

The Infaunal Descendants of the Cycloconchidae: An Outline of the Evolutionary History and Taxonomy of the Heteroconchia, Superfamilies Cycloconchacea to Chamacea [and Discussion]

N. J. Morris and R. M. C. Eagar

Phil. Trans. R. Soc. Lond. B 1978 **284**, 259-275
doi: 10.1098/rstb.1978.0067

References

Article cited in:

<http://rstb.royalsocietypublishing.org/content/284/1001/259#related-urls>

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

To subscribe to *Phil. Trans. R. Soc. Lond. B* go to: <http://rstb.royalsocietypublishing.org/subscriptions>

The infaunal descendants of the Cycloconchidae:
an outline of the evolutionary history and taxonomy of
the Heteroconchia, superfamilies Cycloconchacea to Chamacea

BY N. J. MORRIS

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

[Plates 1 and 2]

The history of the Heteroconchia is traced from the earliest Ordovician, where they occur in shallow, marine sand and silt and inshore mud facies throughout the Palaeozoic, where in contrast to Mesozoic and more recent times they are numerically less important than the Anomalodesmata in the number of species present in the infauna. Evidence for the relationship of the heteroconch superfamilies from Cycloconchacea to Chamacea is discussed and a number of modifications to their existing classification made.

INTRODUCTION

This is an attempt to outline the evolutionary history and relations and to modify the classification of some heteroconchacean superfamilies with particular emphasis on those which are infaunal.

The present paper includes superfamilies up to and including the Chamacea. It is hoped to publish elsewhere an account of the remaining superfamilies which appear in the Mesozoic and are largely siphonate.

The subclass Heteroconchia has been limited by Pojeta (1971) to include the heterodonts, their probable ancestors the actinodontoids, together with the related groups, the unionaceans and the trigoniaceans. At a later date he included the earliest known bivalve genus *Fordilla* (Pojeta 1975). This paper follows Pojeta's interpretation of the subclass Heteroconchia but with the addition of the Hippuritoida. The Anthracosiacea and the Archanodontacea are retained in the subclass with considerable reservation.

A BRIEF POST-CAMBRIAN HISTORY OF THE HETEROCONCHIA,
CYCLOCONCHACEA TO CHAMACEA

Examinations of the facies in which early Ordovician fossil bivalves occur show that their distribution was strictly controlled by the environment. Lower Ordovician (Arenig or its equivalent Upper Canadian), fossiliferous rocks are known from several parts of the world but bivalves are of extremely restricted distribution (figure 25). In the Arenig rocks of South Wales a series of broad depth zones has been recognized based on the occurrence of different trilobites which are restricted to particular sedimentary environments. The depth zones range from intertidal to 'deep' water offshore (Fortey & Owens 1977). Bivalves are restricted to the most inshore sandy muds. Arenig bivalves also occur in Brittany in the Grès Armoricaïn, the most inshore sands of the local succession. However, in the Montagne Noire area (Thoral 1935) of

those of *Babinka* (MacAlester 1965) and *Coxiconcha* [*? = Synek*] (Babin 1977), but later Cycloconchidea have the pedal scars reduced in number and positioned high in the umbones. It seems likely that this change in size of the mantle cavity reflects elaboration of the gills and it is likely that at least in the early stages they were of protobranch type.

By Middle and Upper Ordovician times deposit feeding nuculoids became numerically important among infaunal bivalves and occur in distinctive, mainly deposit-feeding bivalve communities. Cycloconchacea are rather rare in the Upper Ordovician except for the Lyrodesmatidae and less commonly *Cycloconcha* itself. Few Cycloconchacea are known in the Silurian but this reflects the paucity of the bivalve fossil record during this period. Lyrodesmatidae occur in the Lower Silurian and the cycloconchid *Actinodonta* in the Middle Silurian. Both occur in inshore, sandy sediment communities which are rich in bivalves and poor in brachiopods.

An important minor radiation into the later heteroconchian groups must have taken place during the Silurian as Trigoniacea occur in late Silurian rocks (Newell & Boyd 1975) and by Lower Devonian times the astartids *Eodon* and *Prosocoelus* and the mecnodontid *Hefteria* all occur in inshore sand and silt facies.

Each of these groups has their pedal muscle scars high on the shell side and therefore had relatively large mantle cavities of proportions similar to their descendants and each had presumably advanced beyond the protobranchiate stage of the gills. Each of the groups also has a well defined ligament nymph and a reduced number of teeth compared with their actinodont ancestors. The advanced gills and hinge may have been necessary for what were to become the most successful groups of active infaunal filter feeding bivalves. By Middle Devonian times these groups have spread into the tropical limestone facies, in which a higher diversity of mecnodonts, trigoniaceans and astartids (*Prosocoelus*) occur along with *Megalodon*. However, *Cypricardella* and the astartid, *Eodon*, remained restricted to the silt and sand facies.

Devonian and Carboniferous times were marked by a rise and the acme of some early anomalodesmatans such as the Edmondiidae and the Sanguinolitidae as well as a number of siphonate forms. The Heteroconchia were numerically less important. Of 83 probably distinct species of marine unattached infaunal bivalves known from the Viséan of Britain (omitting the protobranch nuculoids and solemyoids), 62 are here considered to belong to the Anomalodesmata, while 9 belong to the Crassatellacea and 12 to the Trigoniacea. It must, however, be remembered that the British Viséan is essentially a limestone sequence and bivalve rich sandstones are not well represented.

The Upper Palaeozoic invasion of land by plants led to the increasing complexity of non-marine aquatic environments. This probably gave bivalves the chance to spread into fresh water. The first definite non-marine bivalves are the late Devonian Archanodontacea. Later, in the Carboniferous, the Anthracosiacea, which are possible descendants of the Cycloconchacea, spread and diversified in the Coal Measure swamps.

In Permian times Crassatellaceans, *Astartella* and *Oriocrassatella*, together with a variety of Trigoniacea, including the siphonate Scaphellinidae, known mainly from North America (Newell & Boyd 1975) are widespread in warm, shallow, epicontinental seas. There is little indication of the important changes that were about to take place within the Heteroconchia. Both the Permian and most of the Triassic fossil records are too little known to permit the tracing of the many evolutionary changes which must have occurred. Possibly a greater diversity of infaunal bivalves is yet to be found at the Permian continental margins.

NOTES ON THE EVOLUTIONARY RELATIONSHIPS
OF SUPERFAMILIES OF HETEROCONCHIA

Cycloconchacea

The actinodont origin of the heterodont hinge was first suggested by Douvillé (1913). His outline scheme of the evolutionary relationships of the bivalves has been the source from which more intricate phylogenies have been erected. Cox (1960) and then Vogel (1962) introduced a more detailed scheme which has since been modified by Newell (1965) and others.

The Cycloconchidae have been reviewed by Pojeta (1971, p. 10) La Roque & Newell in the *Treatise* (1969), and Babin (1966). They are referred to the sub-class Heteroconchia by Pojeta (1971, p. 28) and are considered ancestral to other members of that subclass (Vogel 1962). They are also considered to be closely related to, and may have given rise to, the largely epi-faunal Pterioidea, the Arcoidea, and the Mytiloidea, because of the actinodont hinge found in some of the earliest members of all those orders. Their close common ancestry with the Palaeotaxodonta has been previously demonstrated (Vogel 1962; Morris & Fortey 1976). Contrary to the opinion of MacAlester (1965), I do not think that the Lucinoidea has a separate origin to other bivalves. The characters that were supposed to separate them, the multiple paired pedal muscle scars, do in fact occur widely in primitive members of other groups of bivalves including the Cycloconchacea (Pojeta 1971). Multiple paired pedal muscle scars certainly also occur in *Coxiconcha* Babin 1966 (? = *Syneke* Barrande) which I now think is a primitive edmondian anomalodesmatid. It therefore appears likely that the Cycloconchacea, Lucinoidea and the Anomalodesmata all shared a common ancestry in latest Cambrian or earliest Ordovician times.

The Cycloconchacea range from the early Arenig (L. Ordovician) to Devonian. Several of their characters are considered to be primitive for the Bivalvia and indeed the Cycloconchacea have, since Douvillé (1913), been thought as the 'root stock' of the bivalves.

During the Lower Arenig, actinodont teeth appear in the Cycloconchacea and taxodont teeth in the Nuculoida; this suggests that they are equally primitive. However, the presence of teeth, some of which are actinodont in an early nuculoid (Morris & Fortey 1976) suggests that these two hinge types have a close common ancestry and led us to conclude that the actinodont type is the more primitive. The actinodont pattern basically consists of several teeth radiating below the umbones on opposing vertical hinge plates that mutually interlock. The pattern occurs in the Cycloconchidae and the Lyrodesmatidae (L. Ordovician–L. Silurian). In the latter there is often a secondary dentition of striae on the side faces of the teeth. Actinodont teeth also occur in the Redoniidae but in that family the anterior teeth are rather reduced.

It would appear that the later patterns of hinge teeth that occur in the heteroconchians (heterodont in the Veneroidea and schizodont in the Trigonioidea) have evolved from the primitive actinodont type by direct reduction of the number of teeth. The presence of posterior lateral teeth in some early Trigonioidea, the Eoschizodidae (Newell & Boyd 1975), and in some species only of the Mecynodontidae (figures 5 and 7–9†) suggests that these posterior laterals as well as those in the earliest Veneroidea, the astartid *Eodon*, have evolved from the partial isolation of elongate posterior cardinal teeth.

The ligament attachment of the Cycloconchidae is simple and consists of a narrow elongate

† Figures 1–16 appear on plate 1 and figures 17–24 on plate 2.

groove behind the umbones. This is seen in *Cycloconcha* (Pojeta 1971, pl. 2) and in *Glyptarca naranjoana* (Verneuil & Barrande) (figure 2). A cast of the actual ligament is preserved in *Actinodonta cuneata* (Phillips) (figure 1). Although it is not possible to distinguish different ligament layers, it is most similar to type *C* of Trueman (1969). This type cannot exist in an amphidetic form except where there is a virtually straight hinge line, extending in front of the umbones. As this is not the condition in any of the earliest Ordovician bivalves it must be concluded that its presence in the arcoids, pteriaceans and pectinaceans is secondary.

