
Origin and Evolution of the Class Rostroconchia [and Discussion]

B. Runnegar, C. B. Goodhart and E. L. Yochelson

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Origin and evolution of the Class Rostroconchia

BY B. RUNNEGAR

Department of Geology, University of New England, Armidale, Australia 2351

[Plates 1 and 2]

The pseudobivalved Rostroconchia, first recognized as a separate class of molluscs in 1972, may be the only extinct molluscan class. Until recently, primitive rostroconchs (ribeirioids) were generally thought to be the carapace of crustacean arthropods and advanced rostroconchs (conocardioids) were considered to be unusual pelecypods. In fact, rostroconchs were a diverse class of molluscs (2 orders, 8 families, 31 genera, 400+ species known) that grew a bivalved adult shell from a univalved larval and juvenile shell. They were bilaterally symmetrical animals that probably had an anterior mouth, posterior anus, a pair of lateral gills, and a pelecypod-like foot. Most are believed to have been deposit feeders that used enlarged anterior mantle tissue to collect food, but some were clearly suspension feeders. They lived on top of the sea floor (rarely) or partly buried within it (commonly).

Rostroconchs are known only from Palaeozoic rocks and range in age from earliest Cambrian to latest Permian (approximately 575–245 Ma ago). They evolved from untorted univalved molluscs (helcionellacean monoplacophorans) in the late Precambrian, remained an inconspicuous component of the biota through the Cambrian, and then radiated rapidly in the palaeotropical seas of the Early Ordovician. Relatively few genera survived the Ordovician, possibly because of competition by the Pelecypoda, but many species of these are found in younger Palaeozoic rocks. The last refuge of the class seems to have been the cool-temperature regions of the Permian Earth.

By the middle Early Cambrian, the first pelecypod *Fordilla* had evolved from a primitive rostroconch. Rostroconchs were preadapted to exploit the pelecypod form, and the appearance of *Fordilla* may have been a relatively insignificant step. Somewhat later, probably in the Late Cambrian or Early Ordovician, the Scaphopoda were also derived from the Rostroconchia. This evolutionary event seems to have required the ventral fusion of an elongate rostroconch shell at the post-larval stage of development.

Animals resembling primitive rostroconchs were required as theoretical links between monoplacophorans and pelecypods before the Class Rostroconchia was well studied. These hypothetical intermediates differ from the real thing in only one important respect; it was predicted that such forms would have many pedal muscle insertions on each valve, which they do not. The single anterior and posterior pedal muscle insertions of primitive rostroconchs therefore indicate a secondary simplification of the molluscan stock; this probably occurred after the anatomy of *Neopilina* was attained, but before the main radiation of the phylum.

INTRODUCTION

Rostroconchs are bilaterally symmetrical pseudobivalved molluscs known only from fossils of Palaeozoic age. They comprise an extinct class of molluscs (Pojeta, Runnegar, Morris & Newell 1972; Runnegar & Pojeta 1974; Pojeta & Runnegar 1976). Unlike pelecypods, rostroconchs grew a bivalved adult shell from a univalved larval and juvenile shell, and therefore had no ligament or adductor muscles. After a brief but effective radiation in the Early Ordovician (figure 1), rostroconchs were largely supplanted by the more efficient pelecypods, but they remained a minor component of the biota until their extinction at the close of the Palaeozoic.

The first rostroconchs to receive scientific names were described in 1809 and 1815 from limestones in Derbyshire and Ireland (Pojeta & Runnegar 1976). The larger form, *Hippocardia hibernica* (J. de C. Sowerby) from the Carboniferous of Cork (figure 1, 26), superficially resembles living heart-cockles (e.g. *Corculum*), so that it and other advanced rostroconchs such as *Conocardium* (figure 1, 29) were considered for about 150 years to be unusual pelecypods, allied to cardiids or pteriids.

By contrast, primitive rostroconchs, including the genus *Ribeiria* Sharpe, 1853 (figure 1, 6), were generally thought to be the carapace of crustacean arthropods (Phyllocarida). Some

