THE EARLY PHYLOGENY OF THE CLASS BIVALVIA

by JOHN C. W. COPE

ABSTRACT. Differences between zoologists and palaeontologists over high-level bivalve taxonomy reflect the hitherto poorly understood early phylogeny of the class Bivalvia. Recent description of a diverse early Arenig fauna and recognition that explosive radiation of early Ordovician bivalves can be correlated with evolution of the filibranch gill within the palaeotaxodonts, together with parsimonious analysis of early bivalve shell characters, has allowed the production of a modified scheme of high-level taxonomy reflecting phylogeny. Shell microstructure has proved of use in detecting phylogenetic links. The subclass Palaeotaxodonta, primitively with prismato-nacreous shells, includes the earliest bivalves and gave rise to the subclass Lipodonta. A new family of palaeotaxodonts, Cardiolariidae, is proposed to include palaeotaxodonts with a modified hinge and probably with filibranch gills; the subclass Palaeoheterodonta, also with prismato-nacreous shells, was derived from these. Radiation from the palaeoheterodonts produced the subclasses Anomalodesmata and Neotaxodonta by the early Ordovician. The Neotaxodonta probably had a shell microstructure with both crossed-lamellar and complex crossed-lamellar elements, and gave rise to the Pteriomorphia, characterized by a calcitic outer shell layer, in early Ordovician times. The shell microstructure of the Neotaxodonta suggests that the Heterodonta evolved from this group, probably by mid or late Ordovician times, but their early fossil record is very poor. A new neotaxodont, *Alytodonta gibbosa* gen. et sp. nov., is described from the lowermost Silurian of Girvan, Scotland. The genus *Babinka* is recorded for the first time from Britain, from the Arenig of South Wales, and the new genus *Homilodonta* is proposed for some mid and late Ordovician palaeotaxodonts from Ireland and North America.

ALTHOUGH bivalves are abundant and varied organisms at the present day and have an excellent fossil record, their high-level classification has been in a state of flux for over a century. This arises from the different series of taxonomic criteria used by various workers; in particular, there is an immediate divergence between the approaches to the problem of high-level classification used by zoologists and palaeontologists. Whilst the former have used many features of soft part morphology and produced different classifications based on different organs, palaeontologists have used shell morphology and those of the soft parts which can be determined from the shell (e.g. musculature). Thus Linnaeus (1758) used the degree of fusion of the margins of the mantle; Lankester (1883) relied on the pedal development, whilst for many zoologists (e.g. Fischer 1880–87; Pelseneer 1889) the gill grade was the definitive criterion in high-level taxonomy of the class. More recently, the stomach type (Purchon 1959, 1960) or labial palp development (Stasek 1963) have been advocated as providing the best taxonomic indicators. For the palaeontologist, however, most of these attributes are not discernible from the fossil shell, although where there are clearly established fossil ancestors of extant forms, it is often possible to draw conclusions as to the nature of certain soft parts. In drawing up bivalve classifications, palaeontologists have used shell form, in particular the dentition (e.g. Neumayr 1884; Bernard 1898), or features of the soft parts which can be deduced from the shell, such as the musculature (e.g. von Zittel 1881–85) or ligament type, together with consideration of the fossil record (e.g. Douvillé 1912) to provide the basis for the high-level taxa. The result has been a conflicting series of classifications of the group (e.g. Starobogatov 1992; Cope 1995).

One of the problems that palaeontologists have faced repeatedly in their quest for a classification of the bivalves is that of homeomorphy. Bivalves are, perhaps unsurprisingly, frequently held up as an example of a group which shows many adaptations of the shell to different modes of life. The

same shell shapes are repeated in forms which we now recognize cannot be related phylogenetically. This still causes problems; for example, were the Devonian–Recent mytilids derived from the Ordovician–Permian modiomorphoids (as suggested for example by Pojeta 1978) or are the mytilids an unrelated homeomorphic stock which evolved to occupy the same ecological niche? We do not yet know the answer, but the lack of any convincing intermediates (see Carter 1990b, p. 273) suggests that the latter explanation may be more likely. Other bivalve characteristics are also homeomorphic; for example, dentition patterns are repeated in unrelated stocks essentially because the number of ways two calcified valves can be articulated is limited. Thus the taxodont dentition of the arcoidean bivalves was for several decades the cause of their direct linking to the nuculoids (e.g. Douvillé 1912; Davies 1947) and this idea was not finally dispelled until Cox (1959) showed that the two stocks were totally unrelated.

One other important tool in the search for fundamental taxonomic criteria in the bivalves has been the advent of shell microstructural studies, made possible through the use of the scanning electron microscope. A major initial monograph by Taylor et al. (1969, 1973) showed the potential of such studies as a taxonomic tool; this has been succeeded by many smaller studies of individual fossils or groups. The work has been carried forward more recently in a major compilation by Carter (1990a). In the course of these studies, some caveats have emerged, for instance that shell microstructures as complex as crossed-lamellar structure can be evolved by unrelated groups of molluscs. Shell microstructure allows other homeomorphies to be detected. For example, the dentition of the heterodonts is at times similar to that of the palaeoheterodonts, so that the two groups have been combined in the subclass Heteroconchia Hertwig, 1895 by some authors (e.g. Pojeta 1978, 1987), although shell microstructure now suggests the two groups are quite distinct and that the similarity in dentition is purely homeomorphic.

The ideal for which to aim, in erecting a high-level taxonomy, is clearly a phylogenetic scheme which uses knowledge of extant bivalves to apply some anatomy to the fossil forms. The Treatise on invertebrate paleontology. Volume N. Mollusca 6 (Cox et al. 1969–71) was a serious attempt at such a scheme but suffered, in particular, because of the lack of knowledge of early fossil forms, and thus details of some of the most fundamental diversifications of the class were lacking. At the time of publication of the Treatise, for example, the earliest bivalve was thought to be the Middle Cambrian genus Lamellodonta Vogel, 1962; this has been shown subsequently to be a distorted obolid brachiopod (Havlíček and Kříž 1978). However, for more than a decade this spurious bivalve fuelled a major debate about whether actinodont or taxodont dentition was the primitive bivalve condition. Over the past 30 years, however, knowledge of early bivalves has increased dramatically, largely through the works of Pojeta (e.g. 1966, 1971, 1978, 1988) and Babin (e.g. 1966, 1982a), and we are now reaching the position of establishing the primary evolutionary pathways along which bivalves diversified.

It is now firmly established that two genera of bivalves existed in the early Cambrian; Fordilla Barrande, 1881 and Pojetaia Jell, 1980 are now both accepted as belonging to the same family, Fordillidae, which in turn is assigned to the subclass Palaeotaxodonta (Runnegar and Pojeta 1992). These latter authors showed that the shell structure in these forms consisted, at least in part, of nacre prisms, and Carter (1990b) showed that a Devonian palaeotaxodont had very similar shell microstructure. From the Middle Cambrian, in addition to Pojetaia, two other bivalve genera are known (MacKinnon 1982; Berg-Madsen 1987; Hinz-Schallreuter 1995); all are now accepted as palaeotaxodonts. Berg-Madsen (1987) also recorded a specimen of the mid Cambrian genus Tuarangia from an erratic block from Western Pomerania, Poland, which has also yielded the conodont Westergaardodina tricuspidata Müller, indicating an early late Cambrian age. This remains the only unequivocal record of a bivalve from the upper Cambrian, but ten species are known from the Tremadoc Series of the Ordovician from three localities (Argentina – Harrington 1938; Australia – Pojeta and Gilbert-Tomlinson 1977, southern France – Babin 1982a). The Australian locality was initially recorded as of probable early Arenig age by Pojeta and Gilbert-Tomlinson (1977); however, more recent work has shown that the fauna is of late Tremadoc age (Shergold et al. 1991). The Tremadoc faunas include palaeotaxodonts, palaeoheterodonts and

cyrtodonts. In the early part of the succeeding Arenig Series, bivalves are now known from five localities world-wide (Cope 1996) and the known fauna totals about 35 species. Of these, the majority come from one locality in South Wales which has recently yielded a bivalve fauna consisting of 20 species belonging to 18 genera (Cope 1996), and includes representatives of the subclasses Palaeotaxodonta, Lipodonta, Palaeoheterodonta, Pteriomorphia and Anomalodesmata. This fauna emphasizes the fact that a significant part of the evolutionary history of the class Bivalvia must have occurred in pre-Arenig times, yet our knowledge of pre-Arenig bivalves is very poor and contributes little to the resolution of the problems of the earliest radiation of the class. The fact that the hitherto described Tremadoc bivalve species include forms which may now be presumed to have been of filibranch gill grade, demonstrates that there must be significant Tremadoc faunas yet to be discovered, and to judge from the fossil record it appears that the Gondwanan shelves are the places where other early bivalve faunas should be sought. Babin (1995) has emphasized the role of the western high latitude Gondwanan shelves in early bivalve evolution, but the Australian Tremadoc faunas show that the low latitude Gondwanan shelves were also important. It is probable that the filibranch gill evolved during the early part of the Tremadoc Epoch and priority should thus go to the search for ancestors of these forms on the peri-Gondwanan shelves, where it seems most likely that they will be found. In contrast, the Laurentian continent seems to be devoid of early Ordovician bivalves; there, rostroconchs occupied the shallow infaunal habitats in much the same way as bivalves did on the Gondwanan shelves. It was not until the mid Ordovician that the bivalves migrated to Laurentia.

Compared with the one known family of bivalves (belonging to one subclass) in the Cambrian, no fewer than 18 families belonging to six subclasses have hitherto been identified as existing before the end of the early Ordovician. The seventh subclass appeared probably by mid or late Ordovician times. Beyond this time, no further bivalve subclasses appeared, and all seven subclasses existing in the late Ordovician are represented at the present day. It is thus clear that the early Ordovician explosive evolutionary outburst represents the most important phase of bivalve evolutionary diversification. Not only did bivalves become noticeably more diverse at this time, and employed an increasing variety of modes of life, but they simultaneously became significantly larger. Compared with the 1–2 mm length of Cambrian bivalves, early Arenig bivalves (apart from the palaeotaxodonts) are regularly 10–15 mm long, and by the Llanvirn Epoch regularly exceed 25 mm. Cope (1995) correlated this increase in size, diversity, and mode of life with the evolution of the filibranch gill. He suggested that amongst the palaeotaxodonts there were forms with a modified hinge indicating an adaptation for greater valve opening commensurate with the acquisition of the feeding gill.

There are demonstrable gaps in the bivalve fossil record because that of the early Ordovician is clearly so incomplete. However, parsimonious analysis of shell characters enables us to reconstruct parts of this cryptogenetic past. Even when the fossil record is more complete, it is often remarkably disjunct; as an example, solemyoid bivalves are unknown from Britain between the lower Arenig and the Lower Carboniferous, although many thousands of bivalves have been collected (and exist in museum collections) from this long interval. Such disjunct fossil ranges provide an added complication to the unravelling of the early phylogeny of some bivalve groups. As a corollary of this, it is clear that the order of occurrence of bivalves in the fossil record cannot be an infallible guide to their respective origins.

The taxonomic scale adopted herein is the same as that of the *Treatise* (Cox *et al.* 1969–71) and of Pojeta (1978, 1987); that is, to treat the major divisions of the class Bivalvia as subclasses. However, I show below that we can now establish plausible phylogenetic links between these major taxonomic units; they are not now discrete entities without connections, as was the case at the time of publication of the *Treatise*. It may be, therefore, that a taxonomically more defensible position would be to regard these major divisions of the class as superorders rather than subclasses.

Subclass PALAEOTAXODONTA Korobkov, 1954

(Pl. 1, figs 1–7, Text-fig. 3)

The palaeotaxodonts include the most primitive living bivalve, the cosmopolitan genus *Nucula*, which has survived, apparently differing little from its Ordovician ancestors. *Nucula* has protobranch gills, a prismato-nacreous shell and a hinge-plate bearing a row of subequal teeth and sockets – the taxodont dentition. It lives as an infaunal sessile deposit feeder.

The fossil record from the early Cambrian through to the early Ordovician suggests that the Palaeotaxodonta were the earliest bivalves, and supports the view that *Pojetaia* and *Fordilla*, not only the earliest unequivocally accepted bivalves but also, in all probability, palaeotaxodontids, could well have given rise to later bivalve stocks. The shell structure of both *Pojetaia* and *Fordilla* has been shown by Runnegar and Pojeta (1992) to be similar to that of a Devonian palaeotaxodont (Carter 1990*b*). Modern nuculoid palaeotaxodonts have a three-layered aragonitic shell: the inner layer consists of sheet nacre, the middle layer of lenticular nacre, and the outer layer is prismatic (Taylor *et al.* 1969). The same three-layered structure also characterizes the Monoplacophora and the Archaeogastropoda, confirming the likelihood that this was the primitive molluscan shell microstructure (Text-fig. 1). However, in contrast to the nuculoids, modern nuculanoid palaeotaxodonts have a homogeneous aragonitic shell (Taylor *et al.* 1969). This change appears to have happened geologically recently, as Cox (1959) reported nacreous structure in a Jurassic *Nuculana*, an observation subsequently confirmed by Taylor *et al.* (1969, p. 68).

The dentition of bivalves is designed to lock the valves accurately on closure, to provide a mechanism allowing rotation along the hinge axis, and to prevent a shearing motion of the valves when open. These characteristics provide bivalves with protection against current action and predation. The taxodont dentitions of the palaeotaxodonts 'provide strong juncture between the valves and in addition oppose rotation in the plane of commissure' (Kauffman *in* Cox *et al.* 1969, p. N173). However, it is clear that the dentition of most of the palaeotaxodonts (e.g. Pl. 1, figs 1–7)

EXPLANATION OF PLATE 1

Fig. 1. *Ctenodonta nasuta* (Hall, 1847); USNM 14718; upper Ordovician, Ottowa, Canada; RV; ×1. Photograph supplied by J. Pojeta. Figured Pojeta 1971, pl. 4, fig. 6.

Fig. 2. *Homilodonta* cf. *regularis* (Portlock, 1843); USNM 162705; middle Ordovician, Kentucky; RV; ×3. Palaeotaxodont figured as *Deceptrix* sp. nov. by Pojeta 1978, pl. 1, fig. 1.