The likelihood that neither the known Cambrian bivalves nor their monoplacophoran ancestors had such a straight hinge line or dorsum (Runnegar & Pojeta 1974) suggests that the bivalve hinge system developed largely behind the umbones.

Pedal/body attachment scars occur in multiple pairs in *Cycloconcha* (Pojeta 1971) and in *Davidia* cf. *carinata* (Barrois 1891) (author's observation). In *Davidia*, which is the earlier of the two, they occur lower on the shell flank, as in *Babinka* (MacAlester 1965). Such attachment scars must occur above the top of the mantle cavity and this shows that the mantle cavity size is a variable feature in Ordovician cycloconchaceans, the later ones being larger. It is therefore suggested that primitive protobranch gills may have been replaced by larger, more complicated gills.

Pedal muscle attachment scars have been described in a number of early bivalves (MacAlester 1965; Babin 1977). Later Cycloconchidae such as *Actinodonta cuneata* (Phillips 1848) have well preserved anterior and posterior pedal retractor scars but no other attachment scars have been seen. This suggests that in the Cycloconchidae themselves the locomotory musculature was modified from a generalized to a more specialized state.

The classification of the Cycloconchacea here adopted is based on that of Pojeta (1971). The genera *Davidia* and *Glyptarca* are added, and, furthermore, *Tanaodon*, which was doubtfully placed in the Modiomorphidae by La Roque and Newell (in Moore (ed.) 1969), is now placed in the Cycloconchidae close to *Actinodonta*. The Silurian and Devonian genus *Cypricardinia* can only be doubtfully included in the Cycloconchidae as its hinge is imperfectly known.

As far as can be judged from Haffer's (1959) figure of his species, *Cypricardinia montiumacutorum*, from the Lower Devonian of Spitzbergen and from Beushausen's illustrations (1895), the ligament appears not to be inserted into a distinct nymph, as in most later Heteroconchia, but was set in a slight furrow at the dorsal margin of the shell behind the umbones, as in other Cycloconchacea. The dentition of *Cypricardinia* differs from those of the early Crassatellacea in some respects. In the right valve there is a large central tooth which articulates between a pair of cardinals in the left valve. These, in turn, articulate between two outer, smaller, teeth in the right valve. Well developed posterior laterals are separate from the cardinals. *Cypricardinia* has teeth that are somewhat intermediate between heterodont and actinodont. The teeth are arranged in the opposite order to those of the earliest astartid, *Eodon*, and have more in common with those of the Mecynodontidae. The muscle scars of *Cypricardinia* are unknown. The tooth pattern, which is more simple than in most other Cycloconchidae, is (in the Steinmann notation adapted by Boyd & Newell 1968) **post. (1)01 | 010(1) ant.** in the right valve and **post. 1 | 0101(0) ant.** in the left valve. The inclusion of *Cypricardinia* in the Cardiniidae (Moore (ed.) 1969) is clearly wrong.

Species normally attributed to *Cypricardinia* (e.g. *C. planulata* Conrad) occur quite commonly in the European Silurian rocks. They have fairly strong concentric ribs reminiscent of the mecynodontid *Hefteria* and similar umbonal regions to that of *Mecynodon* itself. The hinges of

these species are unknown. However, the hinge plate of *C. montiumacutorum* has no hint of the hiatus in the right valve described by Boyd & Newell (1968) in early Trigoniacea, this also occurs in the Mecynodontidae and to some extent in *Megalodon*.

Evolution from the Cycloconchacea to its descendant Orders Trigonoidea, Hippuritoida and Veneroidea in all cases entailed reduction in the number of cardinal teeth. This was accompanied by the development of a clearly defined ligament nymph, presumably reflecting an advance in the design of the ligament. Reduction of the number of hinge teeth could have been a simple step in which neotony played a part. During the ontogeny of both 'cyrenoid' and 'lucinoid' heterodont hinge teeth patterns there is an early stage where there are one or two lamellar teeth in each valve (Cox 1969, *after* Bernard). This is also true in the primitive nuculoid, *Tironucula* (Morris & Fortey 1976). Since this stage, with a limited number of teeth, occurs in the assumed descendants of the Cycloconchidae and in a primitive nuculoid which is contemporaneous with the Cycloconchidae and also thought to have a close common ancestry with them (Morris & Fortey 1976) it is reasonable to suggest that this early stage may also have occurred in the Cycloconchidae themselves.

It is therefore suggested that the Cycloconchacea required many large, long teeth to aid

DESCRIPTION OF PLATE 1

Explanation of symbols used in plates: a.a., anterior adductor muscle scar; a.p.r., anterior pedal retractor muscle scar; e, ligament; n, ligament nymph; p.a., posterior adductor muscle scar; r, internal or semi-internal ligament attachment area; 1, hinge tooth; 0, hinge socket.

All the figured specimens are in the British Museum (Natural History), the fossils in the Department of Palaeontology and the Recent specimens in the Department of Zoology.

FIGURE 1. *Actinodonta cuneata* Phillips, Middle? Silurian, Freshwater East, Pembrokeshire, U.K., LL 35210, oblique dorsal view of latex rubber mould (magn. $\times 2.3$).

FIGURE 2. *Glyptarca naranjoana* (Verneuil & Barrande), U. Llanvirn, L. Ordovician Shelve inlier, Shropshire, U.K., LL 35211, right valve, view of hinge (magn. $\times 6.5$).

FIGURES 3 AND 4. *Cypricardella parallela* (Phillips), Tournaisian, L. Carboniferous, Tournai, Belgium. Figure 3. L45476, left valve (magn. $\times 4.4$). Figure 4. L19047. Right valve (magn. $\times 3.3$).

FIGURES 5 AND 6. *Mecynodon oblongus* (Goldfuss), M. Devonian, Stringocephalus Ls., Sötenich, Eifel, W. Germany. Figure 5. L25306, left valve, interior with hinge (magn. $\times 1.4$). Figure 6. L25299, (a) dorsal view, (b) right valve (magn. $\times 1.6$).

FIGURE 7. *Mecynodon carinatus* (Goldfuss), M. Devonian, Bensberg, nr Cologne, W. Germany, L14842, left valve, interior (magn. $\times 1.5$).

FIGURES 8 AND 9. *Mecynodon* sp., M. Devonian, Stringocephalus Ls., Sötenich, Eifel, W. Germany. Figure 8. L25315, right valve (magn. $\times 1.0$). Figure 9. L25318, left valve (magn. $\times 1.5$).

FIGURE 10. *Megalodon cucullatus* J. de C. Sowerby, M. Devonian, Stringocephalus Ls. Paffrath, Eifel, W. Germany, 30509, interior of right valve with hinge (magn. $\times 1.5$). H, hiatus.

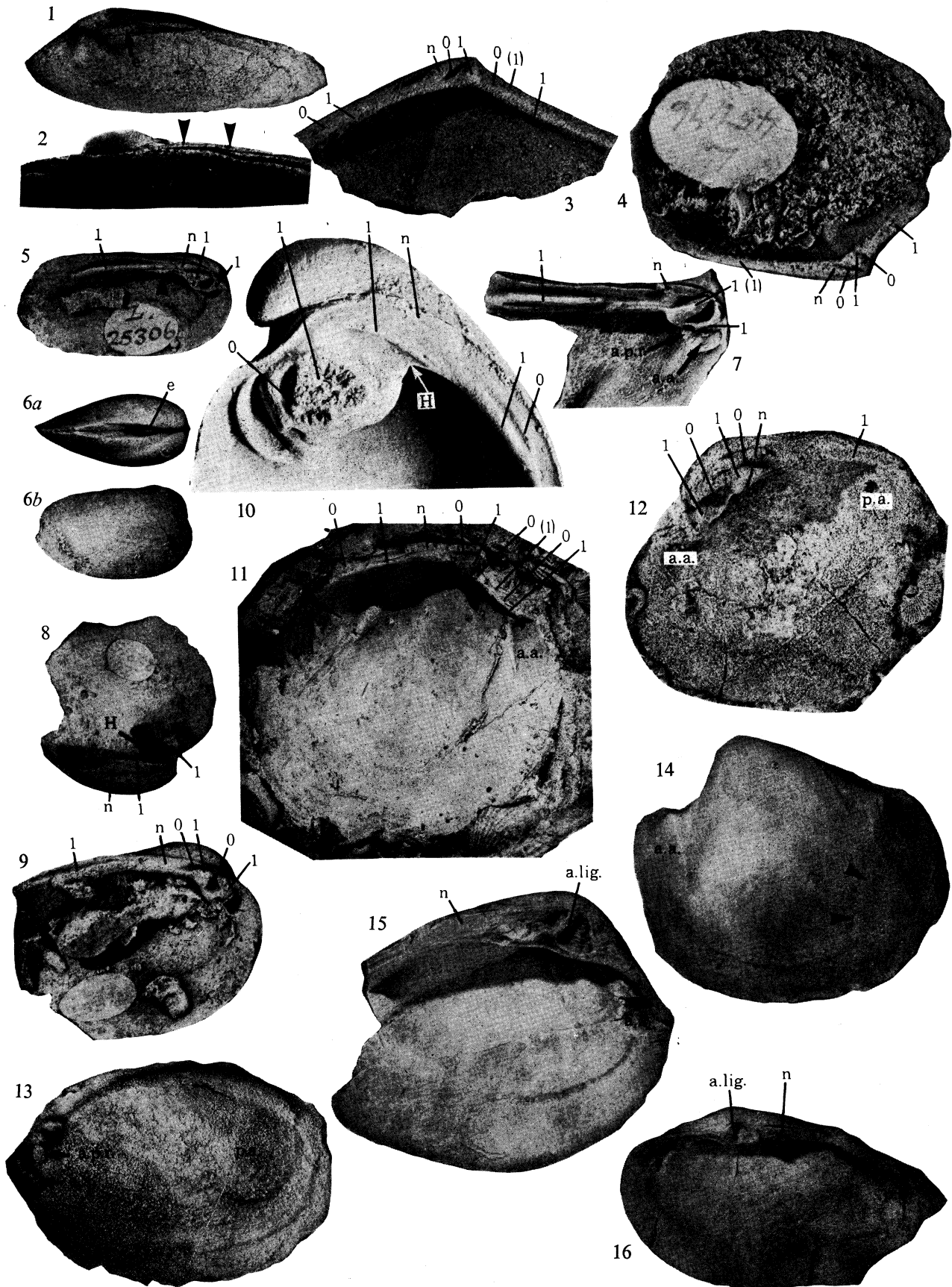
FIGURE 11. *Eodon* aff. *bicostula* (Krantz), Siegenian, L. Devonian, Humerich, nr. Oberstadtfeld, Eifel, W. Germany, L25256, interior of left valve, latex rubber mould (magn. $\times 1.9$).