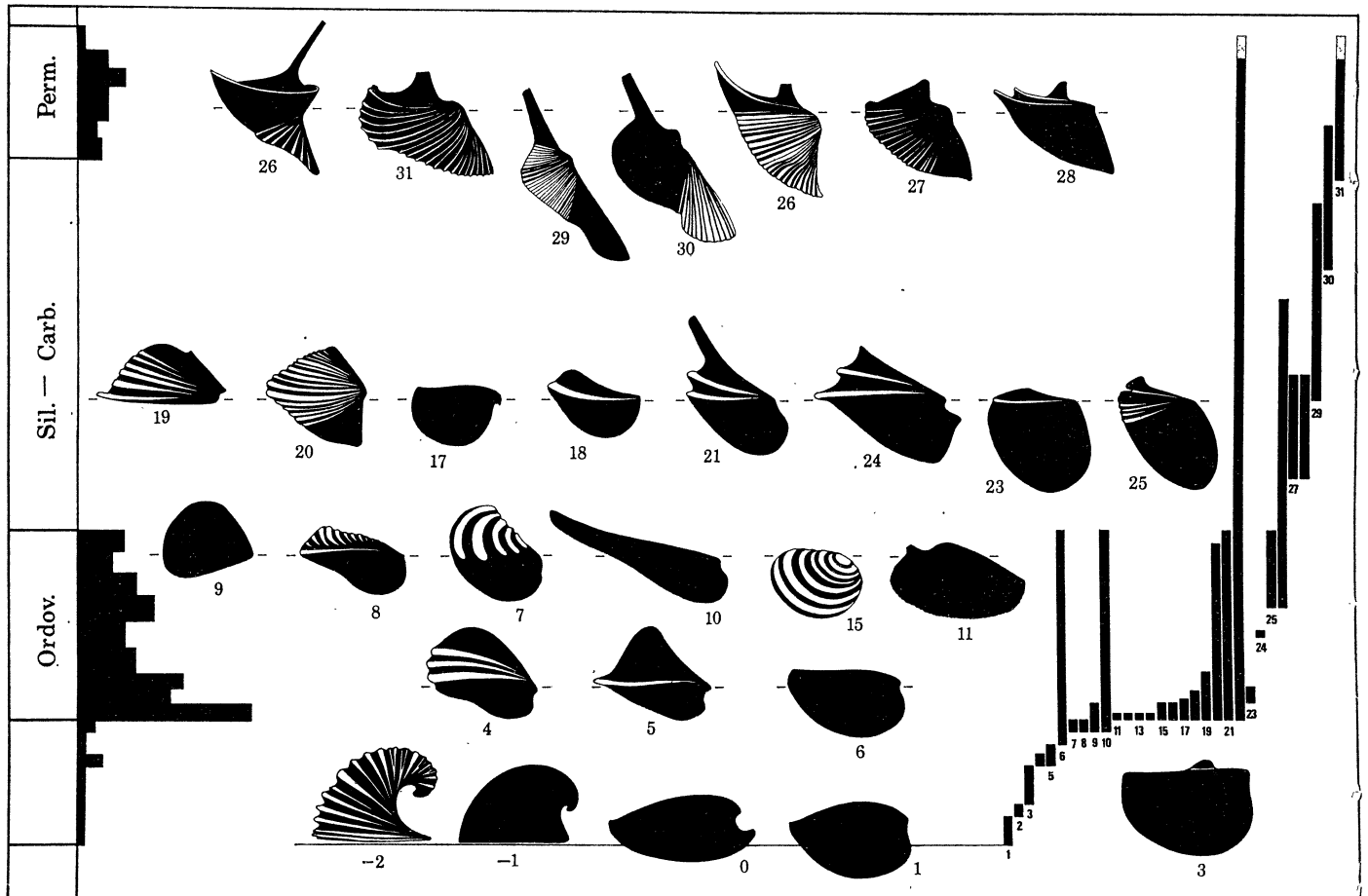


FIGURE 1. The radiation of the Rostroconchia. Silhouettes depict most rostroconch genera (1–31) and the probable ancestors of the Rostroconchia (–2–0), all in probable life orientation. Vertical bars (right) show the stratigraphic ranges of all known rostroconch genera; numbers on bars correspond to numbers on silhouettes. Horizontal bars (left) show the number of rostroconch species known to have existed during the Cambrian, Ordovician and Permian periods. Key: –2, *Latouchella* Cobbold; –1, *Anabarella* Vostokova; 0, *Mellopegma* Runnegar & Jell; 1, *Heraultipegma* Pojeta & Runnegar; 2, *Watsonella* Grabau; 3, *Myona* Kobayashi; 4, *Pleuropegma* Pojeta, Gilbert-Tomlinson & Shergold; 5, *Oepikila* Runnegar & Pojeta; 6, *Ribeiria* Sharpe; 7, *Cymatoppegma* Pojeta, Gilbert-Tomlinson & Shergold; 8, *Kimoppegma* Pojeta, Gilbert-Tomlinson & Shergold; 9, *Pinnocaris* Etheridge; 11, *Pseudotechnophorus* Kobayashi; 12, *Eoischyrinia* Kobayashi; 13, *Wanwanella* Kobayashi; 14, *Wanwanoidea* Kobayashi; 15, *Ptychopegma* Pojeta, Gilbert-Tomlinson & Shergold; 16, *Tolmachovia* Howell & Kobayashi; 17, *Apotoppegma* Pojeta, Gilbert-Tomlinson & Shergold; 18, *Anisotechnophorus* Pojeta & Runnegar; 19, *Euchasma* Billings; 20, *Eopteria* Billings; 21, *Technophorus* Miller; 22, *Bransonia* Pojeta & Runnegar; 23, *Pauroppegma* Pojeta, Gilbert-Tomlinson & Shergold; 24, *Myocaris* Salter; 25, *Ischyrinia* Billings; 26, *Hippocardia* Brown; 27, *Mulceodens* Pojeta & Runnegar; 28, *Bigalea* Pojeta & Runnegar; 29, *Conocardium* Bronn; 30, *Arceodomus* Pojeta & Runnegar; 31, *Pseudoconocardium* Zavadovskiy.

received names such as *Pinnocaris*, which reflect this belief. This is not altogether surprising, as the two kinds of fossils may occur together, and at sites of poor preservation are difficult to distinguish. But perceptive palaeontologists such as Robert Etheridge Jr had some doubts, for in proposing *Pinnocaris* in 1878, Etheridge noticed several features which suggested that *Pinnocaris* might be a mollusc. Ironically, he decided that it was probably an arthropod, because the early growth lines are concentric about a single 'central point or apex'. This is the diagnostic univalved larval shell of all rostroconchs.