Fig. 3. *Pensarnia laeviformis* Cope, 1996; NMW78. 17G. 1071; latex cast of holotype; figured Cope 1996, pl. 1, fig. 2; Lower Arenig, Llangynog, Carmarthenshire; RV; ×4.

Fig. 4. *Similodonta similis* (Ulrich, 1892); USNM 47037*a*; upper Ordovician, Minnesota; LV; ×5. After Pojeta 1978, pl. 2, fig. 7.

Fig. 5. *Praenucula filistriata* (Ulrich, 1894); USNM 40487; upper Ordovician, Ohio; LV; ×5. Palaeotaxodont figured as *Deceptrix filistriata* by Pojeta 1978, pl. 2, fig. 1. Photograph supplied by J. Pojeta.

Fig. 6. *Myoplusia bilunata perdentata* (Barrande, 1881); Barrande Collection, Národní Museum, Prague; middle Ordovician, Czech Republic. After Babin and Gutiérrez-Marco 1991, pl. 4, fig. 8; RV internal mould; ×5.

Fig. 7. *Nuculoidea lens* Liljedhl, 1983; SGU Type 842; Wenlock, Gotland; holotype, RV; ×3·8. After Liljedahl 1994, fig. 30A. Note central resilifer on the hinge-plate, a Silurian innovation.

Fig. 8. *Ovatoconcha fragilis* Cope, 1996; NMW78. 17G. 1175; lower Arenig, Llangynog, Carmarthenshire; composite mould RV; ×2·5. After Cope 1996, pl. 4, fig. 2. Note large anterior adductor.

Fig. 9. *Psiloconcha grandis* Ulrich, 1894; USNM 46283*a*; upper Ordovician, Ohio; RV; ×1·3. Photograph supplied by J. Pojeta. Figured Pojeta 1988, pl. 17, fig. 1.

Fig. 10. *Solemya radiata* Meek and Worthen, 1860; AMNH 42616; Upper Carboniferous, Ohio; ×1·7. Photograph supplied by J. Pojeta. Figured Pojeta 1988, pl. 22, fig. 1.

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PLATE 1
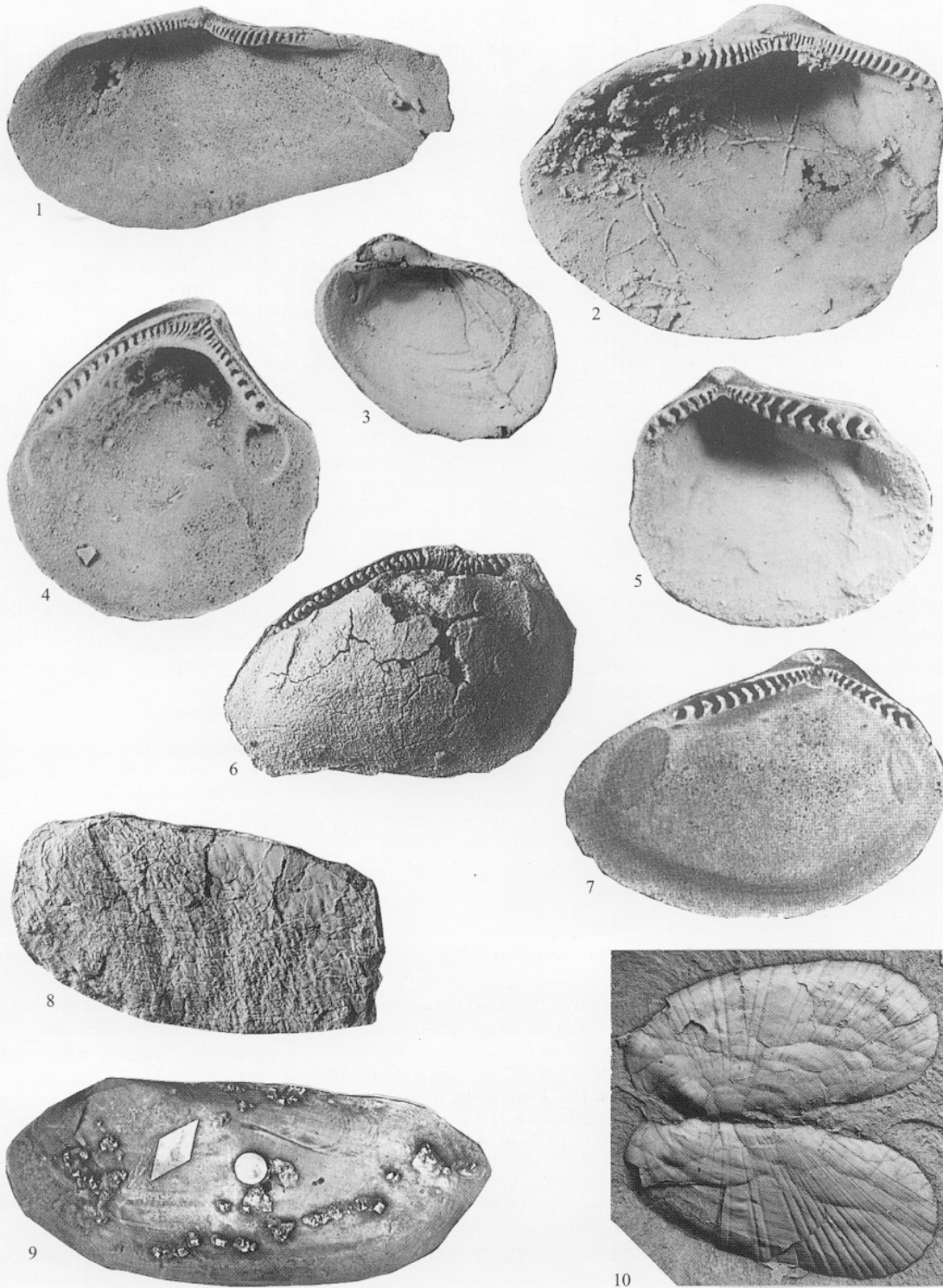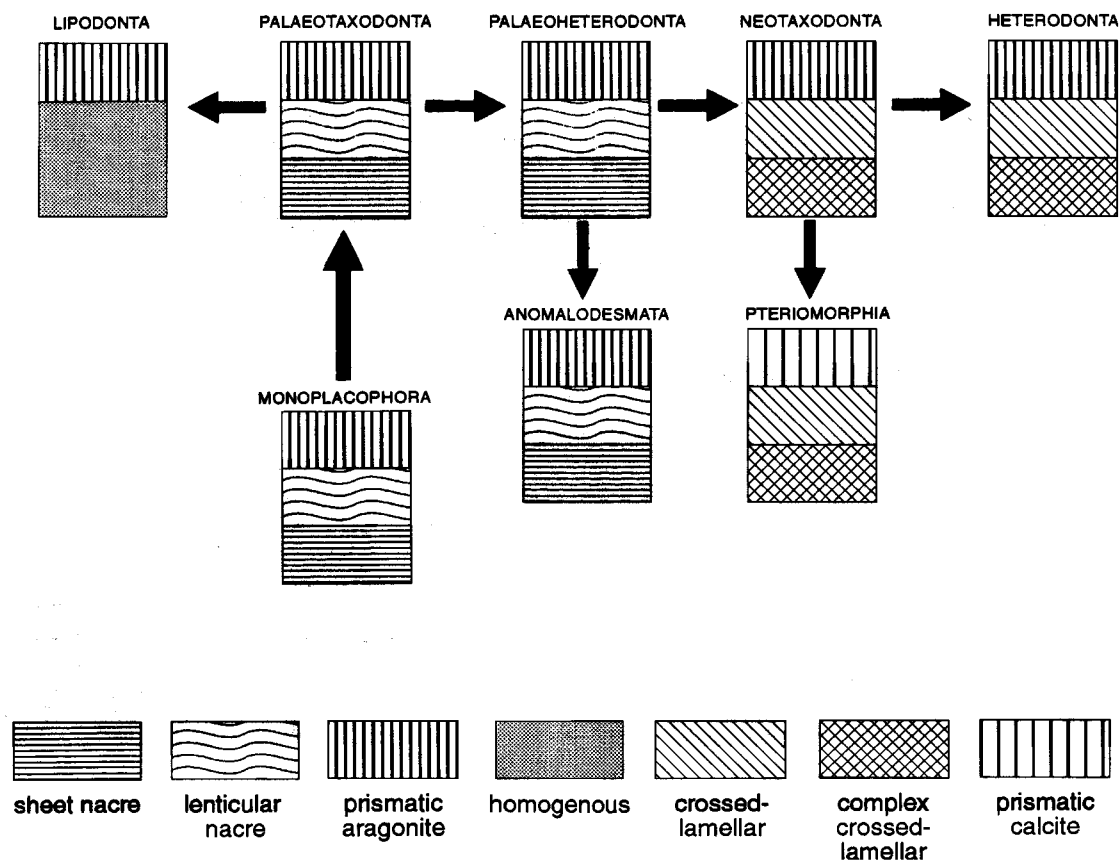
TEXT-FIG. 1. Parent shell microstructures of the bivalve subclasses. The forms depicted are those from which all shell microstructures known within each subclass can readily be derived. Thus, in the neotaxodonts (and also in some heterodont families), modern forms have a two-layered shell; this could be readily derived from the presumed parent shell structural type by loss of the outer layer. In the pteriomorphians, many extant forms possess the parent shell structural type; others have extended the calcite to other shell layers, etc.

would only perform in this way with a restricted degree of valve opening. Other palaeotaxodonts (e.g. Text-fig. 3) have a differentiated taxodont hinge which would prevent shearing motions with a greater degree of valve opening.

The palaeoheterodonts can be derived from such a palaeotaxodont ancestor (Cope 1995, and below), and several examples are now known of palaeotaxodonts which have similarly differentiated teeth. Previously (Cope 1995), I suggested that these examples could represent forms in which the hinge mechanism was modified to allow pseudofaeces to be expelled, and could represent the earliest filibranch grade bivalves (see below); these forms could provide ideal ancestors for the diverse early Ordovician palaeoheterodonts. I believe that the fact that all living palaeotaxodonts are protobranch has pre-conditioned our views of extinct forms and thus has hitherto constrained our interpretations of the gill grade of Ordovician palaeotaxodonts. There is no a priori objection to the belief that several genera of advanced palaeotaxodonts had filibranch gills. Following this hypothesis, the feeding gill could have been evolved within the palaeotaxodonts and its evolution could well have provided the trigger which unleashed the evolutionary burst amongst the Bivalvia in the earliest Ordovician, presumably during the early part of the Tremadoc.

If the palaeotaxodonts were the earliest bivalves, at least one of the other subclasses must have evolved directly from them. Earlier (Cope 1995), I presented evidence to show that the palaeotaxodonts were the rootstock of the palaeoheterodonts. All extant palaeoheterodonts are of filibranch or eulamellibranch gill grade, and I suggested (Cope 1995) that the filibranch grade evolved within the palaeotaxodonts. This hypothesis removed one of the most awkward obstacles in the way of producing a convincing model of early bivalve evolution. If we accept this hypothesis, it provides a reason for the sudden explosive evolution of the bivalves in the early Ordovician, concomitant with their rapid increase in size and abundance; the development of the feeding gill enabled bivalves to develop their infaunal feeding strategies further and allowed them, for the first time, to develop epifaunal modes of life and to compete, on increasingly equal terms, with the articulate brachiopods.

With the evolution of the filibranch gill, one significant disadvantage accrued: the gill could not differentiate between food and non-food particles, and as water and ciliary currents directed these particles mouthwards, a method of sorting was required unless the animals were to ingest large amounts of useless sediment during normal feeding activity. The solution the bivalves adopted was to eject the sedimentary particles as pseudofaeces, but this material could not be carried away by the already existing internal shell water currents, as these were in the wrong direction, so they employed a vigorous flapping of the valves to expel the pseudofaeces accumulated along the ventral margin of the shell (Cox et al. 1969). This, it seems to me, is the reason why differentiated dentition was developed concomitantly with the filibranch gill and with larger size.

It appears most unlikely that the filibranch gill, the more primitive grade of the feeding ctenidium, could have evolved more than once. On the other hand, it also seems clear that the eulamellibranch grade could have evolved several times, as it is found in seemingly unrelated stocks of bivalves. The difference here is that the demibranchs of the filibranch gill, lying as they do in close proximity to each other, are likely to have developed organic connections to each other in different groups of bivalves; this would have resulted wholly from their organic proximity and the consequence is a polyphyletic grouping of bivalves of eulamellibranch grade (as first demonstrated by Ridewood 1903).

A group of early and mid Ordovician–Devonian palaeotaxodonts has now been identified that are united by their differentiated hinge and that are believed to have developed filibranch gills; these are grouped together in the new family Cardiolariidae (see below and Text-fig. 3).

The subclass Palaeotaxodonta is thus here identified as the group which included not only the earliest bivalves, but also that in which the filibranch gill type evolved. *Pojetaia* is confirmed as being close to the ancestral bivalve. It therefore now seems clear that the long controversy over which was the earliest type of dentition, and how the primary radiation of the bivalves occurred is now over. The palaeotaxodonts were the rootstock of the bivalves, and the most fundamental radiation – associated with the evolution of the feeding gill – occurred within that subclass, probably during the earliest Ordovician or possibly latest Cambrian.

Subclass LIPODONTA Cope, 1995

(Pl. 1, figs 8–10)

This subclass includes the extant genus *Solemya* which is an infaunal mobile detritus feeder. Like *Nucula*, *Solemya* has protobranch gills, but differs in its marked anterior elongation with a dominant anterior adductor muscle, and an edentulous hinge. *Solemya* itself has survived little changed since Devonian times. Solemyoids are specialized bivalves adapted to a deeply infaunal habitat, particularly in shallow-water silty muds; they have a much reduced gut, which was the cause of much speculation on their physiology by zoologists, until Cavanaugh (1983) demonstrated that they lived symbiotically with sulphur-oxidizing chemoautotrophic bacteria. Solemyoids have a shell with anterior and posterior gapes which has a thick periostracum that extends ventrally beyond the calcified portion of the valves.