FIGURE 12. *Prosocoelus priscus* (Roemer), L. Devonian, Spiriferensandstein, Kahleberg, N. W. Hartz, W. Germany, L14780, right valve, interior, latex rubber mould (magn. $\times 1.4$).

FIGURE 13. *Megalomoidea canadensis* (Hall), Ludlow, U. Silurian, Hespeler, S. of Guelph, Ontario, Canada, L38555, left side of steinkern (magn. $\times 1.1$).

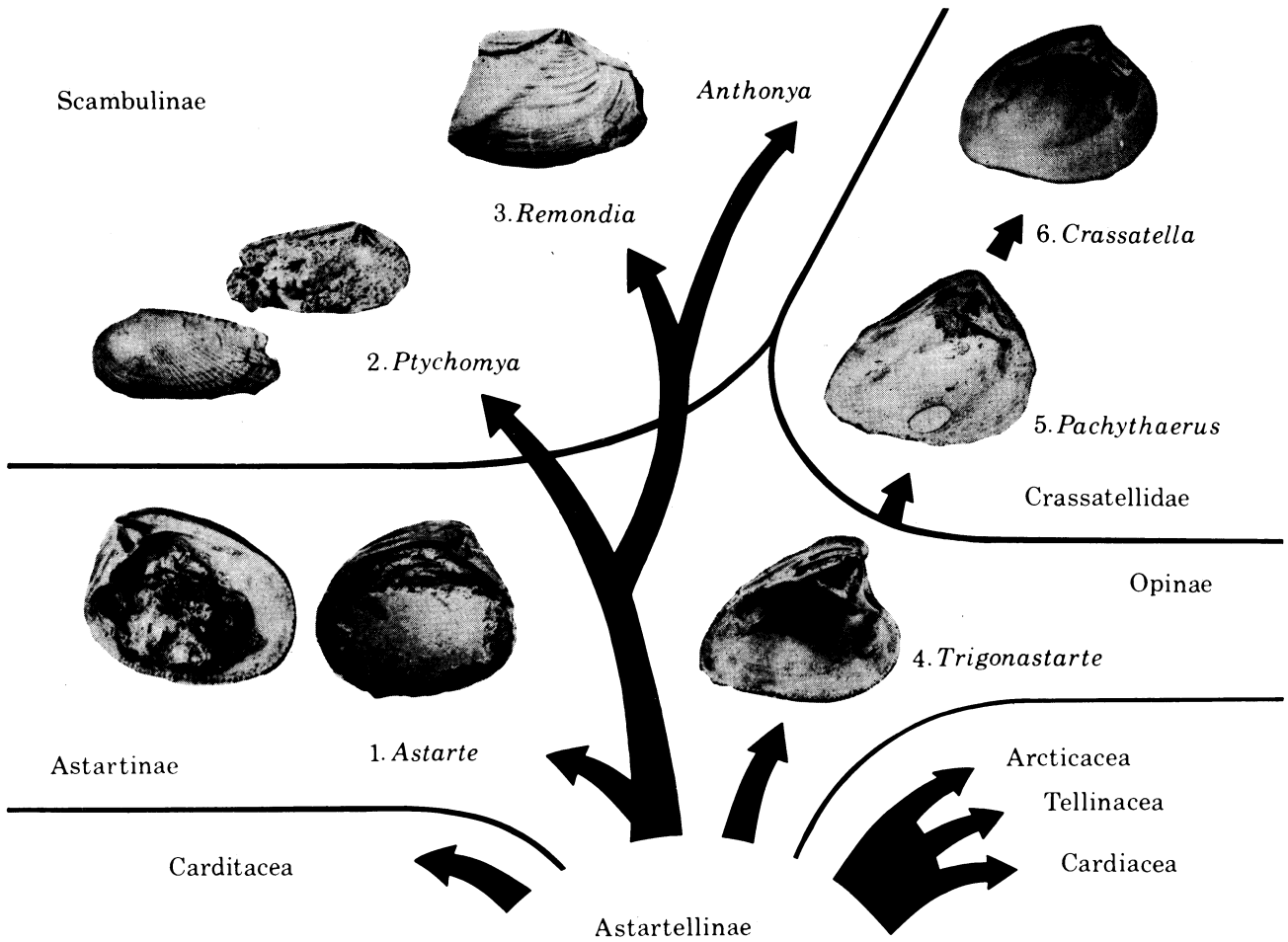
FIGURE 14. '*Astarte*' *duboisiana* d'Orbigny, Volgian, U. Jurassic, 'Russia', LL 24396 left side of steinkern (magn. $\times 1.3$). Pallial sinus arrowed.

FIGURES 15 AND 16. *Carbonicola* cf. *acuta* (J. Sowerby), Upper Carboniferous, Coal Measures, a. lig. = pit thought to contain hypertrophied anterior outer ligament layer. Figure 15. L44706, left valve (magn. $\times 1.3$), roof of 10 ft coal nr Adderley Green Longton, Staffordshire, U.K. Figure 16. Right valve (magn. $\times 1.3$), L876a nr Hanley, Staffordshire, U.K.

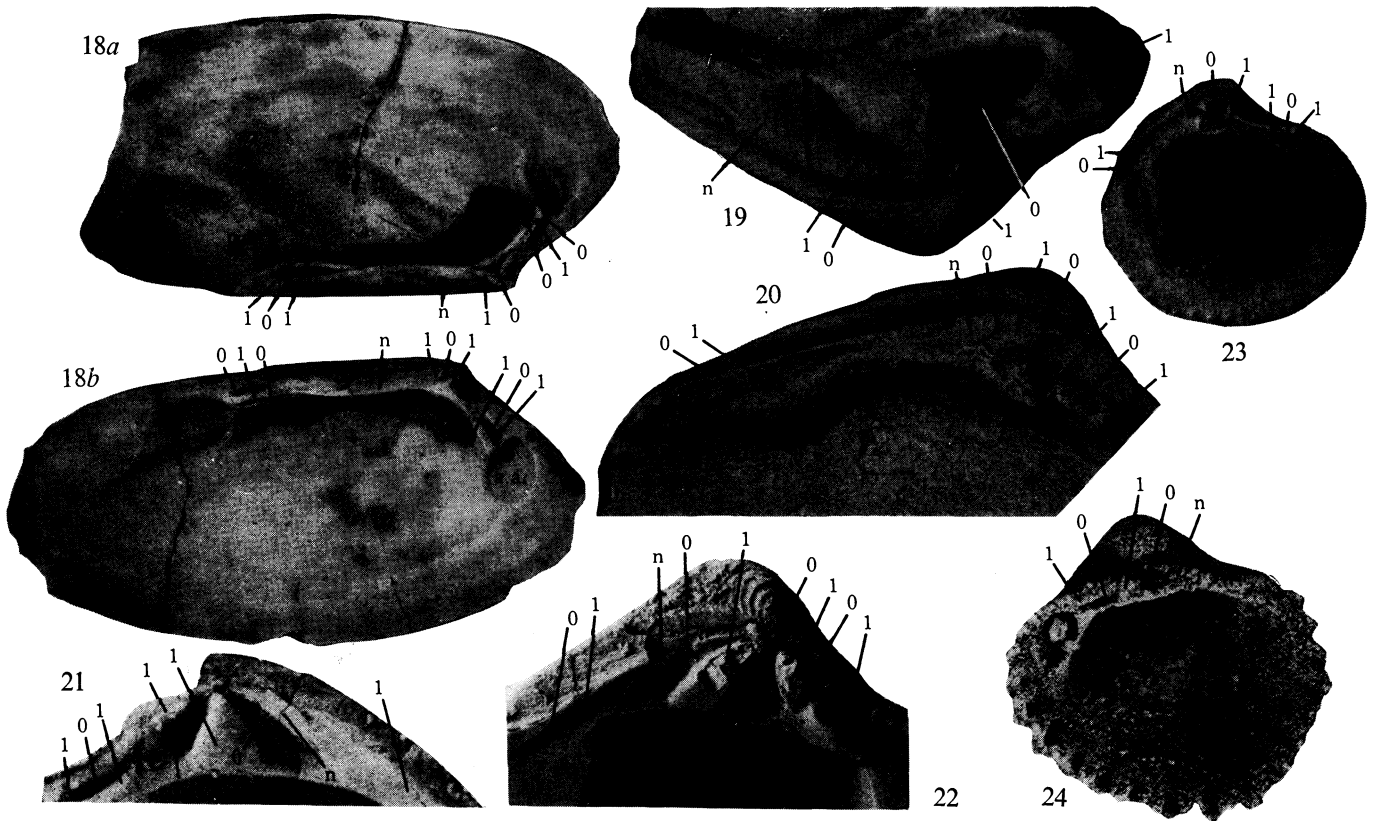


FIGURES 1-16. For description see opposite.

(Facing p. 264)



Astartellinae
FIGURE 17



FIGURES 17-24. For description see opposite.

and protect a relatively weak form of ligament. When that ligament evolved into a stronger system involving a nymph, the large number of teeth were no longer necessary and the simpler heterodont teeth of the descendants might have developed from a simple, early ontogenetic stage of the Cycloconchidae.

Anthracosiacea

The origin of the Anthracosiacea has always been in some doubt. A link with the Modiomorphacea has been suggested more than once but in one case (Morris 1967) this was based on the general similarity of shape of the early Mytiloida to *Archanodon* and the supposed heteromyarian condition of some Anthracosiacea. However, this late Devonian non-marine genus is usually so poorly preserved as to show no characters other than shell shape. The inference then made was that the Archanodontacea were ancestral to the Anthracosiacea, but beyond both being non-marine superfamilies they have little in common.