In 1960, in a Presidential Address to the Malacological Society of London, Cox presented a new classification of the Bivalvia which he commended for use in the *Treatise on invertebrate paleontology*. One novel section of this classification highlighted the unique characters and separate history of advanced rostroconchs, by placing *Conocardium* and allied genera in a new order, the Rostroconchida. In 1967 Morris transferred the ribeirioids from the Arthropoda to the Bivalvia, and viewed the Ribeirioida and Conocardioida as the two most primitive orders of bivalves. Both groups were subsequently removed from the Bivalvia and placed in the new class Rostroconchia (Pojeta *et al.* 1972). All known genera and many species of the class have since been described by Pojeta & Runnegar (1976), Runnegar & Jell (1976), and Pojeta, Gilbert-Tomlinson & Shergold (1977). I am grateful to the last three authors for providing the results of their major study for this review.

ROSTROCONCHIA: FEATURES OF THE CLASS

Skeletal anatomy and functional morphology

Rostroconchs are shelled molluscs that grew a pseudobivalved adult shell from a conical larval and juvenile shell (figures 2 and 3†). All skeletal structures including muscle insertion areas are bilaterally symmetrical, except where comarginal plicae, radial ribs, or valve-edge denticles interlock at the commissure. Rostroconchs lived with their plane of symmetry vertical, either on the sea floor (rarely: figure 1, 19) or partly buried within it (commonly: figure 1). A variety of ornamental structures (carinae, plicae, ribs etc.: figure 1) seems to have been developed to reduce scour, to improve water circulation around the exposed part of the shell, and possibly to increase the camouflage of the animals. Few such structures seem to be designed to increase burrowing efficiency, but the comarginal plicae of *Ptychopegma* (figure 1, 15) may have operated in this way.

Primitive rostroconchs (ribeirioids) and some advanced rostroconchs (conocardioids) have a calcareous plate called a *pegma* connecting right and left valves. It leaves a characteristic notch in the anterior dorsal margin of internal moulds (figures 12*h* and 15). The phylogenetic origin of the pegma probably lies in shell geometry, but in primitive rostroconchs its posterior face was used as the insertion area for the anterior part of the shell-attached pedal musculature (figure 12*h*). When this function was no longer required, the pegma disappeared or was retained, possibly to help separate a feeding apparatus from the mantle cavity (figure 12*m*).

While the mantle cavity remained relatively narrow (as in *Ribeiria*, figure 1, 6), the pegma did not greatly impede shell growth. But those forms with an inflated shell and a large pegma (such as *Euchasma*, figure 1, 19) needed to resorb the edges of the older parts of the pegma to allow the valves to open slowly during growth. In such shells only the distal edges of the pegma are connected to the left and right valves.