In the *Treatise* (Cox *et al.* 1969), the solemyoids were included as members of the subclass Cryptodonta Neumayr, 1884. Even at the time of publication of the *Treatise*, the members of this subclass appeared an ill-matched medley of forms, whose only factor in common was the lack of knowledge of the hinge. Since 1969, a great deal more information has been obtained on many of these forms and it is now realized that some of them can be assigned to the subclass Pteriomorphia (e.g. Kříž 1979), whilst others include some rostroconchs. Pojeta (1978) suggested that solemyoids were derived from palaeotaxodonts and thus they could be included in the same subclass. He later (1988) figured a series of anteriorly elongated palaeotaxodonts and suggested that these may well have been the origin of solemyoids in the mid Ordovician. Cope (1996) described a new solemyoid, *Ovatoconcha fragilis*, from the Lower Arenig of South Wales, showing that the solemyoids were already a distinct group at this time. Thus Pojeta's claimed intermediate forms could be interpreted either as surviving intermediate stocks, or as a separate mid Ordovician evolution of anteriorly elongated palaeotaxodonts, unrelated to the solemyoids. Another possible early Arenig solemyoid is the *Cymatonota*? sp. figured by Babin (1982*a*, pl. 11, fig. 17) from the Montagne Noire; if this is indeed a solemyoid, the orientation of the shell proposed by Babin (1982*a*, p. 45) would need to be reversed.

As early as 1969, Newell (*in* Cox *et al.* 1969, pp. N212–N213) noted that it was reasonable to conclude that solemyoids were only distantly related to palaeotaxodonts; the only criterion for grouping them together was that they were the only two bivalve cohorts sharing the protobranch gill. Apart from this one feature in common, they 'differ in almost every feature'. With the recognition that some palaeotaxodonts may well have had filibranch ctenidia (see above), it appears that the gill grade now has less of an importance in taxonomy and so this one common factor is of less relevance, except to show that the solemyoids must have originated from the palaeotaxodonts.

Since solemyoids occurred in the early Ordovician, their probable divergence from the palaeotaxodonts must have occurred earlier. In view of this early divergence and their fundamental morphological differences, it is clear that a separate high-level taxon is necessary for the solemyoids. I thus (Cope 1995) introduced the subclass Lipodonta to accommodate them. It is evident that this subclass has had a long geological history. The retention of the protobranch gill and a shell consisting of an outer prismatic layer and an inner homogeneous laminated layer, a microstructural

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EXPLANATION OF PLATE 2

Fig. 1. *Lyrodesma majus* (Ulrich, 1879); USNM 46223; upper Ordovician, Ohio; RV; × 3. Photograph supplied by J. Pojeta. Figured Pojeta 1971, pl. 3, fig. 15. A lyrodesmatid palaeoheterodont.

Fig. 2. *Copidens browni* Pojeta and Gilbert-Tomlinson, 1977; CPC 15593; lower or middle Ordovician; Georgina Basin, NT, Australia; LV, hinge-plate; × 4. Photograph supplied by J. Pojeta. Figured Pojeta and Gilbert-Tomlinson 1977, pl. 28, figs 4–5. A cycloconchid actinodont.

Fig. 3. *Ananterodonta oretanica* Babin and Gutiérrez-Marco, 1985; CUM SP-IV 2 073/OR; lower Llanvirn, Toledo, Spain; holotype LV; × 1. After Babin and Gutiérrez-Marco 1991, text-fig. 9f. A cycloconchid actinodont.

Fig. 4. *Cycloconcha mediocardinalis* Miller, 1874; WM 8893; upper Ordovician, Ohio; RV; × 4. After Pojeta 1971, pl. 2, fig. 16. A cycloconchid actinodont.

Fig. 5. *Actinodonta cuneata* Phillips, 1848; BGS GSM 59825; Upper Llandovery, Marloes Bay, Pembrokeshire; latex cast of RV lectotype; × 1·75. After Pojeta 1978, pl. 4, fig. 9. A cycloconchid actinodont.

Fig. 6. *Colpomya constricta* Ulrich, 1895; USNM 162746; upper Ordovician, Kentucky; × 2·5. After Pojeta 1971, pl. 12, fig. 2. A colpomyid modiomorphoid.

Fig. 7. *Carminodonta crossi* Cope, 1996; NMW78. 17G. 1183; lower Arenig, Llangynog, Carmarthenshire; × 3. After Cope 1996, pl. 3, fig. 8. A cycloconchid actinodont.

Fig. 8. *Modioliodon oviformis* (Ulrich, 1890); USNM 247856; middle Ordovician, Kentucky; × 1·5. After Pojeta 1978, pl. 13, fig. 15. A modiomorphoid palaeoheterodont with a simple pseudocardinal dentition.

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PLATE 2
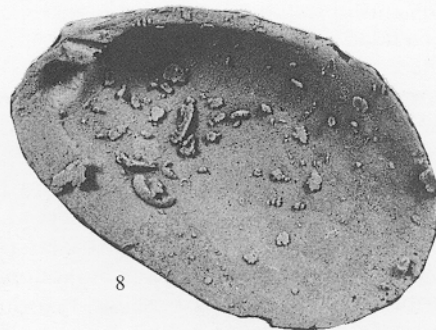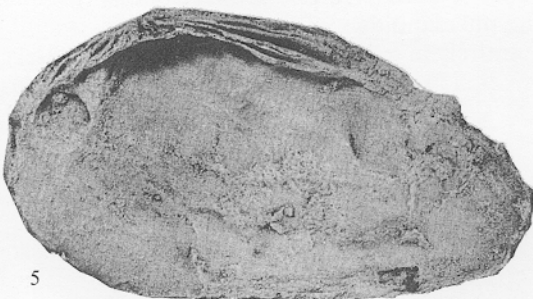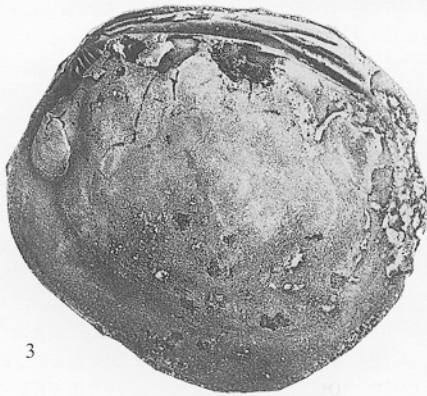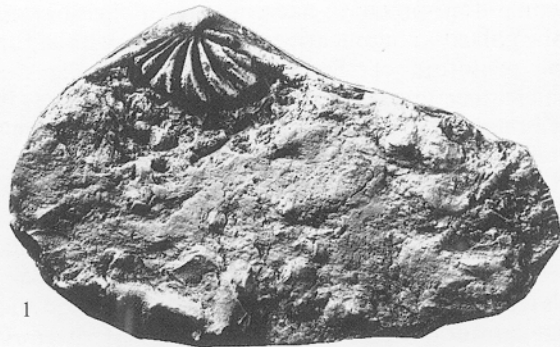
type which could be readily derived from a palaeotaxodont prismato-nacreous shell (Taylor *et al.* 1969, 1973), suggests very early derivation from a palaeotaxodont ancestor, perhaps within the Cambrian; their origin may have preceded the evolution of the filibranch gill among the palaeotaxodonts. The time of origin of the shell microstructure exhibited by modern solemyoids is unknown; Early Palaeozoic forms could well have retained the primitive prismato-nacreous shell microstructure but earlier Cope (1996, p. 989), I presented evidence to show that early Arenig forms had a high organic content in their shell, suggesting the possibility that they already had a thick periostracum.

Lipodonts are essentially edentulous and these forms are included in the superfamily Solemyoidea Adams and Adams, 1857, which contains one family, Solemyidae Adams and Adams, 1857. However, some other forms, which have been related to the solemyoids, possessed teeth, and the extant genus *Nucinella* develops an actinodont-like dentition (Allen and Sanders 1969). Cox *et al.* (1969) assigned *Nucinella* to the family Manzanellidae Chronic, 1952 of the order Arcoida Stoliczka, 1871 (therein placed within the subclass Pteriomorphia) with a query. Allen and Sanders' zoological work suggested, however, that its affinities were solemyoid, and Pojeta (1988) referred it to the family Nucinellidae Vokes, 1956, whilst recognizing Manzanellidae Chronic, 1952 as a separate family within the superfamily Nucinelloidea Vokes, 1956. Pojeta (1988) referred this superfamily to the solemyoids.

Taylor *et al.* (1973), however, whilst admitting that *Nucinella* had some anatomical resemblances to *Solemya*, reported that other features more closely resembled those of the palaeotaxodonts. Unlike other lipodonts, nucinelloideans have teeth; they also are monomyarian (or have a very reduced posterior adductor). Nucinelloideans have a much smaller shell than solemyoideans; they are usually between 1 mm and 5 mm long; the shell margins do not gape, and the periostracum does not extend ventrally beyond the calcified parts of the shell (Pojeta 1988). Taylor *et al.* (1973, p. 287) reported that the shell structure of *Nucinella* was of similar homogenous type to that occurring in *Nuculana*, but unlike that of *Solemya* or the nuculoideans. Clearly, the affinities of the superfamily Nucinelloidea are not fully resolved, but the balance of evidence suggests to me that both of its families (Nucinellidae and Manzanellidae) are better placed within the palaeotaxodonts as anteriorly elongated forms, possibly derived from the nuculanoids.

On this basis, the subclass Lipodonta remains entirely a rather homogeneous but entirely endentulous group, comprising the single order Solemyoida Dall, 1889, containing one superfamily, Solemyoidea Adams and Adams 1857.

Subclass PALAEOHETERODONTA Newell, 1965

(Pl. 2, figs 1–8; Pl. 3, figs 1–6; Pl. 4, figs 2, 7)

The palaeoheterodonts include the extant genera *Neotrigonia* and *Unio*, but the subclass also includes important fossil forms such as the actinodontoids and the modiomorphoids. The origins of this subclass appear to be in the cardiolariid palaeotaxodonts which, as explained above, were probably of filibranch gill grade. Cope (1995, text-fig. 30.1) demonstrated that the dentition of the Cardiolariidae, in particular of *Cardiolaria* itself (Text-fig. 3), is remarkably similar to that of the palaeoheterodont *Glyptarca* Hicks, 1873 (Pl. 4, fig. 2). Newell (*in* Cox *et al.* 1969, p. N256) designated *G. primaeva* Hicks as type species of the genus which has been subject to misinterpretation because of the inadequate nature of Hicks' type material (lectotype of the type species designated by Carter 1971). Previously (Cope 1996), I figured a new species, *G. serrata*, from rocks of identical early Arenig (Moridunian Stage) age from Llangynog, some 65 km to the east of Hicks' locality, and figured forms with perfectly preserved moulds of the dentition (see also Pl. 4, fig. 2). The similarity of the overlap of the two sets of teeth in *Glyptarca* and *Cardiolaria* is remarkable. *Cardiolaria* is undoubtedly a palaeotaxodont, whilst *Glyptarca*, although a palaeoheterodont, has a posterior tooth developing a pseudo-taxodont separation. Cope (1995) suggested that these genera provide clear evidence of a link between the palaeotaxodonts and the palaeoheterodonts. The
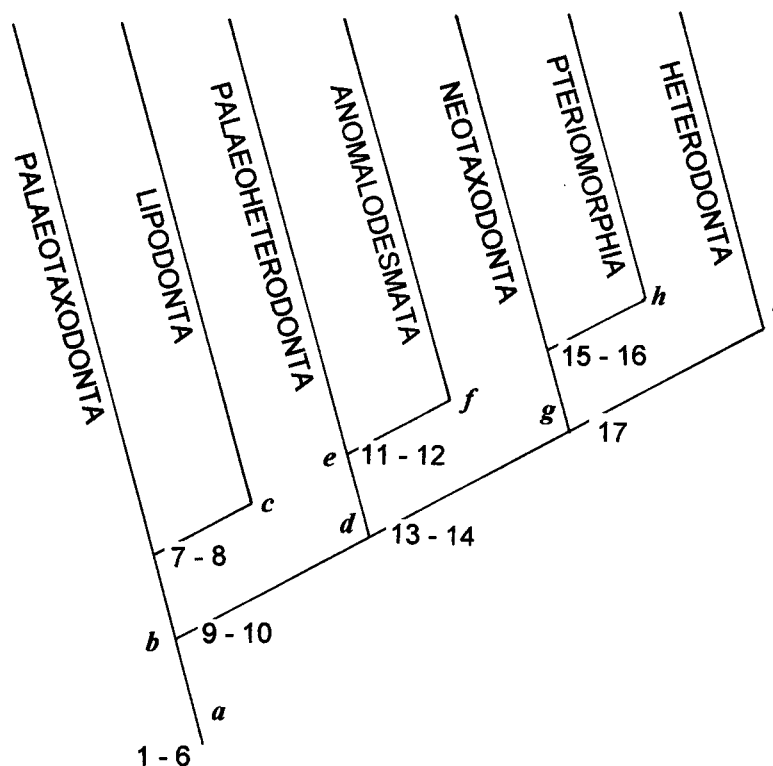
TEXT-FIG. 2. Cladogram showing the postulated relationships between the bivalve subclasses and positions of key genera, families and superfamilies. 1. Prismato-nacreous shell. 2. Protobranch gills. 3. Approximately equal adductors. 4. Two equal valves. 5. Simple opisthodetic ligament. 6. Simple row of teeth on hinge. 7. Anterior adductor dominant. 8. Loss of teeth. 9. Filibranch gill. 10. Differentiated dentition. 11. Loss of teeth. 12. Granulose shell ornament. 13. Duplivincular ligament. 14. Middle shell layer crossed-lamellar; inner layer complex-crossed lamellar. 15. Outer shell layer calcite. 16. Loss of subumbonal teeth. 17. Loss of duplivincular ligament. *a. Pojetaia. b.* Cardiolariidae. *c. Ovatoconcha. d.* Glyptarcoidea. *e. Cosmogoniophora. f. Arenigomya. g. Catamarcaia. h. Cyrtodonta. i.* Crassatelloidea.

overlap of the two sets of teeth appears in the Ordovician only in these two genera; it appears also to be a very rare attribute of bivalve dentition through any part of their geological range. *Cardiolaria* has anterior dentition which displays a similar contrast in size to the posterior dentition as in *Glyptarca*; it lacks, however, the characteristic dorsally divergent arrangement of the anterior dentition of the latter genus. In turn, the dentition of *Glyptarca* is such as would provide an ideal ancestor for the dentition of the neotaxodontids (see below). Thus, the subclass Palaeoheterodonta appears to be readily derivable from the Palaeotaxodonta; it forms the principal plexus of Ordovician filibranch bivalves from which, it is now apparent, two other bivalve subclasses may be readily directly derived.