The first obstacle to understanding the correct relationships of the Anthracosiacea is the hinge (figures 15 and 16), which is somewhat irregular and usually poorly preserved. This is partly because the ligament, which lies in a narrow ligament groove above a well formed nymph behind the umbones, extends forward into a socket below the umbones and immediately behind the lunule; this leaves little room for hinge teeth.

The well formed nymph is similar to those typical of the Crassatellacea, Trigoniacea and Mecynodontidae. It is less like any known in the contemporary Anomalodesmata and quite unlike the arrangement of the attachment of the ligament in the Mytiloida. The shell shape, although somewhat elongate, is similar to that of Crassatellacea, Trigoniacea, Cycloconchacea and indeed some later Unionacea. This leads on to the supposition, that like the extant members of these superfamilies, they were capable of at least sluggish movement. If ancestry were sought among the Palaeozoic Anomalodesmata, it would therefore be reasonable to eliminate the deeper burrowing stationary forms such as *Cuneamya* and *Wilkingia*. Relatively active burrowers that were the right shape occur only in the Edmondiidae and the Sanguinolitidae.

DESCRIPTION OF PLATE 2

FIGURE 17. Mesozoic radiation of some Crassatellacea. Figure 17.1. '*Astarte*' *subtetragona* Goldfuss, Toarcian, L. Jurassic, Nailsworth, Gloucestershire, U.K. L74549–50 (magn. $\times 1.1$). Figure 17.2. *Ptychomya robinaldina* (d'Orbigny), L. Aptian, L. Cretaceous, Trigoniaschwartzi Beds, Niungola, locality S. of Mbemkuru River, Tendaguru area, Tanzania, L51211 (magn. $\times 0.4$). Figure 17.3. *Remondia (Mediraon)* sp., L. Cretaceous, N. America (exact locality uncertain), LL 35212 (magn. $\times 0.6$). Figure 17.4. *Trigonastarte trigonalis* (J. Sowerby), M. Bajocian, M. Jurassic, Half-way House, Dorset, U.K. L4734 (magn. $\times 0.4$). Figure 17.5. *Pachythaerus vindinensis* (d'Orbigny), Cenomanian, U. Cretaceous, Le Mans, France, 81181 (magn. $\times 0.7$). Figure 17.6. *Crassatella vadosa* Morton, L. Maastrichtian, U. Cretaceous, Ripley Fm, Coon Creek, Ala., U.S.A. LL 35213 (magn. $\times 0.7$).

FIGURE 18. *Cardinia elongata* Dunker, M. Hettangian, L. Jurassic, Halberstadt, E. Germany, L867. (a) Right valve interior; (b) left valve interior (magn. $\times 1.8$).

FIGURES 19 AND 20. *Palaeocardita crenata* (Goldfuss), Carnian, U. Triassic, St Cassian, Italy. Figure 19. 36383, right valve hinge (magn. $\times 5.7$). Figure 20. L4053, left valve hinge, (magn. $\times 4.1$).

FIGURES 21 AND 22. *Ludbrookia tenuicosta* (J. de C. Sowerby), M.–U. Albian, Gault, Folkestone, U.K. Figure 21. L4965, right valve hinge (magn. $\times 3.7$). Figure 22. L4966, left valve hinge (magn. $\times 3.2$).

FIGURE 23. *Tutcheria submulticostata* (d'Orbigny), Pliensbachian, L. Jurassic, Fontaine Etoupe Four, France, 81124, left valve interior (magn. $\times 3.1$).

FIGURE 24. *Septicardia peruwiana* (Cox), Norian, U. Triassic, North of Junin, Cerro de Pasco region, Peru, LL 35219, right valve interior (magn. $\times 8.0$).

This second family, in particular, includes forms which to some extent resemble later heterodonts but no species with either a hinge or accessory musculature that is clearly similar to those of *Carbonicola* (an example of the Anthracosiidae) has been found (J. M. Dickins & N. J. Morris, unpublished information).

The remaining possibilities for Anthracosiacean ancestors are the Cycloconchacea and the Trigoniacea. By Carboniferous times the Crassatellacea have already adopted their veneriform shape. The Anthracosiaceans such as *Carbonicola* and *Anthracosia* have a general shape close to Cycloconchaceans, such as *Actinodonta*, as well as elongate species of the Schizodidae. If either of these were the ancestor it would mean that the hinge teeth had been completely reduced or had been masked by the ligament. It seems to be a choice between a group (the Sanguinolitidae) which, at a period of relatively high diversity, spreads into a new non-marine environment or a group that was living on in a marginal environment which diversified as that environment itself became more varied (the Cycloconchacea).

The hinge is so greatly modified that it leaves no clue as to which group was ancestral. Possible cycloconchacean ancestry would include *Actinodonta cuneata* Phillips (Middle Silurian) which occurs in an inshore sandy facies. The genus also occurs in non-marine silts of Lower Devonian age in Britain. It is possible that this early invasion of non-marine waters led to the origin of the Anthracosiacea. Alternatively the Devonian Cycloconchacean family Carydiidae which is known only from rather poorly preserved material, the best of which has been illustrated by Haffer (1959), has the actinodont teeth reduced to two in each valve and does have a similar shape to some early members of the Anthracosiidae.

In addition, it is not easy to distinguish between the musculature of the Trigoniacea and some Cycloconchacea, so that an ancestry from early Schizodidae, although rather doubtful, cannot be entirely ruled out.

As there is a slightly greater similarity between the Anthracosiacea and the Heteroconchia rather than with the Anomalodesmata, the superfamily is tentatively retained in the Heteroconchia until further evidence is obtained.

Megalodontacea

The Mecynodontidae are interpreted here to range from infaunal shallow burrowers and semi-faunal nestlers to byssate epifaunal species. *Mecynodon* itself comprises species of all these types. The hinge teeth resemble those of *Eoschizodus*. The hiatus in the hinge plate at the median socket of the right valve is *Mecynodon* sp. is of exactly the same type as illustrated by Newell & Boyd in *Schizodus* (Newell & Boyd 1975, text-fig. 12E) and in *Eoschizodus* (Newell & Boyd 1975, text-fig. 28A). Species of *Mecynodon* show a different development of posterior lateral teeth (figures 5–9).

In *Mecynodon oblongus* (figure 5) and *Mecynodon* sp. (figure 9) the posterior lateral of the left valve enlarges posteriorly from a point in line with the base of the ligament nymph and is similar to *Eoschizodus* (Newell & Boyd 1975, p. 94) but in *M. carinatus* the posterior lateral in the same valve occurs in an approximately similar position but starts abruptly with a rounded anterior end and continues posteriorly with parallel sides (figure 7). In this species, particularly, the teeth should be described as heterodont; the lateral teeth are better demarcated than in the early Astartid *Eodon*.

However, the teeth are also similar to those of *Megalodon* (figure 10). *Megalodon* has exactly the same pattern of teeth in the right valve (figures 8 and 10), including a similar though

relatively weaker hiatus. But in *Megalodon* the umbones are much more incurved and the teeth and whole hinge plate relatively much more substantial. It is thought that *Megalodon* is an end member of a series of species where the umbones are becoming enrolled and the hinge hypertrophied partly to increase weight for stabilization in an umbones downwards semi-infaunal, possibly byssate, nestling position.

The similarity of the hinge of these genera highlights the close phylogenetic relationship of the Crassatellacea, Megalodontacea and Trigoniacea.

The particular similarity between some species of *Mecynodon* and *Megalodon* suggests that they have the closest common ancestry, and for that reason the Mecynodontidae are referred to the Megalodontacea within the Hippuritoida. If this proposal is correct it means that the Hippuritoida most probably have an infaunal Cycloconchacean ancestry.

The Lower Devonian genus *Hefteria*, rejected by Newell & Boyd (1975, p. 95) from the Trigoniacea, has similar ornament to that which occurs on the umbonal regions of the Middle Devonian *Mecynodon oblongus*, and the hinge of the left valve (Newell & Boyd 1975, fig. 29) is very similar to that of *Mecynodon*, although the posterior lateral forms only rather a faint ridge. For these reasons *Hefteria* is included in the Mecynodontidae. The similarity between *Hefteria* and the permophorids (Newell & Boyd 1975, p. 95) is probably due to convergence.

The earliest genus attributed to the Megalodontidae in the Treatise (La Roque & Newell 1969) is *Megalomoidea* (Middle Silurian) (figure 13). However, this genus resembles and is best interpreted as a much enlarged form of the modiomorphid, *Modiolodon*. It is only known from the shallow warm water calcarenite facies occurring in North America and Sweden. The Devonian genus *Montanaria*, placed by Chavan (1969a, p. N511) in the family Mactromyidae, of the Lucinacea, also appears to be related to the *Modiolodon* group. The Devonian genera *Eomegalodon* and *Cumularia* have a hinge pattern less enlarged than *Megalodon* and more closely resembling *Mecynodon* and are therefore better placed in the Mecynodontidae than the Megalodontidae.

The Megalodontidae are first prominent in the Mid-Devonian when there was a radiation of shallow burrowers and nestlers in areas of warm shallow calcarenite sedimentation. They are then absent from the fossil record until the Triassic when they occur in a similar environment and often in great profusion. The gap in the record between the Devonian and the Triassic, a period of approximately 140 Ma, remains unexplained. This is remarkable because rocks, which would appear to have been deposited in an environment which would have suited the Megalodontidae, are well known in the Lower Carboniferous and contain a large number of well documented bivalves. However, some of the Triassic species are virtually identical with the Devonian ones. It therefore seems much more likely that there is a real gap in the record rather than a case of homeomorphy.

Although the Triassic genera *Physocardia*, *Cornucardia* and *Dicerocardium* were placed in the Glossacea (Cox 1969b) they seem only to be convergent and should not be placed in that superfamily. *Dicerocardium* appears to foreshadow the bizarre shape of the Diceratidae while *Physocardia* and *Cornucardia* resemble *Megalodon* except for their reduced hinge plates. At present both seem best placed in the Megalodontacea.

