Bulletin of the British Museum (Natural History), Zoology Series, Supplement*, **3**, 125 pp., 29 pls.

——— 1973. The shell structure and mineralogy of the Bivalvia. II. Lucinacea–Clavagellacea Conclusions. *Bulletin of the British Museum (Natural History), Zoology Series*, **22**, 256–294, pls 1–15.

TAYLOR, P. D. and COPE, J. C. W. 1987. A trepostome bryozoan from the Lower Arenig of South Wales: implications of the oldest described bryozoan. *Geological Magazine*, **124**, 367–371.

THORAL, M. 1935. *Contribution à l'étude paléontologique de l'Ordovicien inférieur de la Montagne Noire et révision sommaire de la faune cambrienne de la Montagne Noire*. Imprimerie Charité, Montpellier, 363 pp., 35 pls.

TOMLIN, J. R. 1931. Some preoccupied names – III. *Proceedings of the Malacological Society, London*, **19**, 174–175.

TUNNICLIFF, S. P. 1982. A revision of late Ordovician bivalves from Pomeroy, Co. Tyrone, Ireland. *Palaeontology*, **25**, 43–88, pls 7–13.

ULRICH, E. O. 1890. New Lamellibranchiata. No. 2. On two new genera and six new species. *American Geologist*, **6**, 173–181.

—— 1892. New Lower Silurian Lamellibranchiata chiefly from Minnesota rocks. *Minnesota Geological and Natural History Survey*, **19**, 211–248.

—— 1894. The Lower Silurian Lamellibranchiata of Minnesota: from Volume 3. *Final Report of the Geological and Natural History Survey of Minnesota*, 475–628. (Published and distributed under separate cover prior to publication of the entire Volume 3 in 1897).

—— 1895. New and little known Lamellibranchiata from the lower Silurian rocks of Ohio and adjacent states. *Report of the Geological Survey of Ohio*, **7**, (2), 627–693, pls 45–56.

VERNEUIL, D. de and BARRANDE, J. 1856. Description des fossiles trouvés dans les terrains siluriens et dévoniens d'Almaden, de la Sierra Morena et des montagnes de Tolède. *Bulletin de la Société Géologique de France, 2ème Série*, **12**, 964–1025.

VOKES, H. E. 1956. Notes on the Nucinellidae (Pelecypoda) with description of a new species from the Eocene of Oregon. *Journal of Paleontology*, **30**, 652–671.

WALLER, T. R. 1978. Morphology, morphoclines, and a new classification of the Pteriomorphia (Mollusca: Bivalvia). *Philosophical Transactions of the Royal Society of London, Series B*, **284**, 345–365.

WHITEAVES, J. F. 1897. *Palaeozoic fossils. 3, Part III, The fossils of the Galena-Trenton and Black River formations of Lake Winnipeg and its vicinity*. Geological Survey of Canada, Ottowa, 129–242, pls 16–22.

WHITFIELD, R. P. 1882. Part 3, Palaeontology, 163–363, pls 1–27. *In Geology of Wisconsin, Survey of 1873–1879*. Vol. 4. Commissioners of Public Printing, Beloit, xxiv + 779 pp.

WHITTARD, W. F. 1979. (compiled by DEAN, W. T.). An account of the Ordovician rocks of the Shelve Inlier in west Salop and part of north Powys. *Bulletin of the British Museum (Natural History), Geology Series*, **33**, 1–69.

WILLIAMS, H. S. 1912. Some new Mollusca from the Silurian formations of Washington County, Maine. *Bulletin of the United States National Museum*, **42**, 381–398, pls 49–50.

—— and BREGER, C. L. 1916. The fauna of the Chapman Sandstone of Maine. *Professional Paper of the United States Geological Survey*, **89**, 347 pp., 27 pls.

YU WEN 1985. *Yangtzedonta* – a problematical Bivalvia from Lower Cambrian Meishucunian Stage, China. *Acta Micropalaeontologica Sinica*, **2**, 401–408. [In Chinese with English summary].

JOHN C. W. COPE

Department of Earth Sciences
University of Wales Cardiff
P.O. Box 914
Cardiff CF1 3YE, UK

Typescript received 14 July 1995
Revised typescript received 23 January 1996

NOTE ADDED IN PROOF

Since this paper was submitted, a paper by I. Hinz-Schallreuter (1995, Muscheln (Pelecypoda) aus dem Mittelkambrium von Bornholm, *Geschiebekunde aktuell*, **11**, 71–84) has been published, describing *Pojetaia* and two further palaeotaxodont genera from the Middle Cambrian of Bornholm. Amendment is thus needed to the first paragraph of this paper.