Some actinodontoideans, such as the family Redoniidae (see Pl. 3, figs 1, 4) have reduced dentition, but the reduction reaches its maximum in the modiomorphoids (Pl. 2, figs 6, 8; Pl. 3, fig. 2), which otherwise appear very close to the actinodontoideans. Pojeta (1978) related the modiomorphoids to the mytilids and suggested that the former may ultimately have been derived from *Fordilla*. He re-introduced Iredale's (1939) group Isofilibranchia as a subclass to include these forms. This suggestion is not accepted herein, as there is no convincing link between the mytiloids and modiomorphoids. Furthermore, the shell structure of *Fordilla* has been shown to be identical

to that of *Pojetaia*, resulting in a unification of the two early Cambrian genera in the family Fordillidae (Runnegar and Pojeta 1992); thus *Fordilla* is now regarded as a palaeotaxodont. Some modiomorphoids have teeth of reduced actinodontoid type (e.g. Pl. 2, fig. 8) and thus link clearly with the palaeoheterodonts, whilst in others, teeth are totally missing (e.g. Pl. 3, fig. 2). I find myself in accord with the views of Bailey (1983) who was unable to accept Pojeta's inclusion of the modiomorphoids in the Isofilibranchia. Bailey (1983, p. 200) concluded that the modiomorphoids were best included with the actinodontoids in the subclass Palaeoheterodonta as '*Modio-morpha*...has a heterodont arrangement with weak posterior laterals...other modio-morphoids...have strong posterior elements as part of a continuous actinodont series'. I would agree with Bailey (1983) in regarding modiomorphoids as an example of a bivalve group which has very variable dentition: at times it appears edentulous, at others that of some members is actinodont-like. Like other groups of bivalves, the modiomorphoids were able to repeat different styles of dentition at different times. The fact that the modiomorphoids seem closely allied to the actinodontoid palaeoheterodonts in the early Ordovician suggests that they were directly linked phylogenetically. However, some other occurrences of actinodontoid dentition appear to be unrelated homeomorphies. Thus, some modern solemyoids (see above, for discussion of affinities of these forms) can produce pseudo-actinodont dentition (Allen and Sanders 1969) as also can some modern palaeotaxodonts (Allen and Sanders 1973). These appearances of apparent actinodont dentition imply no more of a phylogenetic link to the actinodonts, than neotaxodontid dentition implies a phylogenetic relationship to palaeotaxodontid dentition – a putative relationship finally refuted by Cox (1959). Thus the presence, or absence, of teeth in the modiomorphoids should be regarded as a feature which appears and disappears. It does not detract from the hypothesis that

EXPLANATION OF PLATE 3

Fig. 1. *Dulcineaia manchegana* Babin and Gutiérrez-Marco, 1991; CUM PZ-III 2 105/OR; lower Llandeilo, Ciudad Real, Spain; ×2·8. After Babin and Gutiérrez-Marco 1991, pl. 7, fig. 7. A redoniid actinodont with a microcrenulated anterior tooth and single posterior tooth.

Fig. 2. *Modiodonta gothlandica* (Hisinger, 1831); RMMo149878; Wenlock, Gotland; holotype; ×2·5. After Liljedahl 1994, fig. 37G. Internal mould of a modiomorphoid with much reduced dentition.

Figs 3, 6. *Babinka prima* Barrande, 1881; NMW96. 23G. 1*a*; *Bergamia rushtoni* Biozone, Pontyfenni Formation, upper Arenig, Pontyfenni Quarry, Whitland, Carmarthenshire. 3; LV; ×2. 6, close-up to show details of the gill attachment muscle impressions at the end of the pedal muscle scars. The anterior adductor scar is the deeper impression to the left of the print; ×6. Treated herein as an actinodontoid with reduced dentition.

Fig. 4. *Moridunia simplicidens* Cope, 1996; NMW78. 17G. 387; lower Arenig, Llangynog, Carmarthenshire; ×3. After Cope 1996, pl. 5, fig. 6. A redoniid actinodontoid.

Fig. 5. *Goniophora* (*Cosmogonioiphora*) *extensa* Cope, 1996; NMW78. 17G. 1222; lower Arenig, Llangynog, Carmarthenshire; holotype; RV; ×3. After Cope 1996, pl. 4, fig. 5. A modiomorphoid possibly close to anomalodesmatan origins.

Fig. 7. *Arenigomya carinata* Cope, 1996; NMW78. 17G. 1265; lower Arenig, Llangynog, Carmarthenshire; LV; ×3. After Cope 1996, pl. 7, fig. 12. The earliest species of anomalodesmatan known hitherto.

Fig. 8. *Rhytimya radiata* Ulrich, 1895; USNM 102037; upper Ordovician, New York State; RV; ×3. Photograph supplied by J. Pojeta. Figured Pojeta 1978, pl. 15, fig. 1. A form showing the granulose shell texture of many early anomalodesmatans.

Fig. 9. *Orthonota undulata* Conrad, 1841; ANSP 61406; Middle Devonian, New York State; ×1·5. Photograph supplied by J. Pojeta. Figured Pojeta and Runnegar 1985, fig. 11i. An example of a group of Ordovician–Devonian soleniform shells of uncertain affinities; the group may be either anomalodesmatans or modiomorphoid palaeoheterodonts.

Fig. 10. *Cuneamya* sp.; USNM 92331*b*; middle Ordovician, New York State; RV; ×1·5. Photograph supplied by J. Pojeta. Figured Pojeta 1978, pl. 15, fig. 7.

Fig. 2 published with permission from the Lethaia Foundation.

PLATE 3
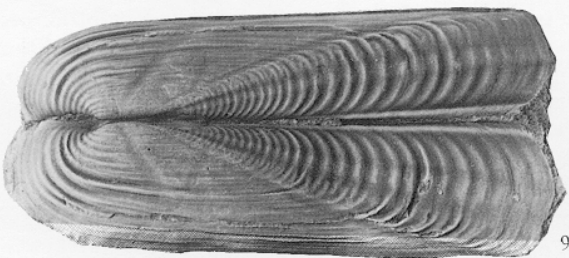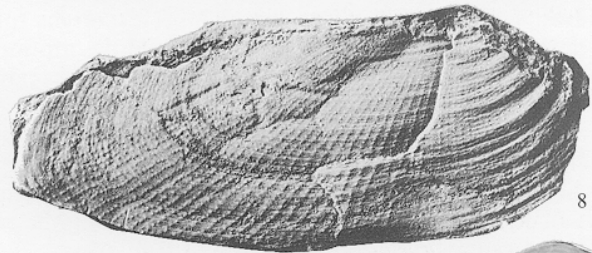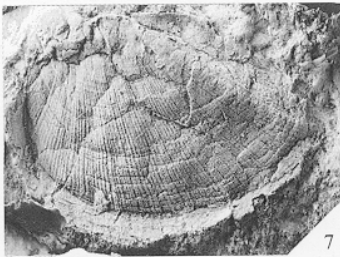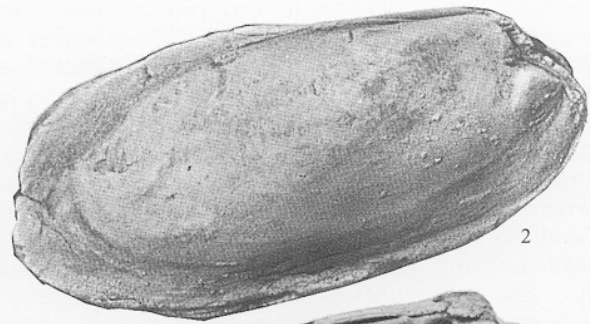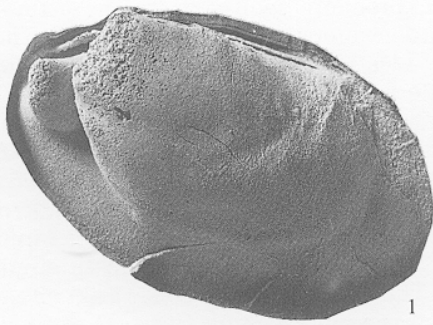
COPE, palaeoheterodonts, anomalodesmatans

the modiomorphoids, with their prismato-nacreous shell, probably evolved from the actino-dontoidean palaeoheterodonts which had similar prismato-nacreous shell microstructure. The shell structure of most modern palaeoheterodonts is identical to that of the nuculoid palaeotaxodonts (Taylor *et al.* 1969), supporting their origin from that group (Text-fig. 1).

One extant group of palaeoheterodonts has filibranch grade gills: this is the trigonioids, which can be traced back plausibly to the Ordovician lyrodesmatid palaeoheterodonts (Pl. 2, fig. 1). In turn *Lyrodesma*, first recorded from the middle Ordovician, can be readily derived from the mid Ordovician genus *Tromelinodonta* Babin, 1982*b* and this from *Noradonta* Pojeta and Gilbert-Tomlinson, 1977 (Babin 1982*b*). *Noradonta* shows some similarity in dentition to the cardiolariid palaeotaxodont *Inaequidens* Pojeta and Gilbert-Tomlinson, 1977 (Text-fig. 3F), and may thus link the trigonioids ultimately back to palaeoheterodont origins. The whole lineage is likely to have been of filibranch gill grade if the evolution of the filibranch gill was a unique event. Cox (*in* Cox *et al.* 1969, p. N21) recorded the possible preservation of gills in Jurassic *Laevitrigonia*, based on the evidence of an unpublished nineteenth century plate, apparently showing this feature. Spamer *et al.* (1989, pl. 1) have reproduced the plate illustrating these forms and Whyte (1991) has located several specimens of *Laevitrigonia* showing phosphatic gill supports consistent with filibranch ctenidia.

In the other group of living palaeoheterodonts, the unionoids, all extant members are eulamellibranch. However, Whyte (1992) has demonstrated that while preserved gill structures in Cretaceous unionoids indicate that these forms were eulamellibranch, late Triassic forms had filibranch gills. This constitutes the only example hitherto known of the change from filibranch to eulamellibranch gill grade occurring within a single lineage. However, as first demonstrated by Ridewood (1903), this is a transition which has probably occurred several times in unrelated bivalve stocks, resulting in the polyphyletic nature of the eulamellibranch gill.

Subclass ANOMALODESMATA Dall, 1889

(Pl. 3, figs 7–10)

Anomalodesmatan bivalves are essentially edentulous burrowing forms. Modern anomalodesmatan forms are, apart from one septibranchiate group, of eulamellibranch gill grade; it is thus likely that their ancestors in the Ordovician would have been of at least filibranch grade. Modern anomalodesmatans have three-layered prismato-nacreous shells identical in structure to those of nuculoids (Taylor *et al.* 1973) and it is thus likely that the subclass was derived from forms with prismato-nacreous shells (Text-figs 1–2). This origin must now go back to at least the early Ordovician, following my earlier (Cope 1996) description of the early Arenig anomalodesmatan genus *Arenigomya* (Pl. 3, fig. 7). The first anomalodesmatans are likely to have been of filibranch gill grade, and the eulamellibranch and septibranch forms developed subsequently. Other characteristic features of the anomalodesmatans are the obsolescent hinge teeth, often resulting in an edentulous hinge or, in some cases, a single, rather amorphous tooth beneath the umbo; they never have lateral teeth and commonly have (throughout their geological range) a fine reticulate ornament with a granulose texture developed along the radial ornament and especially where the elements of radial and concentric ornament intersect.

In the early Ordovician, there was one group of bivalves which appears to have all the characters required of an anomalodesmatan ancestor. That group is the modiomorphoid palaeoheterodonts; they are often edentulous, and probably had a prismato-nacreous shell (as in all extant palaeoheterodonts and all fossil forms with the shell structure preserved). Harrington (1938) recorded the modiomorphoid *Cosmogoniophora* from the Tremadoc of Argentina, and Pojeta and Gilbert-Tomlinson (1977) recorded the genera *Colpantyx* and *Xestoconcha*, both colpomyid modiomorphoids, from the late Tremadoc Pacoota Sandstone of the Amadeus Basin of Australia. Modiomorphoids thus appear in the fossil record before anomalodesmatans. Instead of conventional dentition, the colpomyid modiomorphoids have on their hinge what Pojeta and Gilbert-Tomlinson (1977) referred to as a 'blunt articulating device' (Pl. 2, fig. 6) which could again

provide a satisfactory link between the modiomorphoids and the anomalodesmatans. In the genus *Arenigomya* (Cope 1996), the hinge structure consists of two spoon-shaped subumbonal structures which would appear to have articulated with each other (see Cope 1996, text-fig. 7). This, however, is rather different from the 'blunt articulating device' in each valve of the colpomyids, which resembles a blunt tooth. It is possible that the structures in *Arenigomya* could have housed an internal ligament, as in some modern anomalodesmatans, and the structure would then be a chondrophore. This is in accord with the hinge structures of modern anomalodesmatan forms.

As far as the origin of the shell ornament is concerned, the modiomorphoid *Goniophora* (*Cosmogoniophora*) *extensa* Cope, 1996 (Pl. 3, fig. 5) has a fine reticulate ornament, and it would require small change to this ornament type to produce the characteristic anomalodesmatan granulose texture. Thus, it appears that all the features of the early anomalodesmatans could be readily derived from a modiomorphoid ancestor, and I believe that there is no need to look any further for the origin of this subclass.