Two Jurassic genera, *Pterocardia* and *Pachyrismella*, usually included in the Megalodontidae, have the hinge and shell shape of the Cardiidae while in addition *Pachyrismella* has the short pallial sinus, adductor and pedal muscle scars typical of the Cardiacea. In consequence these two genera are removed to the Cardiacea.

Trigoniacea and Unionacea

The Palaeozoic history of the Trigoniacea is not treated at length here, as it is dealt with in great detail by Newell & Boyd (1975), who have traced them back to the Upper Silurian. They concluded that the Devonian genus *Eoschizodus* is reminiscent of actinodont ancestors and they considered that *Lyrodesma* was an early development similar to, but independent of, the early Trigoniids (Newell & Boyd 1975, p. 86). This is contrary to the opinion of Pojeta (1971) who suggested that the Trigoniacea are directly descended from the Lyrodesmatidae. The occurrence of posterior lateral teeth in the early Trigoniacean *Eoschizodus* and the similarity of the early Trigoniacea to both the Mecynodontidae and the early Megalodontidae which also have posterior lateral teeth, suggests that the lateral hinge teeth are a primitive feature of these closely related groups. It is easier to derive a hinge with lateral teeth from that of the Cycloconchidae, where the outer elongate teeth are as widely placed as the laterals, by reduction of the number of hinge teeth, than from the Lyrodesmatidae where the teeth are bunched on a hinge plate that is shaped like the segment of a circle (see Pojeta 1971, pl. 3).

As seems to be the case with the Crassatellacea, the reduction of the number of hinge teeth from a presumed actinodont ancestor corresponds with the acquisition of a short, well defined ligament nymph. Possibly a stronger ligament allowed experimentation with different arrangements of hinge teeth.

The Upper Silurian genus *Pseudaxinus* almost certainly belongs in the Trigoniacea but unfortunately its hinge and muscle scars are not known.

Newell & Boyd (1975, pp. 83–85) pointed out both the similarities and differences that exist between the Trigoniacea and the Unionacea. Their inclusion of both superfamilies in the same order, the Trigonoida, reflects the greater similarity between them than between the Unionacea and the Anthracosiacea and it is likely that the Unionacea are the result of a separate invasion by Trigoniaceans of the non-marine habitat in either the late Palaeozoic or early Mesozoic.

Crassatellacea

The earliest known Veneroida belong to the genus *Eodon* (L.–U. Devonian), an Astartid which resembles *Cycloconcha* in shape, musculature and some hinge details, but the teeth are of a simpler pattern. The characters of *Eodon* and *Cycloconcha* are compared in table 1 and figure 26.

There is no record of a Silurian astartid, and *Actinodonta*, the only well known Silurian cycloconchid, is the wrong shape to be an astartid ancestor. As a whole, the Silurian bivalve fauna is poorly known. The ancestry of *Eodon* cannot therefore be traced. All that can be said is that, sometime during the Silurian, actinodont teeth became modified into the simpler patterns of the early Veneroida, Hippuritoida and Trigonoida. This change from a relatively large number of cardinal teeth to a smaller number of teeth coincides with the development of a well defined ligament nymph. It is suggested that advances in the design of the ligament may have allowed simplification of the rather cumbersome actinodont hinge.

The lateral teeth of *Eodon* are in a position on the hinge plate similar to the outer teeth of *Cycloconcha* (figures 26): there is therefore a strong suggestion that these teeth are homologues.

A possible problem in accepting a cycloconchid as the ancestor of the Veneroida lies in the suggestion that the development of different types of teeth may be controlled by separate groups of genes. In recent Veneroida the posterior lateral teeth originate from a different

lamella from the other teeth (Cox 1969*a*, after Bernard). Boyd & Newell (1968), in their study of Permian Crassatellacea, interpret the occasional reversal of all the teeth except the posterior lateral as evidence for the latter's development being genetically distinct from that of the other teeth. On the other hand, in the Cycloconchidae, there is no apparent reason to suggest that any of the teeth, all originating from a point below the umbo, are genetically distinct. However,

TABLE 1. A COMPARISON OF *CYCLOCONCHA* AND THE EARLY ASTARTID, *EODON*

	<i>Cycloconcha</i>	<i>Eodon</i>
shell shape	equivalve, orbicular disk-shaped umbones prosogyral with slight lunule	equivalve, orbicular disk-shaped umbones prosogyral with slight lunule
ornament	concentric growth lamellae	concentric growth lamellae
hinge	ligament groove at dorsal shell margins, posterior to umbones, nymph not clearly delimited teeth radiate from initial point below umbones, all are cardinals	ligament nymph clearly defined posterior to umbones teeth radiate from initial point below umbones but laterals originate some distance from this point
muscle scars	fairly numerous teeth present adductors sub-equal, posterior slightly larger than anterior anterior adductor well inset pallial line simple and entire pedal attachment scars multiply paired and sub-equal, grouping almost regular	few teeth present adductors sub-equal, posterior slightly larger than anterior anterior adductor well inset pallial line simple and entire pedal attachment scars multiply paired and sub-equal, grouping less regular

the study of *Tironucula* (Morris & Fortey 1976) provides evidence to suggest that the genetically distinct development of teeth originated very early in the history of bivalves. In its ontogeny, only anterior teeth are present at the earliest growth stages seen. In this case, where anterior teeth occur earlier than posterior ones, it is reasonable to postulate that more than one set of genes is responsible. *Tironucula* is a nuculoid of early Ordovician age and clearly shows a very close common ancestry with the Cycloconchidae. There is therefore a strong possibility that the dentition of Cycloconchidae had genetically distinct development and that clear visible expression of this difference is exhibited in descendant Veneroida.

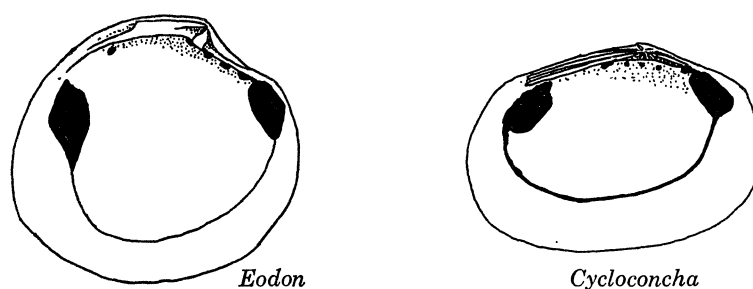


FIGURE 26. A comparison of *Eodon* and *Cycloconcha*: (a) *Eodon* aff. *bicostula* Krantz, L. Devonian, Eifel, W. Germany; (b) *Cycloconcha* cf. *mediocardinalis* Miller, composite (after Pojeta 1971) U. Ordovician, eastern U.S.A.

The hinge of early Astartidae is described as early 'Lucinoid' type both by Haffer (1959) and Boyd & Newell (1968) and is generally accepted as giving rise to the more advanced 'Cyrenoid' pattern by an increase in the number of cardinal teeth either by bifurcation of already existing teeth or growth of additional ones. This reflects the ontogeny of more advanced heterodonts (Cox 1969*a*). It is evidence by Haffer's inclusion of the genera he ascribed to the

Lucinacea that he considered the change from the 'lucinoid' to the 'cyrenoid' hinge also implies an evolutionary series from the Lucinacea to the Crassatellacea and the Veneracea. The evidence shows that such a line of descent is not possible. During the Silurian and Devonian, representatives of the Lucinacea including *Paracyclas* and *Ilionia* (MacAlester 1965; personal observation) have many of the highly specialized attributes of living Lucinacea. These attributes include the hypertrophy of the anterior adductor muscle and muscle attachment scars suggesting the presence of mantle gills, both of which are entirely unknown in the Veneroida as they are interpreted here.

Haffer (1959) postulated an evolutionary progression in the hinge teeth of early Astartidae in which the central cardinal tooth of the left valve in the Devonian genus, *Eodon* (figure 11) (his tooth 2 in *Cypricardella* fig. 17a, as he uses Bernard's classification), has by the Carboniferous given rise to species of '*Cypricardella*' (Haffer 1959, fig. 17b) where there are two cardinals in the left valve. A new tooth (4b) has been introduced behind tooth 2. However, in their Permian species, *Astartella auri*, Boyd & Newell (1968) interpreted the extra tooth as the formation of an anterior cardinal at the lunule margin and pointed out that a further socket must arise between this anterior tooth and the lunule margin to attain the condition of the Mesozoic Astartidae. It is therefore probable that extra cardinal teeth can be introduced both behind and in front of tooth '2'. Several other cases have been observed in which a new cardinal tooth has been developed at the base of or just below the ligament nymph. They become apparent when compared with Palaeozoic Astartellinae which have the more primitive condition with a central tooth '2' only. This condition can be seen in *Cypricardella subelliptica* Hall (on which Boyd & Newell's hypothesis is partly based), other Carboniferous species of *Cypricardella* (figure 3) and *Astartella vera* Hall. The new tooth in the Mesozoic taxa is separate from and behind the original tooth '2' in the manner of Haffer's example.

Examples showing this new tooth are typical Mesozoic Astartidae such as '*Astarte*' *subtetragona* Goldfuss (figure 17). The new tooth is also found in Mesozoic Arcticea and Cardicea.

These different examples of the origin of additional teeth reinforce the value of the use of a modified system of Steinmann hinge notation that does not imply homology (Boyd & Newell 1968).

The Devonian genus *Prosocoelus* (figure 12), which Haffer (1959) referred to the Mecynodontidae, has no hiatus of the hinge plate of the right valve and in this way resembles early astartids rather than the Mecynodontidae. It is here considered to be an early offshoot of the Astartellinae and apparently had no post-Devonian descendants.

The Astartidae have been a very conservative stock in general shell form; those occurring in the Lower Devonian differ little from living ones. The difference in tooth arrangement, although significant, is nevertheless relatively minor. Modification of the hinge structure, when the ligament migrates inwards into a resilifer forming part of the flat hinge plate, could easily happen on a number of occasions with a similar effect on the shape of the hinge. One clear example of this process is the Permian genus *Oriocrassatella*. *Oriocrassatella* differs from the Crassatellinae in that there is a septum on the resilifer which apparently separated the inner and outer ligament layers (Boyd & Newell 1968). There are no known *Crassatella*-like species between the Upper Permian and the Upper Jurassic.