† Figures 2–11 appear on plate 1, and figures 13–31 on plate 2.

Since the valves of rostroconchs were joined dorsally (figure 13) and could not be opened and closed at will, all rostroconchs have one or more permanent apertures in the anterior, ventral, and/or posterior valve margins. These orifices allowed the animals to feed, to move or burrow, to respire by circulating water in and out of the mantle cavity, and to remove foreign or unusable particles (pseudofaeces) and body wastes from the mantle cavity. In the most primitive rostroconchs (e.g. *Heraultipegma*, figure 1, 1; figure 14), the shell aperture is long and continuous from anterior to posterior. Other ribeirioids commonly have only anterior and posterior shell apertures (e.g. *Myocaris*, figure 1, 24), or more rarely, were sealed anteriorly and ventrally (e.g. *Technophorus*, figure 1, 21). These latter animals were immobile once the adult shape had been attained.

All advanced rostroconchs have a large anterior shell aperture that was used for feeding and moving. All also have a small posterior orifice that lies at the end of a short to long tubular prolongation of the shell known as a *rostrum* (figure 1, 26–31; figures 8 and 9). This structure is analogous to the posterior shell aperture of scaphopods, is too narrow for suspension feeding, and undoubtedly served to circulate water to the gills in the mantle cavity.

Most advanced rostroconchs have a tiny *ventral orifice* in the posteroventral commissure. It usually occurs where prominent external carinae meet at the valve edges (figure 9). In the bizarre genus *Hippocardia* (figure 1, 26 figures 10 and 11), the ventral orifice occurs at the end of a long narrow tube, but in this case the tube generates a curved structure known as a *hood* that surrounds the rostral area of the shell.

Two closely related advanced rostroconchs (*Conocardium* and *Arceodomus*: figure 1, 29, 30) have no ventral orifice, and one genus (*Bigalea*: figure 1, 28) has two, each associated with a pair of prominent carinae. It seems likely that the ventral orifices were outlets for pseudofaeces carried to them by ciliated tracts on the mantle and visceral mass, and were analogous to the fourth apertures of some pelecypods with extensively fused mantle margins (Yonge 1948). Their absence in *Conocardium* and *Arceodomus* probably reflects the elaborate food sorting apparatuses of these genera, which prevented sediment and other foreign matter from entering the mantle cavity.

The internal edges of the valves of many primitive rostroconchs are smooth, but more evolved forms invariably have rows of denticles lining the edges of the anterior shell aperture (figure 7).

DESCRIPTION OF PLATE 1

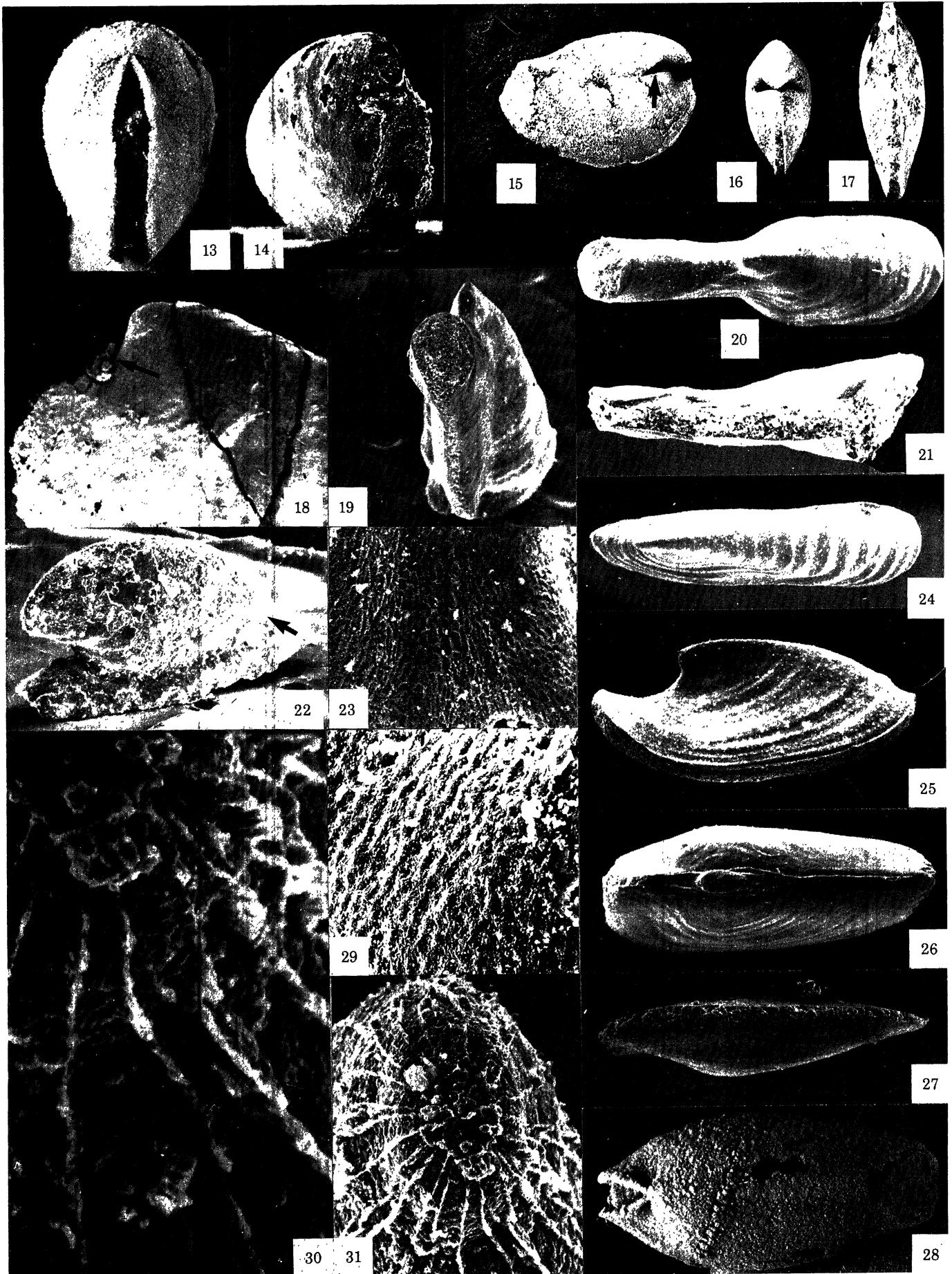
Shell morphology of advanced rostroconchs (conocardioids).