Subclass NEOTAXODONTA Korobkov, 1954

(Pl. 4, figs 1, 3–6, 8–9)

Previously (Cope 1995), I reintroduced the subclass Neotaxodonta for the superfamilies Arcoidea and Limopsoidea which together constituted a restricted order Arcoida. The latter includes several familiar extant forms such as the ark shells and glycymerids. My justification for separating out the superfamilies Arcoidea and Limopsoidea from the subclass Pteriomorphia, as in the *Treatise*, was that extant members of the subclass Neotaxodonta are characterized by their unique combination of duplivincular ligament (secondarily lost in some limopsoids), with a two-layered shell consisting of an outer crossed-lamellar layer and an inner complex crossed-lamellar layer, together with dentitions which are continuous along the hinge-plate. In contrast, the pteriomorphians have a calcitic outer shell layer, dentition which has a subumbonal lacuna, together with a ligament which is primitively duplivincular (although many extant forms have lost it). The origins of the neotaxodonts are believed to lie within the glyptarcoid palaeoheterodonts (Pl. 4, figs 2, 7), from which they differ most significantly in the possession of a duplivincular ligament, but probably also in shell microstructure. The two-layered shell of modern neotaxodonts is most likely to have arisen through loss of the outer aragonitic prismatic layer of a three-layered shell (Text-fig. 1).

In the *Treatise* (Cox *et al.* 1969), the earliest arcoidean is quoted as *Parallelodon*. However, the first occurrence, in the lower Ordovician, reported for that genus was based partly on Newell's placing (*in* Cox *et al.* 1969, p. N256) of *Glyptarca* Hicks, 1873 in synonymy with *Parallelodon*. It has since been shown unequivocally by several authors, including Carter (1971) and Cope (1996, who re-defined *Glyptarca* on the basis of better material), that it is a palaeoheterodont. The fact that its age was early Arenig, rather than Tremadoc as quoted by Newell, has been known since Pringle (1930) demonstrated Hicks' error. The other possible early Ordovician *Parallelodon* is *P. antiquus* Barrois from the upper Arenig of the Grès Armoricain of Brittany. However, Babin (1966, p. 146) reported that Barrois' specimen, on which the dentition was based, was lost, but that a gutta percha mould on which Barrois (1891) based his figure (pl. 3, fig. 3) suggested that the dentition was far less clear than shown in the figure and was 'd'analyse délicate'. It thus seems that this species must be treated with caution until further material is found.

The genus *Catamarcaia* Sánchez and Babin, 1993 from the upper middle Arenig of Argentina (Pl. 4, figs 4, 6, 9) is a form which appears to be close to the ancestral neotaxodont (Cope 1997). This genus has dentition, which could be derived readily from that of a palaeoheterodont such as *Glyptarca* (Pl. 4, figs 2, 7), together with a grooved ligamental area. Sánchez (1995) compared the development of the dentition of *Catamarcaia* with that of *Glyptarca*, pointing out the similarities. However, it should be noted that this comparison is, in fact, with the glyptarcoid *Hemiprionodonta* Cope, 1996, following the redefinition of *Glyptarca* (Cope 1996). Sánchez and Babin (1993) treated *Catamarcaia* as a pteriomorph lacking the central edentulous space on the hinge-plate, but I would

regard that feature as an essential character state for Early Palaeozoic pteriomorphs. Earlier (Cope 1996), I preferred to regard *Catamarcaia* as a palaeoheterodont, but it has since become clear that this genus possesses a continuous subumbonal dentition combined with a duplivincular ligament, which together are the distinguishing feature of the neotaxodonts. Sánchez and Babin (1993, p. 267) declined to assign *Catamarcaia* to a family. I suggest that it could well belong to the Parallelodontidae Dall, 1898, although Sánchez (1995) suggested that it may have been ancestral to that family.

The shell microstructure of *Catamarcaia*, although not preserved, can be reconstructed confidently as three aragonitic layers: an outer prismatic, a middle crossed-lamellar, and an inner complex crossed-lamellar layer. These microsctructures were derived through modification of the three-layered prismato-nacreous structure of its glyptarcoid palaeoheterodont ancestor, although it is possible that the glyptarcoids already possessed such a shell. From such a parent shell microstructure, the shell types of all neotaxodonts, pteriomorphians and heterodonts can be derived readily (Text-fig. 1).

Newell (*in* Cox *et al.* 1969, p. N256) noted that the phylogeny of the Parallelodontidae was 'difficult to determine and poorly understood'; however, the discovery of *Catamarcaia* seems to demonstrate the origin of the group and, moreover, that of the subclass Neotaxodonta. The new genus *Alytodonta* (see below and Pl. 4, figs 1, 5, 8), from the lowermost Silurian, provides a link between *Catamarcaia* and the Wenlock genus *Freja* Liljedahl, 1984 (Pl. 4, fig. 3).

The characteristic taxodont dentitions, exhibited by many neotaxodonts, were responsible for some of the problems of high-level bivalve taxonomy formerly encountered by palaeontologists, particularly those subscribing to the ideas espoused by Douvillé (1912) whose 'sedentary branch' led directly from *Nucula* to *Arca*. This classification was followed by many European palaeontologists and was adopted by Davies (1947) in one of the two then widely available palaeontological textbooks in Britain. The other textbook (Woods 1946) included both *Nucula* and *Arca* in the order Taxodonta. Although the fundamental differences between the two stocks were recognized by Korobkov (1954) in his subclasses Palaeotaxodonta and Neotaxodonta, confusion still clearly persisted in some quarters, and continued until Cox's (1959) unequivocal demonstration that the taxodont dentitions of the arcoids were totally unrelated phylogenetically to those of the nuculoids.

Of the forms included by Cox *et al.* (1969) in the order Arcoida, I have separated out the superfamily Cyrtodontoidea, which is characterized by anterior and posterior teeth, separated by an edentulous area, and retained it in Pteriomorphia, within a new order Cyrtodontoida (Cope 1996). The order Arcoida *sensu stricto*, on the other hand, is characterized by dentition which is

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EXPLANATION OF PLATE 4

Figs 1, 5, 8. *Alytodonta gibbosa* gen. et sp. nov.; BMNH L. 49858; Mulloch Hill Sandstone, Lower Llandovery, Mulloch Hill, Girvan, Ayrshire; holotype, LV. 1, latex cast of internal mould; ×2. 5, internal mould; ×2. 8, enlarged view of hinge region of latex cast to show details of dentition and insertion points of duplivincular ligament beneath umbo; ×3·5.

Figs 2, 7. *Glyptarca serrata* Cope, 1996; lower Arenig, Llangynog, Carmarthenshire. A glyptarcoid palaeoheterodont probably similar to that from which neotaxodonts were derived. 2, NMW78. 17G. 490; RV internal mould with umbo removed to show dentition; ×6·5. Figured Cope 1996, pl. 2, fig. 10. 7, NMW78. 17G. 801; holotype, LV; ×4. Figured Cope 1996, pl. 2, fig. 1.

Fig. 3. *Freja fecunda* Liljedahl, 1984; SGU Type 3379; Upper Wenlock, Gotland; ×12. Detail of RV hinge to show dentition. After Liljedahl 1984, fig. 18i.

Figs 4, 6, 9. *Catamarcaia chaschuilensis* Sánchez and Babin, 1993; middle Arenig, Western Argentina. 4, CEGH-UNC 10530; RV; ×3. 6, CEGH-UNV 10533; latex cast; ×3·66. 9, CEGH-UNC 10530; close-up of anterior dentition; ×7. After Sánchez and Babin 1994, pl. 1, figs 5–7.

Fig. 3 published with permission from Sveriges Geologiska Undersökning. Figs 4, 6, 9, published with permission from the Societa Española de Paleontologia.

PLATE 4
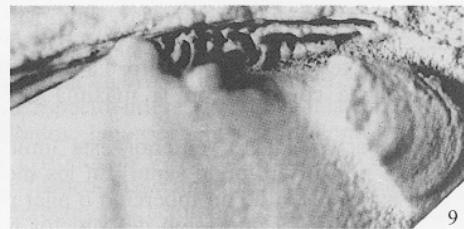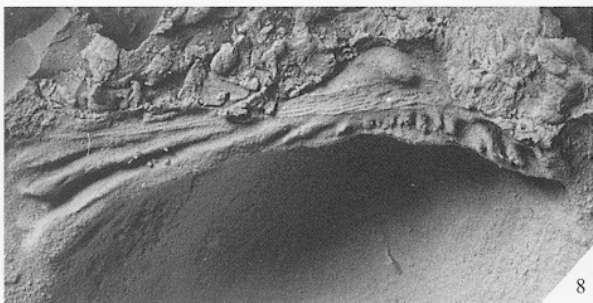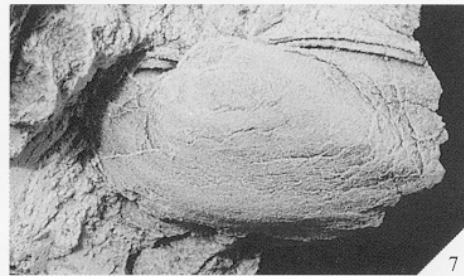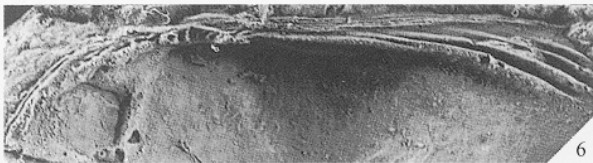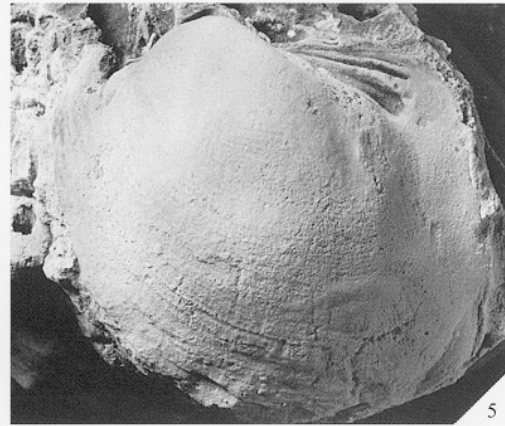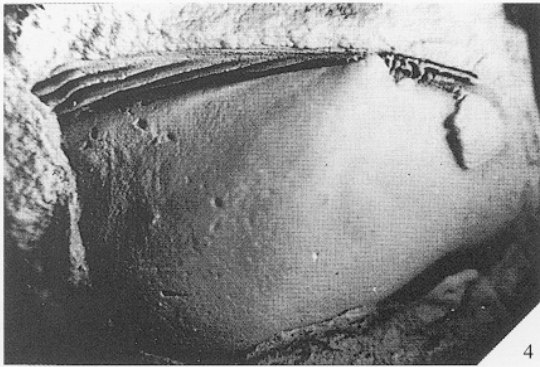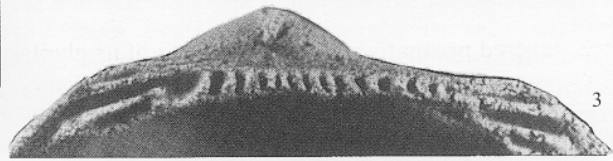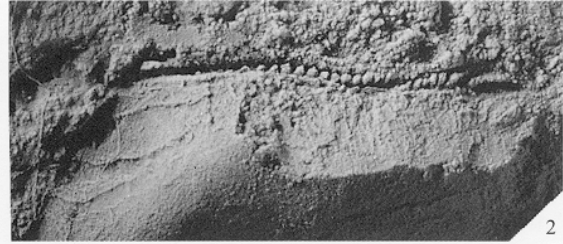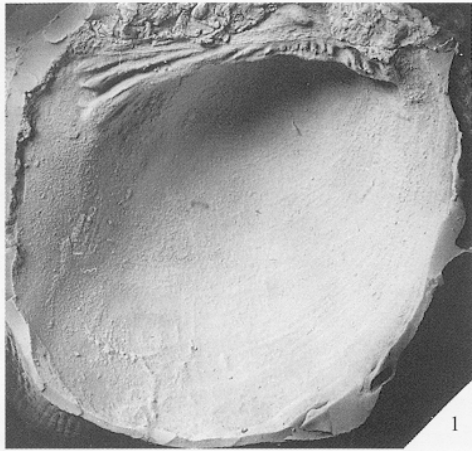
COPE, neotaxodonts, glyptarcoid palaeoheterodonts

continuous beneath the umbo. This leaves the superfamilies Arcoidea and Limopsoidea within the order Arcoida. The latter superfamily is now, however, modified from the entry in the *Treatise*, following the removal of the family Manzanellidae Chronic, 1952 to the Palaeotaxodonta (see above, for discussion of the affinities of the Manzanillidae). One result of this move is that the earliest limopsid is now of late Triassic age (*Hoferia* Bittner, 1894, from the upper Triassic of the Alps).

Subclass PTERIOMORPHIA Beurlen, 1944

(Pl. 5, figs 1–9)

This subclass includes a wide variety of extant forms, such as the oysters, the pectinids and the mussels, that are characterized by shells which have a calcitic outer layer. All groups can be satisfactorily linked phylogenetically to the order Cyrtodontoida (Pl. 5, figs 4–5, 7) which is generally regarded as representing the earliest of the pteriomorphians. The Late Tremadoc Pacoota Sandstone fauna of Pojeta and Gilbert-Tomlinson (1977) includes the hitherto earliest known forms. However, the occurrence of the earliest pterioid in the lower Arenig (Cope 1996) and the earliest ambonychiid in the middle Arenig (Cope 1996) implies that these groups (e.g. Pl. 5, figs 1–2, 6, 8–9) may be of almost equal antiquity. The dentition of the cyrtodontoids, which is characterized by a central edentulous area on the hinge-plate, could have been derived readily from the dentition of the earliest neotaxodonts by loss of the subumbonal dentition. Several authors (e.g. Babin and Gutiérrez-Marco 1991) have noted that there is also agreement between the way in which the teeth of the cyrtodontoids radiate out dorsally from a centre below the hinge-line and the dentition of *Glyptarca*. This dorsally directed divergence was clearly inherited ultimately from the glyptarcoid palaeoheterodonts and, earlier (Cope 1996), I pointed out this significant difference between the actinodontoidean and the glyptarcoidean palaeoheterodonts. It is clear that neotaxodonts form ideal ancestors for the pteriomorphians; the only objection to this hypothesis of cyrtodontoid origins is that it is as yet unsupported by the fossil record. However, as Tremadoc faunas are so poorly known, this is an obstacle that may well be overcome by future finds.