When the Cretaceous genus *Anthonya* is removed from the Crassatellinae and associated with the Scambulinae (figure 17), Cretaceous species of the Crassatellinae show progressive enlargement of the internal resilifer and encroachment of the resilifer on the astartid cardinal

tooth pattern (figure 17.4–17.6). Some of the earlier species such as *Pachythaerus vindinensis* (D'Orbigny 1844) (figure 17.5) have a markedly carinate, rhomboidal appearance. There is strong resemblance between *Pachythaerus* and some genera of the Opinae, particularly *Trigonastarte* (figure 17.4) in which the teeth are of remarkably similar proportions and the external nymph is already reduced when compared with the nymph of the Astartinae and it has dropped well into the top of the dorsal shell margin. These facts lead me to consider that the Crassatellinae were independently derived, not from *Oriocrassatella*, but from a Mesozoic astartid, probably within the Opinae.

The Crassatellacea were arranged in systematic order by Chavan (1969*c*). His classification has been emended first by Boyd & Newell (1968) who introduced two Palaeozoic subfamilies, the Astartellinae in the Astartidae and the Oriocrassatellinae in the Crassatellidae, and since by Runnegar & Newell (1971) who resurrected Beurlen's subfamily Pinzoellinae. Living Crassatellacea have been described by Saleudin (1965, 1967) and by Harry (1966). The close similarity of the Crassatellacea to the Carditacea was pointed out by Yonge (1969). This had been attributed to convergence by Boyd & Newell (1968) but in the present study (unpublished observation by J. M. Dickins and N. J. Morris) the Permophoridae, an early family usually attributed to the Carditacea, are considered to be convergent with the Veneroida and are shown more likely to be offshoots of the Carboniferous family Sanguinolitidae. Furthermore, the Ptychomyidae are removed from the Arcticea and placed in the Crassatellacea and reduced to subfamilial status next to the Scambulinae because their hinge which has previously been misinterpreted (figure 17.2) closely resembles that of both *Remondia Mediraon* (figure 17.3) and *Anthonyia*.

The Hippopodiidae, which do not have heterodont hinge teeth, I consider to be offshoots of the Myoconchinae and, for the present, include them with some doubt in the Anomalodesmata. *Hippopodium ovale* Moore 1867 has homogeneous shell structure as does *Myoconcha*.

Astartidae and Crassatellidae living today have the same amount of mantle fusion with the inner layer fused below the exhalent opening. However, the late Jurassic '*Astarte*' *duboisiana* d'Orbigny 1845 has a slight but definite pallial sinus (figure 14). At approximately the same time siphons appear in the Veneracea, Mactracea, Corbiculacea and Tellinidae. From a comparison with recent species of *Astarte*, the sinus may represent a retractile extended mantle fold or siphon around the exhalent current only. The lower point of the sinus corresponds with the single area of fusion in the living species.

Palmer (1975, p. 39) demonstrated the difference between the Cardiniidae and the Astartidae and other Crassatellaceans. The ornament of the Cardiniidae seems to be the result of episodic growth; only in his rugoids do the imbricating lamellae turn away from the shell surface to form concentric lamellae. As Palmer pointed out, most Astartinae and Crassatellinae have distinct undulations or ribs. These two subfamilies and the Carditidae have marginal crenulae in the larger, growth stages, whereas the Cardiniidae have smooth shell margins. A typical species of *Cardinia* (figure 18) has a hinge with prominent laterals but rather reduced cardinal teeth.

It is apparent that the early evolution of the Cardiniidae took place outside the European Triassic seas. Early records of the family include *Cardinia cordilleranus* (Cox, 1949) from the Norian of Peru and the New Zealand genera *Torastarte* and *Balantoselena*. *Torastarte* has been shown to belong to the Cardiniidae by Fleming (1957) and clearly has the appearance of this family. *Balantoselena* has the external appearance and the lateral teeth of the Cardiniidae; its better developed cardinal teeth resemble those of many Crassatellacea and Carditacea but as

the umbones are much coiled to the anterior, the teeth are more prosocline than is usual for the Astartidae.

Although there are some similarities between the dentition of the Cardiniidae and that of certain Lucinidae with reduced cardinals (Palmer 1975), this seems to be a result of convergence. The Cardiniidae do not have the hypertrophied anterior adductor of the Lucinacea and their descendants. On the contrary, the attachment pattern of the musculature resembles that of the Veneroida, particularly the Crassatellacea and the Arcticacea.

It is considered here that *Torastarte* and probably *Balantioselena* are correctly placed in the Cardiniidae and this family has descended from some as yet unknown Palaeozoic crassatellacean, presumably belonging to the Astartellinae.

Since the family does not have the particular tooth arrangement of the Arcticacea (Casey 1952) and since it has no pallial sinus, there is no reason either to include the Cardiniidae in the Arcticacea or to raise its status above family level. The family is retained here in the Crassatellacea.

The family Myophoricardiidae consists of a number of genera which were widespread in Triassic times. All the species known are of rather small size. Their hinge is comparable to that of some Late Palaeozoic Astartellinae and some other Astartidae; few other details are known. But their hinge and general shape suggests that their place in the Crassatellacea (Cox & Chavan 1969) may be correct.

Carditacea and Chamacea

The close similarity between the Carditidae and the Astartidae has long been recognized. The similarity of the hinge is mentioned by Davies (1935) and that of the whole animal by Yonge (1969). Hinges of Mesozoic genera *Palaeocardita*, *Tutcheria* and *Ludbrookia* (figures 19–23) may be compared with the Jurassic '*Astarte*' *subtetragona* Goldfuss (figure 17.1). However, it is not clear whether the second cardinal tooth of *Palaeocardita* has been produced behind the original tooth '2', as previously described in Haffer's '*Cypricardella*', and appears to have happened in the Mesozoic Astartidae, or at the lunule margin as described by Boyd & Newell (1968) in *Astartella auri*.

The carditids normally have strong radial ribbing. Their umbones are closer to the anterior margin than in the Astartidae, probably reflecting a tendency to produce semi-infaunal and epifaunal, bysally fixed forms. Apart from these differences and the fact that mantle fusion ventral to the exhalent opening does not occur in the Carditidae, there is little difference between the two families.

The earliest Carditacea have for some time been thought to be the Permophoridae (Newell 1957; Chavan 1969*b*) (Carb.–Cret.). The first definite carditid is *Gujocardita* from the Upper Permian of Japan, which resembles the Triassic genus *Palaeocardita*, but apparently lacks marginal crenulae. Nakazawa & Newell (1968) suggest that *Gujocardita* is an evolutionary link between the Carditidae and the permophorid, *Stutchburia*. However, the Permophoridae may be traced back to the Lower Carboniferous sanguinolitid genus *Eopleurophorus* (views held by both J. M. Dickins and N. J. Morris), some species of which have the pustulose outer shell surface typical of the Anomalodesmata. The majority of the Permophoridae do not have cardinal hinge teeth but their development in some genera, described as obsolete or tuberculiform (Chavan 1969*b*) is here thought to be due to convergence. Both the Lower Jurassic *Myoconcha decorata* and a representative of a possibly related family the Hippopodiidae, *H. ovale* Moore had completely homogeneous shell structure. They occurred in a sediment where some other

bivalves had well preserved crossed-lamellar structure. There was no sign of prismatic structure either in myostracum or on an outer shell layer; this may have been due to erosion in the case of the outer layer but could be due to the lack of good preservation of exceptionally thin layers. All the species of Carditacea examined by Taylor, Kennedy & Hall (1973) had crossed-lamella and complex crossed-lamella structure. The Chamacea are similar except that some species have an additional outer calcite layer (Kennedy, Morris & Taylor 1968). Homogeneous shells are more commonly met with in various offshoots of the early Anomalodesmata such as the Pleuromyidae, *Panopea*, *Hiatella* and *Gastrochaena*.

For these reasons the link between the Permophoridae and the Carditidae is not accepted and it is considered more likely that the Carditacea evolved from some later Palaeozoic representative of the Astartellinae that became radially ribbed.

There is no reason to believe that the poorly known, much older Lower Devonian genus *Carditomantea* belongs to the Carditidae. Although the Upper Triassic genus *Septocardia* has been placed in the Cardiidae by Keen (1969), she nevertheless pointed out that it has an affinity with *Palaeocardita* (Carditidae), and forms an evolutionary link between the two. A species of *Protocardia* occurs with *Septocardia* in the Norian (Upper Triassic) of Peru (figure 24); the former has the hinge and shell shape typical of the Protocardiinae. *Septocardia* does not have the typical cardiid lateral hinge teeth and is here placed in the Carditidae rather than the Cardiidae. *Septocardia* has a rather unusual shape with a drawn out siphonal area. Its elongate cardinal hinge teeth are of the general astartid-carditid pattern. Both the teeth and the strong radial ribbing are evidence for its suggested affinity with *Palaeocardita*.

The most common Mesozoic Carditidae are infaunal astartiform species. The more elongate, epifaunal byssate *Cardita* s.s. ranges from the Upper Cretaceous onwards (for example, B.M.P.D. LL 13104 from the high Senonian of Pleven, Bulgaria).

In Chavan's classification of the Carditidae (Chavan 1969*b*) the family is divided into seven subfamilies. Attempts to place Mesozoic genera into these subfamilies suggests that the divisions between them are a little arbitrary and that further work is needed to rationalize the Mesozoic forms.

The possible origin of the epifaunal, cemented Chamacea from a Cretaceous byssate carditid is discussed in an earlier paper (Kennedy, Morris & Taylor, 1970).