EXPLANATION OF PLATE 5

Figs. 1–2. *Carotidens demissa* (Conrad, 1842). 1, FM 8879, upper Ordovician, Ohio; × 5. LV of a pterioid. Photograph supplied by J. Pojeta. Figured Pojeta 1978, pl. 11, fig. 5. 2, USNM 40554, upper Ordovician, Ontario; LV internal mould; × 1·5. Photograph supplied by J. Pojeta. Figured Pojeta 1978, pl. 11, fig. 12.

Fig. 3. *Myodakryotus deigryn* Tunnicliff, 1987; BGS GSM 22041; Caradoc, Llanfyllin, Montgomeryshire; RV; × 2, Negative supplied by S. P. Tunnicliff. Figured Tunnicliff, 1987, pl. 77, fig. 3. An early limoid.

Fig. 4. *Cyrtodonta huronensis* Billings, 1858; USNM 162715; middle Ordovician, Ontario; RV; × 2. After Pojeta 1978, pl. 8, fig. 2.

Fig. 5. *Cyrtodonta saffordi* (Hall, 1859); USNM 46191a; middle Ordovician, Tennessee; RV; × 1·4. Photograph supplied by J. Pojeta. Figured Pojeta 1978, pl. 8, fig. 11.

Fig. 6. *Byssopteria radiata* Hall, 1883; USNM 100540; Upper Devonian, Pennsylvania; lectotype, RV, × 1·15. Showing anterior shortening characteristic of ambonychiids. After Pojeta 1966, pl. 32, fig. 6.

Fig. 7. *Falcatodonta costata* Cope, 1996; NMW78. 17G. 975; lower Arenig, Llangynog, Carmarthenshire; latex cast of holotype, RV; × 3.

Fig. 8. *Ambonychia alata* Meek, 1872, USNM 84928; upper Ordovician, Indiana; RV; × 0·75. After Pojeta 1966, pl. 29, fig. 18. Showing anterior shortening.

Fig. 9. *Palaeopteria* sp.; USNM 162737; middle Ordovician, Kentucky; LV; × 5. After Pojeta 1978, pl. 11, fig. 1. Showing characteristic dentition of early pterioid.

Fig. 10. *Illionia prisca* (Hisinger, 1837); Mo158171; Ludlow, Gotland; lectotype, LV; × 1. After Liljedahl 1991, text-fig. 5c. An early lucinoid heterodont.

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PLATE 5

All extant pteriomorphians are of filibranch gill grade and, if the filibranch gill is the monophyletic feature as I claimed previously (Cope 1995), they were derived from a filibranch ancestor in the neotaxodonts.

The presence of a grooved ligamental area, in some cases at least indicative of a duplivincular ligament (see Pojeta 1978; Waller 1978), is another characteristic feature of many pteriomorphians. It is not known in the cyrtodontoid superfamily Falcatodontoidea Cope, 1996 (Pl. 5, fig. 7), but other features of this superfamily link it closely to the cyrtodonts; it appears to have been derived early from the cyrtodontoid stock and to have lost secondarily the duplivincular ligament (as have many of the younger pteriomorphian groups).

Most extant pteriomorphians have a shell with a calcitic outer layer, and some of them (e.g. the oysters) have a predominantly calcitic shell. However, many of them also have crossed-lamellar and/or complex crossed-lamellar structure in their shell (Carter 1990b). Previously (Cope 1995), I therefore concluded that the early Ordovician pteriomorphs could well have had a shell which included elements of crossed-lamellar microstructure. It seems probable that crossed-lamellar fabric occurred as a constituent shell microstructure in the neotaxodontoid line at the time of origin of the pteriomorphians because crossed-lamellar or complex crossed-lamellar shells are common to many forms which also possess a duplivincular ligament (neotaxodonts and pteriomorphians). The calcitic outer shell layer of the pteriomorphians thus appears to have developed secondarily from this ancestral shell type. The lucinoid and some veneroid heterodonts (see below) probably provide us with the best clue as to what this may have been, as they consist of three layers: an outer composite prismatic layer, a middle crossed-lamellar layer and an inner complex crossed-lamellar layer (Taylor et al. 1973). The calcitic outer shell layer of the pteriomorphians seems to have originated by substitution of prismatic calcite for prismatic aragonite, probably through a single mutation, and the crossed-lamellar portions of the shell (or ligament) reflect the original microstructure of the middle and inner shell layer in early Ordovician forms. Indeed, some modern mytiloids and pectinoids retain the presumed parent shell microstructural plan (Taylor et al. 1969), as depicted in Text-figure 1. It is likely that the calcitic outer shell layer evolved at about the time of the separation of the Pteriomorphia from the Neotaxodonta, as all pteriomorphian groups, some of which had evolved from the cyrtodontoids within the early Ordovician, have a predominantly calcitic outer shell layer. There are as yet no known early Ordovician pteriomorphs with preserved shell microstructure, although Taylor et al. (1973, p. 288) reported that a late Ordovician ambonychiid (e.g. Pl. 5, figs 6, 8) probably had a prismatic calcite outer shell layer.

Other pteriomorphian groups can be derived readily from the cyrtodontoids. The pterioids are now known from the lower Arenig (Cope 1996) and the ambonychiids from the middle Arenig (Cope 1996). The mytiloids seem best derived from the latter group, rather than from the modiomorphoids as preferred by Pojeta (1978) because, in common with all these other groups, they have a shell which is primarily calcitic (but also sometimes including elements of crossed-lamellar and complex crossed-lamellar microstructure; Taylor et al. 1969), as opposed to the aragonitic prismato-nacreous shell of the modiomorphoids. Tunnicliff (1987) described the Caradoc genus Myodakryotus (Pl. 5, fig. 3), with a morphology intermediate between those of cyrtodontoids and limoids; the genus was assigned to the new family Myodakryotidae within the superfamily Limoidea. Subsequently (Cope 1995, text-fig. 30.3), I suggested how the origin of the later pteriomorphians may be related to these primary radiations.

Since the publication of the Treatise, various members of the order Praecardioida Newell 1965, formerly included in the Cryptodonta, have been the subject of further researches (e.g. the major monographical study by Kříž (1979) of the Cardiola group) which have demonstrated clearly that they are pteriomorphian forms. Following the Treatise classification, they would have been included in the order Arcoida but, in its restricted sense (as used herein, as an order within the Neotaxodonta), they cannot belong there. Kříž (1979) may well have been correct in deriving these forms from the Cyrtodontoida (the latter elevated to ordinal status by Cope (1996)), but they differ in many fundamental ways, including the dentition, from the cyrtodonts, and do not find a natural place within that order. The solution adopted herein is to recognize Praecardioida as a separate

order within Pteriomorphia. Some forms included in the *Treatise* in Praecardioida, have been removed subsequently from that group, including the genus *Eopteria* Billings, 1865, shown by Pojeta and Runnegar (1976) to be a rostroconch.

Subclass HETERODONTA Neumayr, 1884
(Pl. 5, fig. 10)

This subclass is the most varied group of living bivalves and includes more than 80 families. It contains many forms familiar on European sea-shores, such as the cockles, razor-shells and myas, and a variety of fossil forms including the Cretaceous rudists. Heterodonts have fused mantle lobes and commonly have siphons; the gills are all of eulamellibranch grade and this subclass appears to be the last major group of bivalves to have evolved. Heterodont radiations are predominantly features of the Mesozoic and Cenozoic; in the Lower Palaeozoic heterodonts are extremely rare fossils and their origins consequently are largely cryptic.

I believe that there are significant differences between the subclasses Palaeoheterodonta and Heterodonta, although some authorities, notably Pojeta (e.g. 1987), combine the two into the subclass Heteroconchia Hertwig, 1895. The palaeoheterodonts are characterized primarily by prismato-nacreous shells and can be derived directly from the palaeotaxodonts (as demonstrated above), whilst the shells of the heterodonts contain both crossed-lamellar and complex crossed-lamellar layers and appear, most probably, to have been derived from the neotaxodonts. There are, of course, major problems in determining the shell microstructure of many fossil forms, particularly those from the Lower Palaeozoic, but probable phylogenetic links, proposed herein, suggest that the palaeoheterodonts and heterodonts should be maintained as distinct entities. All extant heterodonts are eulamellibranch, whilst extant palaeoheterodonts may be filibranch or eulamellibranch (see above).

The complex crossed-lamellar shell structure is shared only by some groups of heterodonts, pteriomorphians and the neotaxodonts; this provides strong evidence for the close association of these subclasses. Previously (Cope 1995), I suggested that although the subclass Neotaxodonta had originated after the acquisition of the duplivincular ligament, it seemed that the Heterodonta must have arisen before this was acquired, as its members lack this feature. I now believe, on the contrary, that this was unlikely, as the neotaxodonts clearly appeared significantly earlier in the fossil record, and the alternative solution, that the heterodonts were derived from the neotaxodonts, is a more parsimonious explanation of the similar shell microstructures in both groups. This view requires that the heterodont line then lost the duplivincular ligament; this is not a serious problem, as several pteriomorphian groups, including the mytilids, the ostreids and the limids, have also lost the duplivincular ligament which their cyrtodontoid ancestors possessed. In addition, some limopsid neotaxodonts have also lost this feature. Thus, it seems that the probable origin of the heterodonts lies within the neotaxodonts and not in the pteriomorphian rootstock as I earlier surmised (Cope 1995). In this view, there is no direct relationship between the palaeoheterodonts and heterodonts. Hertwig's (1895) combination of the two groups in the Heteroconchia, as followed by Pojeta (1987), is ill-founded; their only shared characteristic is a dentition that, on occasion, can be somewhat similar. However, the posterior lateral teeth in the palaeoheterodonts arise from beneath the umbo and the ligament; in the heterodonts, the posterior lateral teeth, where present, usually arise behind the umbo and the ligament. This latter origin of the posterior dentition would be expected if posterior lateral teeth of neotaxodontid type were combined with a shortened opisthodetic ligament as in the Heterodonta.

Reading of the *Treatise* makes it very difficult to decide what the first heterodont was. Cox (*in* Cox *et al.* 1969, p. N113) recorded the earliest form (disregarding *Babinka* – see below) as the lucinoid *Paracyclas* from the upper Ordovician of Scotland although, according to the systematic sections of the *Treatise*, that genus is restricted to the Devonian (Cox *et al.* 1969, p. N512). Cox's record seems to be based on *P. minor*, recorded from Girvan by Hind (1910, pl. 4, figs 32–35); this appears to be lucinoid in shape, but the lack of preserved dentition makes the assignment uncertain.

However, the middle Ordovician–Devonian genus *Cypricardinia* Hall, 1859 is assigned to the cardiniid crassatelloideans (Cox *et al.* 1969, p. N579), making this record earlier. Other records in the *Treatise* may be dismissed more readily; *Redonia*, assigned to the carditoidean veneroids (Cox *et al.* 1969, p. N546) is now agreed to be a palaeoheterodont, whilst *Matheria* Billings, 1858 (Cox *et al.* 1969, p. N566) is regarded as a cyrtodont, as also suggested in its inclusion there (Cox *et al.* 1969, p. N249). Otherwise, the next youngest recorded heterodont is the genus *Illiona* Billings, 1875 from the Silurian (Pl. 5, fig. 10), belonging to Lucinoidea (Cox *et al.* 1969). From these records, it appears that both the crassatelloideans and the lucinoideans have records which go back into the Ordovician, with the possibility that the former appear earlier.

Reid and Brand (1986) showed that all extant lucinoideans live symbiotically with sulphide-oxidizing bacteria, in much the same manner as the lipodontids (see above); they have usually lost the second gill demibranch through paedomorphosis and, like the lipodontids, have a hypotrophied gut. Living lucinoideans are characterized by the lack of an inhalant siphon and are dependent upon the foot to make an adequate inhalant ventilation tube. Reed and Brand suggested that the ancestral lucinoidean was probably already in symbiotic relationship with bacteria and most probably had a eulamellibranch gill; they also suggested that such ancestral types probably lived as shallow short-siphoned suspension feeders, with extensive adductor muscles (a feature which they point out was already possessed by *Fordilla*), and that the Cretaceous–Recent family Ungulinidae Adams and Adams, 1857, as a non-specialized group, may have some of the characters of the ancestral form. As lucinoideans are clearly a specialized group, it is difficult to envisage them as the stem group of the heterodonts, and the crassatelloideans appear more likely candidates. At the moment, therefore, it appears that we cannot identify the origin of the heterodonts, other than to report that their shell microstructures suggest that their origins were from the neotaxodonts.

Taylor *et al.* (1973) showed that modern lucinoideans, and some veneroideans and tellinoideans have a three-layered shell: the outer layer is composite prismatic, the middle layer crossed-lamellar, and the inner layer complex crossed-lamellar; this may well have been the composition of the shell of the early Ordovician neotaxodonts (see above). In other heterodonts, the shell is composed of two layers (Taylor *et al.* 1969, 1973), the outer consists of crossed-lamellar, and the inner of complex crossed-lamellar aragonite microstructures. As lucinoideans are one of the earliest fossil heterodonts, and also widely regarded as the most primitive members of this subclass, it seems likely that the three-layered shell may have been the original heterodont condition, and the two-layered shell derived from this by loss of the outer layer.