I should like to thank the following people for their invaluable assistance: Mr R. J. Cleavelly, Dr J. M. Dickins, Mr C. P. Nuttall, Mr C. P. Palmer, Dr J. Pojeta Jr, Dr B. Runnegar, Dr P. W. Skelton and Dr J. D. Taylor for their discussions concerning various groups of bivalves dealt with in the paper; Dr R. A. Fortey for his generous assistance with Lower Ordovician stratigraphy; Mr J. V. Brown for taking the photographs; Mr C. P. Nuttall again for his considerable help with and constructive criticism of the manuscript; and Solene Whybrow for drawing the figures.

REFERENCES (Morris)

- Babin, C. 1966 *Mollusques bivalves et céphalopodes du paléozoïque armoricain*. Brest, published by the author.
 Babin, C. 1977 *Géobios* **10**, 51-79.
 Barrois, C. E. 1891 *Annls. Soc. géol. N.* **19**, 134-237.
 Beushausen, H. E. L. 1895 *Abh. preuss. geol. Landesanst* **17**, 1-514.
 Boyd, D. W. & Newell, N. D. 1968 *Am. Mus. Novit.* **2328**, 1-52.
 Casey, R. 1952 *Proc. malac. Soc. Lond.* **29**, 121-176.

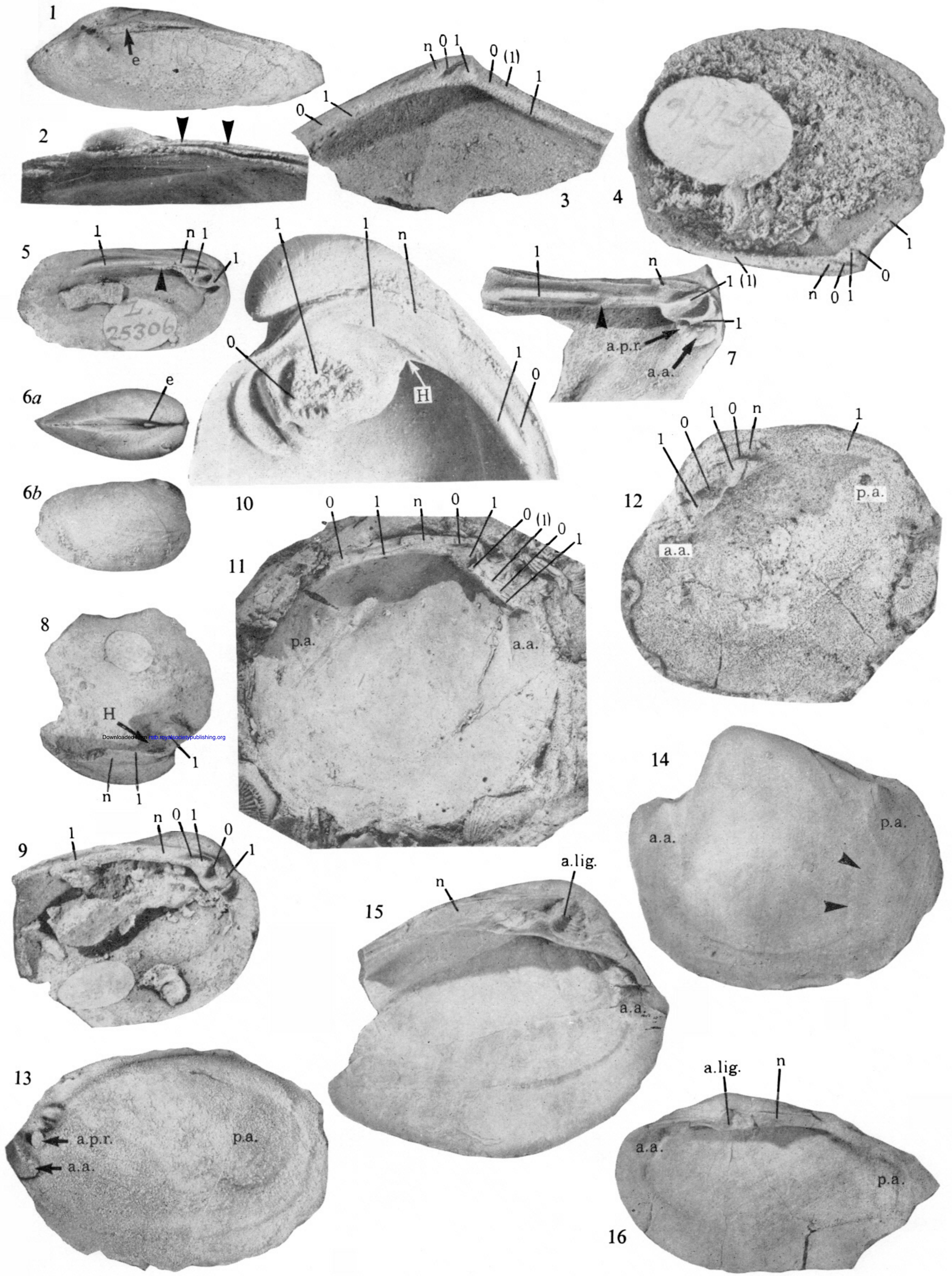
- Chavan, A. 1969a In Moore (ed.) 1969, vol. 2, pp. N491–N518.
 Chavan, A. 1969b In Moore (ed.) 1969, vol. 2, pp. N543–N561.
 Chavan, A. 1969c In Moore (ed.) 1969, vol. 2, pp. N562–N583.
 Cox, L. R. 1960 *Proc. malac. Soc. Lond.* **34**, 60–88.
 Cox, L. R. 1969a In Moore (ed.) 1969, vol. 1, pp. N2–N129.
 Cox, L. R. 1969b In Moore (ed.) 1969, vol. 1, pp. N658–N664.
 Cox, L. R. & Chavan, A. 1969 In Moore (ed.) 1969, vol. 2, pp. N580–N582.
 Davies, A. M. 1935 *Tertiary faunas*, vol. 1. London: Thomas Murphy & Co.
 Douville, H. 1913 *Bull. Soc. géol. Fr.* **12**, 419–467.
 Fortey, R. A. & Owens, R. M. 1977 *Bull. Br. Mus. (nat. Hist.) Geology* **30**. (In the press.)
 Haffer, J. 1959 *Palaeontographica A* **112**, 133–192.
 Harry, H. W. 1966 *Publs Inst. mar. Sci. Univ. Tex.* **11**, 65–89.
 Keen, M. 1969 In Moore (ed.) 1969, vol. 2, pp. N583–N594.
 Kennedy, W. J., Morris, N. J. & Taylor, J. D. 1970 *Palaeontology* **13**, 379–413.
 Kobayashi, T. 1933 *J. Fac. Sci. Tokyo Univ.* **3**, 249–328.
 La Roque, A. & Newell, N. D. 1969 In Moore (ed.) 1969, vol. 1, pp. N393–N401.
 MacAlester, A. L. 1965 *Palaeontology* **8**, 231–246.
 Moore, C. 1867 *Proc. Somerset archaeol. nat. Hist. Soc.* **13**, 119–244.
 Moore, R. C. (ed.) 1969 *Treatise on invertebrate palaeontology*, part N, vols 1 and 2 (of 3) (*Mollusca 6: Bivalvia*) (952 pages). Lawrence, Kansas: The Geological Society of America and University of Kansas.
 Morris, N. J. 1967 In *The fossil record: a symposium with documentation*. The Geological Society of London.
 Morris, N. J. & Fortey, R. A. 1976 *Paleontology* **50**, 701–709.
 Nakazawa, K. & Newell, N. D. 1969 *Mem. Fac. Sci. Kyoto Univ.* **35**, 1–108.
 Newell, N. D. 1957 *Am. Mus. Novit.* **1857**, 1–14.
 Newell, M. D. 1965 *Am. Mus. Novit.* **2206**, 1–25.
 Newell, M. D. & Boyd, D. W. 1975 *Bull. Am. Mus. nat. Hist.* **154**, 52–162.
 d'Orbigny, A. 1844–7 *Paléontologie Française*. Terrains Cretacés, vol. 3. Paris: Arthur Bertrand.
 d'Orbigny, A. 1845 In *Geologie de la Russie d'Europe et des Montagne de l'Oural* (eds R. I. Murchison, E. de Verneuil & A. von Keyserling), vol. 2, part 3, pp. 419–488. London: John Murray, and Paris: Bertrand.
 Palmer, C. P. 1975 *Bull. Br. Mus. nat. Hist. Geology* **26**, 1–44.
 Phillips, J. 1848 *Mem. geol. Surv. U.K.* **2**, 1–330.
 Pojeta, J., Jr 1971 *Prof. Pap. U.S. geol. Surv.* **695**, 1–46.
 Pojeta, J., Jr 1975 *Bull. Am. Paleont.* **67**, 363–384.
 Runnegar, B. & Newell, N. D. 1971 *Bull. Am. Mus. nat. Hist.* **146**, 1–66.
 Runnegar, B., & Pojeta, J., Jr 1974 *Science, N.Y.* **186**, 311–317.
 Saluedin, A. S. M. 1965 *Proc. malac. Soc. Lond.* **36**, 229–257.
 Saluedin, A. S. M. 1967 *Proc. malac. Soc. Lond.* **37**, 381–384.
 Taylor, J. D., Kennedy, W. J. & Hall, A. 1973 *Bull. Br. Mus. nat. Hist. Zoology* **22**, 253–294.
 Thoral, M. 1935 *Contribution à l'étude paléontologique de L'Ordovicien inférieur de la Montagne Notre*. Montpellier: La Charité.
 Trueman, E. R. 1969 In Moore (ed.) 1969, vol. 1, pp. N58–N64.
 Verneuil, E. & Barrande, J. 1855 *Bull. Soc. géol. Fr.* **12**, 964–1025.
 Vogel, K. 1962 *Abh. math.-naturw. Kl. Akad. Wiss., Mainz* **1962**, 192–244.
 Yonge, C. M. 1969 *Proc. malac. Soc. Lond.* **38**, 493–527.

Discussion

R. M. C. EAGAR (*The Manchester Museum, The University, Manchester M13 9PL, U.K.*). Dr Morris has suggested that the Superfamily Anthracosiacea, including the Family Anthracosiidae (*Carbonicola*, *Anthracosia* and *Anthracosphaerium*), may have evolved from descendants of the Lower Palaeozoic Cycloconchidae. I would stress that recent work suggests that the shells formerly assigned to *Carbonicola* in the Viséan of northern England, in the lower Namurian (Pendleian: E₁) of Scotland, Poland and Czechoslovakia, and of the Arnsbergian (E₂) of the latter country differ internally and externally from *Carbonicola*. They have been placed in the new genus *Paracarbonicola* (Eagar R. M. C. 1977 *Phil. Trans. R. Soc. Lond. B*, **271**, 535–570). The new genus is questionably a member of the Anthracosiidae, but its ancestry might possibly prove to be broadly as suggested by Dr Morris. The genus *Carbonicola*, as now restricted, does

not appear until the Marsdenian (R_2) Stage of the upper Namurian. When account is taken of both internal features of the shell, including the pattern of the anterior accessory scar, and external 'ornament', as in the above paper, evidence at present suggests the derivation of *Carbonicola* from a stock of shallow-water highly variable marine bivalves which have been provisionally referred to cf. *Sanguinolites* Hind *non* M'Coy. This conclusion therefore supports the origin of the Anthracosiidae through *Sanguinolites*, a view discussed by Dr Morris. It seems interesting to note that in both *Paracarbonicola* and *Carbonicola* the earliest non-marine shells tended to be edentulous. In *Carbonicola* teeth apparently evolved slowly, commencing with a series of highly variable swellings and depressions on the hinge plate (Eagar, R. M. C. 1946 *Geol. Mag.* **83**, 1–19), the hinge plate deepening with increasing size of the shell. Dental pattern became stabilized only in the succeeding *Anthracosia* of Westphalian B Stage.

N. J. MORRIS. I have only tentatively included the Anthracosiacea in the subclass Heteroconchia because their total characters, as exemplified by *Carbonicola* have a little more in common with the early Heteroconchia than the Sanguinolitidae or other anomalodesmatans. Although some species belonging to the Sanguinolitidae (here taken to include several of the species included in '*Sanguinolites*' by Hind (1905) and to be a family of the Anomalodesmata) and their possible descendants have characters which they share with the Heteroconchia I assume that this is due to convergence. It is, however, quite possible that the similarities between the Anthracosiacea and the Heteroconchia are themselves due to convergence. If Dr Eagar has new evidence that *Carbonicola* can be linked to the Sanguinolitidae through intermediates, it suggests that the Anthracosiacea should be removed from the Heteroconchia and placed in the Anomalodesmata.



FIGURES 1-16. For description see opposite.

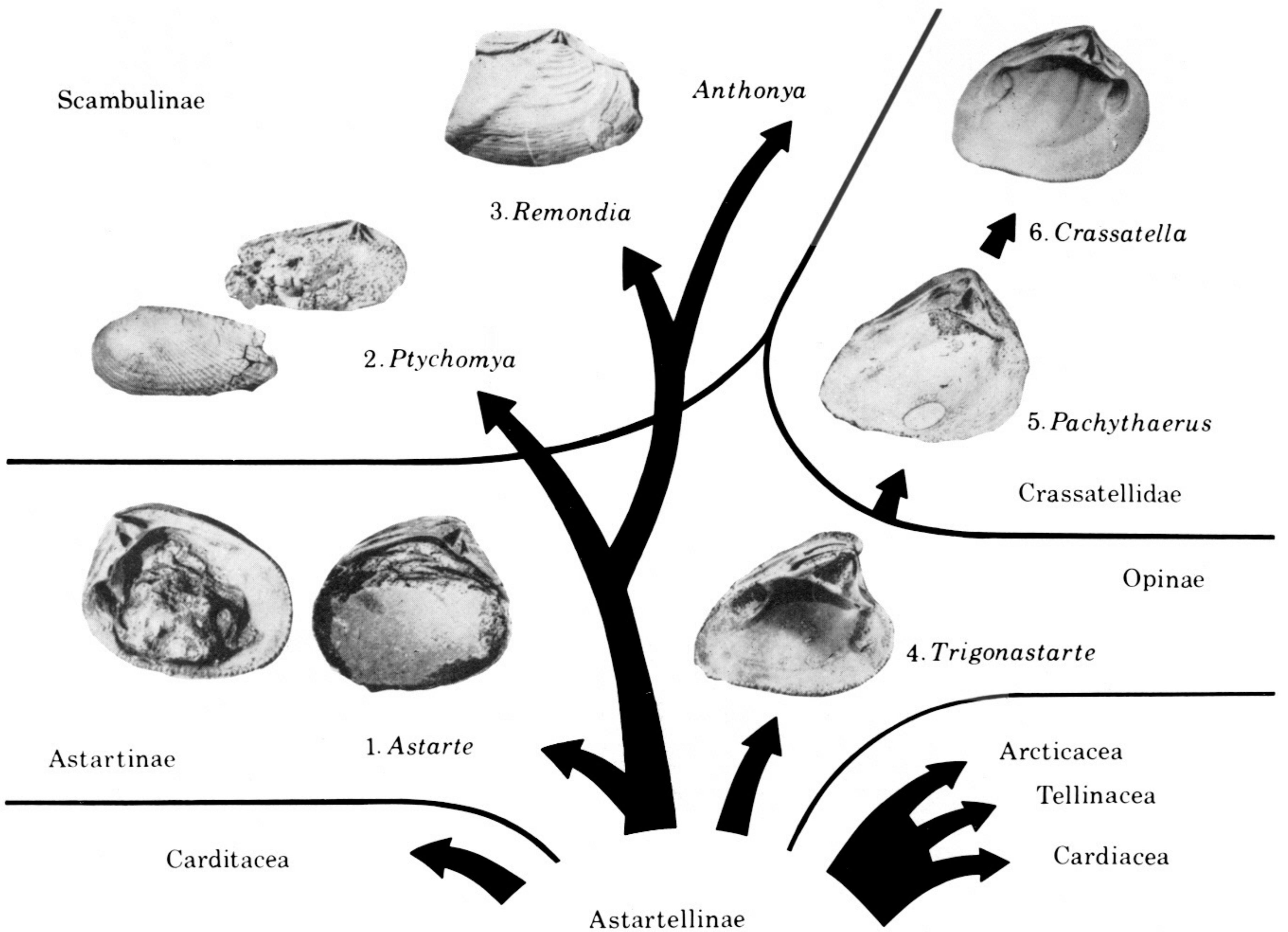
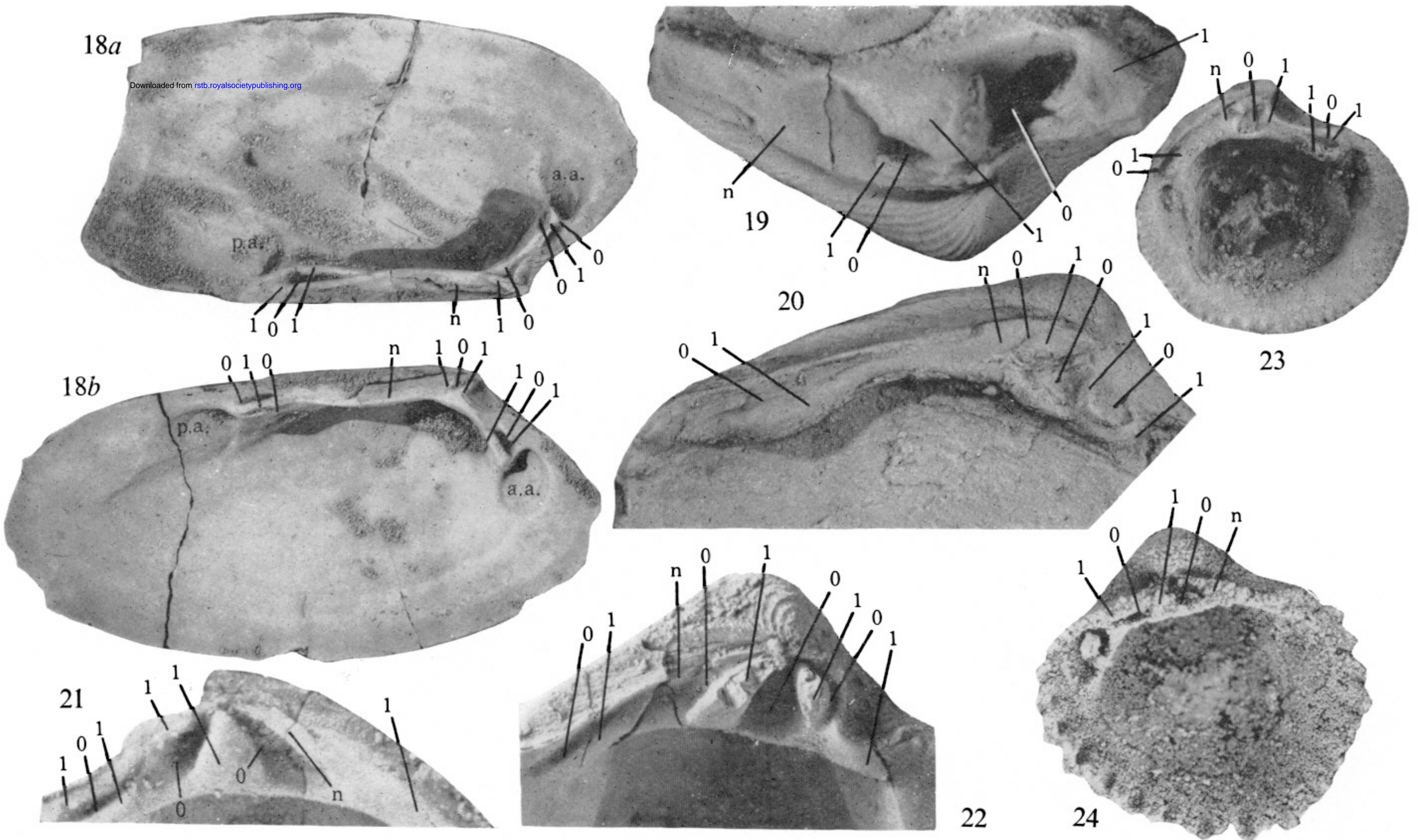


FIGURE 17



FIGURES 17-24. For description see opposite.