McAlester (1965, 1966) claimed lucinoid affinities for the genus *Babinka* Barrande, 1881. However, that form is one of the earliest Ordovician bivalves, being now known from the Tremadoc (Babin 1982*a*), and on that basis alone seems most unlikely to be a heterodont. Indeed, arguments presented herein, suggest that Heterodonta appears to be the most derived bivalve subclass. Of other possible affinities, its dentition could ally it to the cycloconchid palaeoheterodonts, by loss of lateral teeth, as favoured, for example, by Babin (1982*a*). However, Pojeta (1978) suggested that the dentition of *Babinka* was hardly different from that of *Fordilla* and that it could have been directly derived from a *Fordilla*-like ancestor. *Babinka* differs from most other Ordovician bivalves in its multiple pedal muscle insertions, but McAlester's (1965) suggestion that this indicated a direct derivation from a monoplacophoran ancestor, independently of other bivalves (and thus making the class Bivalvia polyphyletic), has been rejected by other authors (e.g. Soot-Ryen 1969; Pojeta 1971). *Babinka* has been recorded widely from rocks of Tremadoc to Llanvirn age and is herein recorded for the first time from Britain (see below and Pl. 3, figs 3, 6). Its early geological appearance makes it difficult to accept *Babinka* as a heterodont. Earlier (Cope 1995), I considered it most likely to be a palaeoheterodont; its multiple pedal muscle insertions are shared by some cycloconchid palaeoheterodonts including *Cycloconcha* Miller, 1874 and *Celtoconcha* Cope, 1996, but also by the nuculoid *Myoplusia* Neumayr, 1884. *Babinka* is certainly not a nuculoid, but several groups of palaeoheterodonts, such as the redoniids and the modiomorphoids, have reduced dentition; I thus concur with Babin (1982*a*) in placing the genus (and the family Babinkidae Horný, 1960) within the order Actinodontoida of the subclass Palaeoheterodonta.

It thus seems that we can exclude *Babinka* from discussions of heterodont origins, in which case, the origin of the heterodonts becomes somewhat more transparent. The shell microstructures which some heterodonts share with the neotaxodonts suggest that these two groups are closely related. The subclass Neotaxodonta appears to have arisen from the glyptarcoid palaeoheterodonts and we now have an early Ordovician genus, *Catamarcaia*, which indicates such a link. The subclass Heterodonta, which evolved somewhat later, probably originated from the neotaxodonts as they share the same shell microstructure; the loss of the duplivincular ligament was a significant feature in this change, and there were concomitant changes in dentition associated with the shortening of the hinge-line. On this reading, the evolution of the heterodonts is a mid Ordovician (or later) phenomenon, and the heterodonts are the most derived of the bivalve subclasses (Text-fig. 2).

CONCLUSIONS

Various factors have contributed towards modifications of the existing schemes of high-level classification within the Bivalvia. The increasing amount of data on bivalve shell microstructures shows that these have considerable taxonomic significance (Text-fig. 1). The consensus of recent work (e.g. Runnegar and Pojeta 1992; Hinz-Schallreuter 1995) suggests that all known Cambrian bivalves were palaeotaxodonts. The discovery of an increasing number of early Ordovician forms has illustrated that the increase in diversity of the class through the early Ordovician represents a truly explosive evolution. The hypothesis that this increase in diversity, coupled with a simultaneous increase in size and abundance of bivalves, could be a direct response to the evolution of the feeding gill, as I proposed previously (Cope 1995), has allowed the construction of new phylogenetic links (Text-fig. 2). The cardiolariids are identified as palaeotaxodonts with differentiated hinge teeth probably indicating the acquisition of the filibranch gill; these form suitable ancestors for the palaeoheterodonts. The lipodonts were evolved from the palaeotaxodonts very early, perhaps during the Cambrian. The modiomorphoid palaeoheterodonts, characterized by reduced dentition, gave rise to the anomalodesmatans in the early Ordovician. One group of palaeoheterodonts, the glyptarcoideans, was characterized by dorsally divergent teeth. Such forms could readily provide the origin of the neotaxodonts by development of the duplivincular ligament. The neotaxodonts, however, had a more sophisticated shell microstructure, which included an outer prismatic layer, a middle crossed-lamellar layer and an inner complex crossed-lamellar layer (Text-fig. 1). Early neotaxodonts with this shell microstructure gave rise to: (1) the modern neotaxodonts, which have lost the outer layer; (2) the pteriomorphians, in which the outer layer of prismatic aragonite is replaced by one of prismatic calcite, and which have developed a subumbonal lacuna in the dentition; and (3) the heterodonts, which retained the inherited shell microstructure (although some forms later lost the outer layer), but in which the duplivincular ligament has been lost.

The links between several of the bivalve subclasses now seem to be reasonably well documented, but some problems remain. In order to answer these problems, specific targets should be addressed; initially, the principal efforts should be directed towards increasing our knowledge of the earliest Ordovician faunas, and here the Gondwanan shelves should be the first target area. It has become evident, in the research for this paper, that we know almost nothing about Tremadoc bivalve faunas, yet this was clearly the time when the major diversification of the class occurred. Areas for possible search include north Africa and Argentina. Subsequently, searches must be made for mid and late Cambrian bivalves to fill the disjunct record of early bivalve evolution; it is likely that the subclass Lipodonta was derived from the Palaeotaxodonta before the Ordovician, and even the Palaeoheterodonta may pre-date the Ordovician. For this search, the area under investigation should be widened, as the records of Cambrian forms show them to have been of widespread occurrence and not restricted to the Gondwanan shelves.

Another problem to be addressed is that of the origin of the heterodonts. It may well be that already described Ordovician forms may in future be found to belong to the heterodonts, but the origin of the heterodonts, as the major bivalve cohort of the Mesozoic and Cenozoic, is a subject which requires investigation. The similarity of the shell microstructure in the neotaxodonts and

heterodonts suggests that the two are closely related, and that the combination of the palaeoheterodonts and heterodonts within a subclass, Heteroconchia, is engendered purely by some degree of homeomorphy of the dentitions.

The fact that no further bivalve subclasses appeared in the geological record later than the subclass Heterodonta in the mid or late Ordovician, and that all seven subclasses that were then in existence are extant, emphasizes the significance of these early Palaeozoic radiations in the phylogeny of the class Bivalvia.

SYSTEMATIC PALAEONTOLOGY

Class BIVALVIA Linnaeus, 1758
Subclass PALAEOTAXODONTA Korobkov, 1954
Order NUCULOIDA Dall, 1889
Superfamily NUCULOIDEA Gray, 1824
Family CARDIOLARIIDAE fam. nov.

(Text-figure 3)

Diagnosis. Palaeotaxodonts with separate anterior and posterior dentitions, in which the hinge lies along line of posterior teeth; anterior teeth, which may be enlarged, lie below hinge axis. Ligament external, opisthodetic.

Remarks. This new family is proposed for palaeotaxodonts which developed separate anterior and posterior dentitions, with a tendency to overlap subumbonally in some of the more advanced forms. The separate dentitions arose because these forms used their dentition in a way different from that of other palaeotaxodonts. In the cardiolariids, the posterior set of more or less equal teeth acted as the hinge and lies below the external opisthodetic ligament. The separate anterior larger teeth served to locate the valves when they were opened more widely to expel pseudofaeces. Previously, I concluded that this hinge type evolved in response to the evolution of the filibranch gill, probably in the early Ordovician (Cope 1995). In the great majority of palaeotaxodonts, which were clearly protobranch, the equal or subequal teeth (gradidentate; Cope 1995) acted in concert, and the hinge lay parallel with the row of teeth (see Pl. 1, figs 1–7). Although the ligament was originally external and opisthodetic, from the early Silurian onwards many gradidentate palaeotaxodonts developed an internal ligament located centrally on the hinge-plate (Pojeta and Runnegar 1985; e.g. Pl. 1, fig. 7).

The family includes a small number of genera, closely related by their similarly differentiated dentition, which can be described as cardiolariid. This dentition is well shown by *Cardiolaria* itself (Text-fig. 2), the type species of which is *C. barrandei* Munier-Chalmas, 1876. McAlester (1968) designated a lectotype, and figured the type material from the middle Ordovician of the Armorican Massif; McAlester (1968) could not find teeth preserved beneath the umbones in any of the specimens. Babin (*in* Babin and Gutiérrez-Marco 1991, p. 116) examined topotypes showing 'an edentulous space beneath the umbo, between the two sets of teeth. This shows it to be attributable to the genus *Cardiolaria.*' Babin and Gutiérrez-Marco (1991) also figured the closely related species *C. beirensis* (Sharpe, 1853) from the upper Lower Llanvirn to Llandeilo of Spain; they showed that in that form there was clear subumbonal overlap of the anterior and posterior dentitions (see Text-fig. 3). Bradshaw (1970) figured the same species from the Llanvirn and Llandeilo of Finistère; her text-figure 1 showed that at a length of *c.* 5 mm, *C. beirensis* has a continuous dentition, but it is noticeable that there is a discordance immediately anterior to the umbo. Bradshaw (1970, text-figs 2–4) also figured other specimens showing the adult stages and indicated areas of resorption; her text-figure 2 shows a clear overlap between the two sets of teeth.

Another genus grouped herein within the family Cardiolariidae is *Deceptrix* Fuchs, 1919 (which ranges from the mid Ordovician to the Devonian). Forms ascribed to *Deceptrix*, but which do not
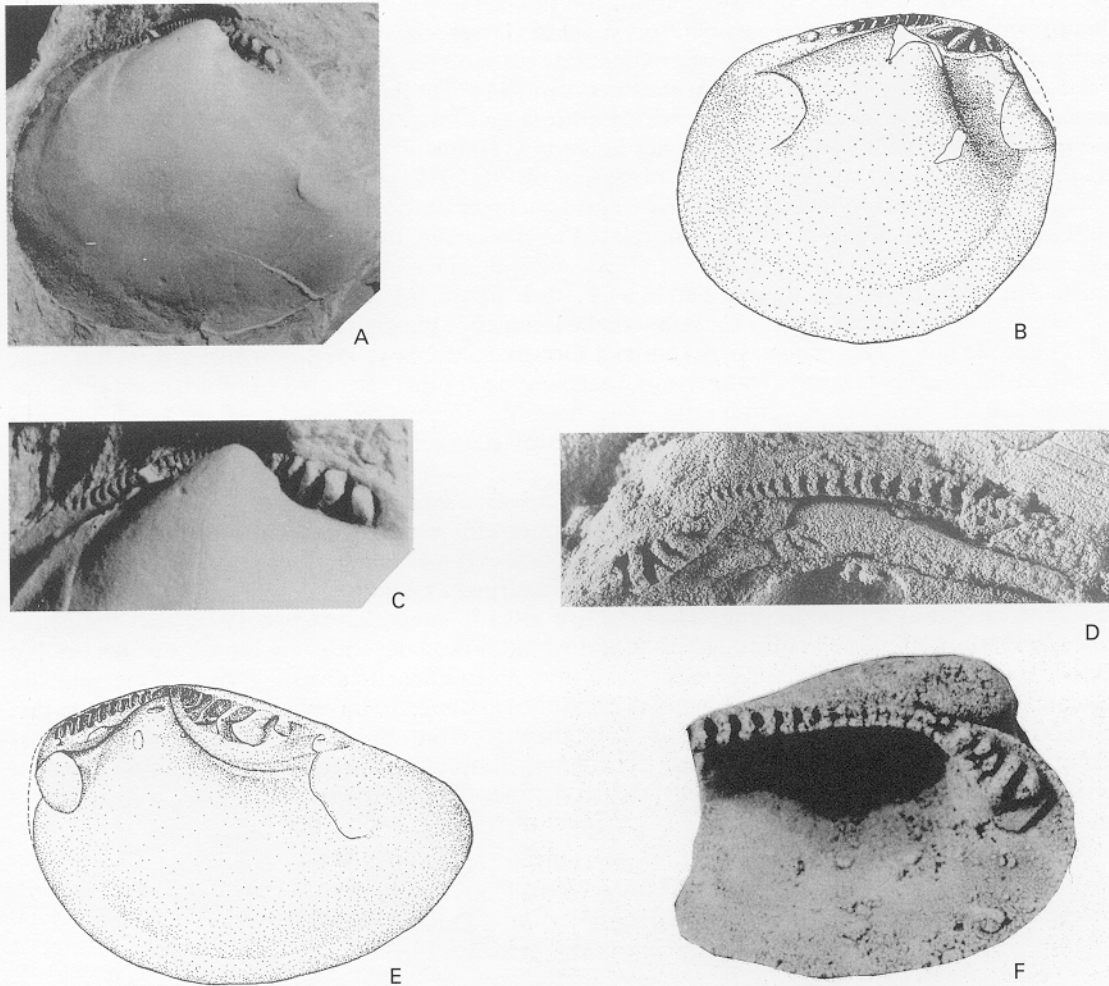
TEXT-FIG. 3. Cardiolariid palaeotaxodonts. A, C. *Deceptrix carinata* Fuchs, 1919; lectotype; Lower Devonian, Sauerland, Germany; collections of the Geologisch-Paläontologische Museums der Humbold Universität, Berlin. A, ×4, after McAlester 1968, pl. 6, fig. 1. C, ×6, after McAlester 1968, pl. 6, fig. 3. B, *Cardiolaria beirensis* (Sharpe, 1853); UCNZ K.3; Llandeilo, Finistère; ×5; after Bradshaw 1970, text-fig. 2. D, *Cardiolaria beirensis* (Sharpe, 1853); UCB FSL 550 110; ?upper Llandeilo, Ciudad Real, Spain; ×4·5; after Babin and Gutiérrez-Marco 1991, pl. 3, fig. 5. E, *Praeleda costae* (Sharpe, 1853); UCNZ C.1.b.; Llandeilo, Finistère; ×5; after Bradshaw 1970, text-fig. 7. F, *Inaequidens davisi* Pojeta and Gilbert-Tomlinson, 1977; UT 94496; middle Ordovician, Tasmania; ×5·5; after Pojeta and Gilbert-Tomlinson pl. 5, fig. 7. A, C. Reproduced by permission of the publisher, the Geological Society of America, Boulder, Colorado USA. Copyright © 1968 by the Geological Society of America, Inc. F. Reproduced by permission of the Australian Geological Survey Organisation.

belong to that genus as exemplified by the type species *D. carinata* Fuchs (see Text-fig. 3) have been figured by several authors, particularly Pojeta (1971, 1978) and Tunnicliff (1982). *D. carinata* (refigured by McAlester 1968) and herein (Text-fig. 3) shows a straight row of posterior teeth and a small number of much larger anterior teeth lying below the hinge-line; it is thus a typical cardiolariid and is not related to the gradidentate types which have been figured as *Deceptrix* by Pojeta (1971, 1978) and Tunnicliff (1982). Some of these forms, however, are well described and

figured, and in order to prevent further confusion of such forms with cardiolariid palaeotaxodonts, I here propose the new generic name *Homilodonta* (Greek: *homilos* (= crowd) and *odontos* (= tooth), referring to the crowded row of gradidentate teeth on the whole hinge-plate). As type species of the genus, I designate *Arca subtruncata* Portlock, 1843. Tunnicliff (1982, pp. 60–61) revised this species, designated a lectotype and provided admirable illustrations (1982, pl. 9, figs 1–7, 9–11). *Homilodonta* also includes the other species figured by Tunnicliff (1982) under the name *Deceptrix*, and the species figured by Pojeta (1971, pl. 5, figs 19–20; 1978, pl. 1, figs 1–2). One of the latter is figured herein as Plate 1, figure 2. *Homilodonta* is a member of the family Praenuculidae (McAlester 1969) and its gradidentate dentition is unrelated to the cardiolariid type. Another species, figured as *Deceptrix filistriata* (Ulrich) by Pojeta (1978, pl. 2, fig. 1), can be readily included in the genus *Praenucula* Pfab, 1934. It is figured herein as Plate 1, figure 5.

Deceptrix seems distinct from *Praeleda*, good examples of which were figured by Bradshaw 1970 and (under the name *Praenucula*) by Babin and Gutiérrez-Marco (1991). *Praenucula* does not show the two distinct series of teeth arranged at an angle to each other, as noted by Bradshaw (1970) for *Praeleda*, and is thus not a cardiolariid. The Australian genus *Inaequidens* Pojeta and Gilbert-Tomlinson, 1977 (Text-fig. 3F), is another mid Ordovician genus which has a typical cardiolariid hinge and is thus assigned to the family.

If the evolution of the feeding gill in the Bivalvia was a single event, then I believe that it must have occurred early in bivalve evolution. If this important evolutionary step occurred within the Cardiolariidae, its members must therefore have possessed a feeding gill, and the evolution of the differentiated hinge in the Cardiolariidae may be construed as a direct response to the evolution of the filibranch gill and filter feeding. Thus, I have already suggested (Cope 1995) that the genus *Cardiolaria* was a filibranch palaeotaxodont and would now claim the same for all members of the family Cardiolariidae – a conclusion which requires amendment to the diagnosis of the subclass Palaeotaxodonta, as hitherto all its members have been assumed to have been protobranch. On this basis, all bivalve stocks arising directly or indirectly from filibranch palaeotaxodonts must themselves have been of filibranch grade. The eulamellibranch grade ctenidium is thus seen as a polyphyletic feature which evolved separately in distinct filibranch cohorts.

Subclass PALAEOHETERODONTA Newell, 1965
Order ACTINODONTOIDA Douvillé, 1912
Superfamily ACTINODONTOIDEA Douvillé, 1912
Family BABINKIDAE Horný, 1960

Genus BABINKA Barrande, 1881

Type species. Babinka prima Barrande, 1881, by monotypy.

Babinka prima Barrande

Plate 3, figures 3, 6

1881 *Babinka prima* Barrande, pl. 266, VI, figs 1–16.
1935 *Babinka prima* Barrande; Thoral, p. 162, pl. 13, figs 4–5.
1954 *Babinka prima* Barrande; Vokes, p. 235, fig. 1.
1960 *Babinka prima* Barrande; Růžička and Prantl, p. 48.
1960 *Babinka prima* Barrande; Horný, p. 480, pl. 1.
1962 *Babinka prima* Barrande; Vogel, p. 235, pl. 5, figs 5–6.
1965 *Babinka prima* Barrande; McAlester, p. 242, pl. 26, figs 3–12; pl. 27, figs 2–5; pl. 28, figs 1–4, 9–14.
1969 *Babinka prima* Barrande; Soot-Ryen, pl. 34, figs 6–8.
1971 *Babinka prima* Barrande; Pojeta, p. 12, pl. 1, figs 12–14.
1977 *Babinka prima* Barrande; Babin, p. 52, pl. 4, figs 1–14; pl. 5, figs 1–3, 6, 9–10.
1978 *Babinka prima* Barrande; Pojeta, p. 242, pl. 14, figs 10–11.

1982a   *Babinka prima* Barrande; Babin, p. 40, pl. 11, figs 8–9.
1991   *Babinka prima* Barrande; Babin and Gutiérrez-Marco, p. 128; pl. 5, fig. 5.

Material. One specimen, NMW 96. 23G. 1a and 1b (part and incomplete counterpart).

Horizon and locality. From the Pontyfenni Formation, *Bergamia rushtoni* Biozone, Fennian Stage, upper Arenig, at Pontyfenni quarry, Carmarthenshire, South Wales (see Fortey and Owens 1987).

Description. If one accepts the orientation of *Babinka* which was proposed by McAlester (1965), the genus is elongated anteriorly. Starobogatov (1971) disagreed with this interpretation of the orientation but, as shown by Pojeta (1978, p. 242), there are valid reasons for accepting it. The single specimen figured herein (Pl. 3, figs 3, 6) is thus interpreted as a left valve composite mould. The shell is 22·9 mm long and 17·8 mm high, measurements which are similar to those of the larger of the Bohemian type material. The specimen shows well the multiple pedal muscle scars which characterize the genus. On this specimen, some six or seven of these are visible (Pl. 3, fig. 6); according to McAlester (1965), specimens from Bohemia have six pedal muscle scars. Gill attachment muscle impressions are visible at the end of several of the pedal muscle scars; these show up to three small scars for each pedal muscle (Pl. 3, fig. 6). The anterior adductor is very similar in size and situation to that of the type material, being long and elongated dorsally (Pl. 3, figs 3, 6); the posterior adductor is not so well displayed although it clearly conforms in shape and position to that of the species. Unfortunately, no dentition is preserved on this specimen, the hinge area being poorly preserved, but the shape of the specimen and its musculature leave no doubt of the specific assignment.

There is a well-developed commarginal ornament, with some strong growth increments. At the anterior end of the ventral part of the shell, there is a suggestion of a faint radial ornament. The counterpart of the specimen is only partly preserved and shows no additional features.

Remarks. *Babinka prima* is now recorded from the uppermost Tremadoc and the lower Arenig of the Montagne Noire (Babin 1982a), and from the upper Arenig of South Wales; from the Llanvirn of the Czech Republic (Barrande 1881) and the Hesperan Massif of Spain (Babin and Gutiérrez-Marco 1991). *B. oelandensis* Soot-Ryen, 1969, was described from the upper Arenig of Sweden, it differs from *B. prima* in its shape and details of the musculature. This is the first record of the genus from Britain.

Subclass NEOTAXODONTA Korobkov, 1954
Order ARCOIDA Stoliczka, 1871
Superfamily ARCOIDEA Lamarck, 1809
Family PARALLELODONTIDAE Dall, 1898

Genus ALYTODONTA gen. nov.

Derivation of name. From the Greek *alyton* (= continuous) and *odontos* (= tooth).

Type species. *Alytodonta gibbosa* sp. nov.

Diagnosis. Inflated rounded shell, longer than high with straight hinge-line bearing continuous dentition, with curved anterior pseudolaterals, numerous short pseudocardinals and few long posterior lateral teeth. Ligament amphidetic, duplivincular. Slight posterior alation.

Remarks. *Alytodonta* is shown by its continuous dentition to be a neotaxodontid and falls into place as a genus intermediate in many characters between *Catamarcaia* Sánchez and Babin, 1993 and *Freja* Liljedahl, 1984. It differs from *Cyrtodonta* (and other cyrtodontids) in lacking a subumbonal lacuna in the dentition. It resembles most closely the early Ordovician *Catamarcaia*, from which it is distinguished by shell proportions and in dentition. *Catamarcaia* has one anterior pseudolateral which is strongly hooked, with its dorsal region parallel to the hinge-line; it has more complex pseudocardinal teeth and has more posterior pseudolateral teeth than *Alytodonta*.

Alytodonta gibbosa sp. nov.

Plate 4, figures 1, 5, 8; Text-figure 4

1910   *Cyrtodonta gibbosa* Salter; Hind, p. 512, pl. 4, fig. 17.
1962   *Cyrtodonta gibbosa* Salter; Vogel, pl. 5, fig. 3.
1984   "*Cyrtodonta*" *gibbosa* Salter; Liljedahl, p. 37, fig. 16F; p. 45, figs 20A, 25D.

Derivation of name. From the Latin *gibbosus* (= protuberant).

Material. Only the holotype, BMNH L. 49858.

Horizon and locality. From the Mulloch Hill Sandstone, Lower Llandovery, Mulloch Hill, Girvan, Ayrshire.

Diagnosis. As for genus.

Description. The holotype and only specimen known is an internal mould of a strongly inflated left valve, 28·8 mm long and 24·4 mm high, which is weakly alate posteriorly. The umbo projects above the straight hinge-line and is prosogyral. The anterior adductor is small, oval and moderately well impressed. The posterior adductor is much larger, but it is only slightly impressed and its margins are diffuse, so its total extent is not discernible. There is a well impressed small muscle scar immediately anterior to this, which is presumably a posterior pedal retractor. No pallial line is visible.
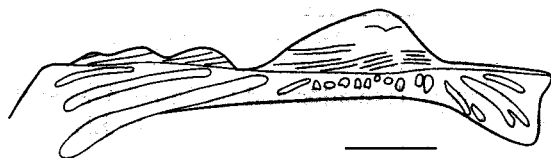
TEXT-FIG. 4. *Camera lucida* drawing of the hinge region of holotype (BMNH L. 49858) of *Alytodonta gibbosa* sp. nov. Scale bar represents 5 mm.

The dentition (Text-fig. 4) is continuous along the hinge-plate. Three anterior pseudolaterals have two smaller ones interspersed between the posterior two; these probably arose through bifurcation. There are 11 small, rather irregularly arranged, pseudocardinal teeth, the most posterior is elongate. The three posterior pseudolaterals are long and the most dorsal of these is slender, whilst the most ventral is quite thick and blunt (see Pl. 4, fig. 8). The other is intermediate in thickness. The grooved ligamental insertions are clearly visible, both anterior and posterior to the umbo, showing that this bivalve possessed an amphidetic duplivincular liagment.

The internal mould bears impressions of commarginal growth increments, but the anterior ventral marginal area also shows a suggestion of fine radial ornament.

Remarks. Hind (1910, p. 512) referred to this species as *Cyrtodonta gibbosa* Salter. This name, however, appears to be merely a copy from the original label on this specimen in the Gray collection. Unusually, with his description of this species, Hind did not give any synonymy, nor did he refer to any work of Salter where this name can be found. The name as used by Hind is also suspect because the supposed author's name (Salter) was not put in parentheses by Hind. However, Salter never used the generic name *Cyrtodonta*, as he believed (wrongly) that the genus *Palaearca* Hall, 1859 predated it (see Salter 1866). Prolonged search by the writer has failed to find any mention either of the species *Palaearca gibbosa* Salter or of *Cyrtodonta gibbosa*, except by Vogel (1962) and Liljedahl (1984), both of whom merely copied Hind's use of the name. Bigsby (1868) referred to *Palaearca gibbosula* Salter as a manucript name for a species from the Trentonian of western Tasmania, but this species appears never to have been described. I have therefore concluded that *Cyrtodonta gibbosa* is a *nomen nudum* and thus invalid. Since at least three previous authors have used this specific name, I believe the best course is to stabilize the nomenclature, and here propose the name *gibbosa* as a new species.

Liljedahl (1984, p. 37) was the first to point out that this species could not belong to the superfamily Cyrtodontoidea as it had continuous subumbonal dentition, whereas the cyrtodontoids

always have a subumbonal lacuna in their dentition, which separates the teeth into discrete anterior and posterior sets. This feature allows the specimen to be assigned to the subclass Neotaxodonta, rather than Pteriomorphia as previously.

Hind's (1910, p. 512) description of the dentition is very inadequate and mentions only two anterior oblique teeth and two long oblique teeth posteriorly. Were it not for his reasonably accurate measurements and figure, it would be difficult to believe that the description of the dentition was in reality from this specimen.

Subclass PTERIOMORPHIA Beurlen, 1944

In my earlier discussion of pteriomorphian taxonomy (Cope 1996, p. 1010), I proposed Cyrtodontida as a new ordinal level taxon to include the superfamilies Cyrtodontoidea Ulrich, 1894 and Falcatodontoidea Cope, 1996. In doing so, however, I overlooked that the Cyrtodontida had been proposed as an order by Scarlato and Starobogatov (*in* Nevesskaya *et al.* 1971) and I am grateful to Mr V. A. Ratter for bringing this to my attention. Although the Rules of Zoological Nomenclature do not apply to taxa higher than the family group level, I nevertheless feel that the authorship of the order Cyrtodonta (which I interpreted in a much more narrow sense than Scarlato and Starobogatov) should be attributed to Scarlato and Starobogatov 1971, *emend.* Cope 1996.

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APPENDIX

Abbreviations used in plate descriptions

AMNH, American Museum of Natural History, Washington DC
ANSP, Academy of Natural Sciences of Philadelphia
BMNH, Natural History Museum, London
BGS, British Geological Survey, Keyworth, Nottingham
CEGH-UNC, Cátedra de Estratigrafia y Geología Histórica, Universidad Nacional di Córdoba
CPC, Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra
CUM, Department of Palaeontology, Complutense University of Madrid
FM, Field Museum of Natural History, Chicago
LV, left valve
Mo, Swedish Museum of Natural History, Stockholm
NMW, National Museums and Galleries of Wales, Cardiff
RM Mo, Swedish Museum of Natural History, Stockholm
RV, right valve
SGU Type, Type Collections, Geological Survey of Sweden, Uppsala
UCB, Université Claude Bernard, Lyon 1
UCNZ, Department of Geology, University of Canterbury, New Zealand
USNM, Department of Paleobiology, United States National Museum, Washington DC
UT, University of Tasmania
WM, Walker Museum Collection at Field Museum of Natural History, Chicago