- FIGURES 2 AND 3. Dorsal and left lateral views of juvenile *Hippocardia*? with well preserved univalved larval shell. (Magn. $\times 44$.)
- FIGURES 4–6. Left external view of *Arceodomus*, plus views of interior and exterior of shell fragment, (photographs by courtesy of Dr Norman D. Newell). (Magn. $\times 2$.) The longitudinal shelves visible in figure 5 occur in the anterior aperture of *Arceodomus*.
- FIGURE 7. Internal mould of *Hippocardia*, viewed from the left side. (Magn. $\times 4$.) Note the well developed pegma and denticles lining the anterior aperture.
- FIGURES 8 AND 9. Posterodorsal and left lateral views of *Pseudoconocardium*, showing the rostral orifice, third orifice (arrowed), and tension fractures that result from shell growth. (Magn. $\times 1.5$.)
- FIGURES 10 AND 11. Natural mould and latex cast of the shell and hood of two specimens of *Hippocardia*. (Magns $\times 0.75$ and $\times 2$.) The arrow in figure 10 points to the tubular extension of the third orifice, now filled by sand. In figure 11, the dorsal surface of the hood is encrusted by an auloporoid coral, indicating that the hood was exposed during the life of the animal.



FIGURES 2-11. For description see opposite.

(Facing p 322)



FIGURES 13–31. For description see opposite.

Through growth, these denticles generated submerged ribs that are buried by the internal shell layers. Because the internal shell layers may be selectively dissolved during fossilization, steinkerns of advanced rostroconchs are frequently ornamented with moulds of these submerged ribs (figure 10).

Obviously the submerged ribs, like the external hood, are formed by the migration of functionally important structures (the denticles) during growth. One explanation of the denticles is that, like the denticles on the aperture of cowrie shells, they formed because copious amounts of mantle tissue had to be folded to be withdrawn into the shell. The denticles are greatly enlarged in the aperture of *Mulceodens* (figure 1, 27), and they are clearly homologous with complex calcareous structures in the anterior aperture of *Arceodomus* and *Conocardium* (Wilson 1970; Pojeta & Runnegar 1976). These latter structures, termed *longitudinal shelves* (figure 5), are submerged ribs that have emerged through the inner shell layers (Wilson 1970, fig. 32) to meet at the mid-line of the shell (Pojeta & Runnegar 1976, pl. 43, fig. 13).

Well preserved specimens of *Arceodomus* show that a series of longitudinal shelves produce a tortuous passage to the interior of the shell. The shelves suggest that a complex series of ciliary or tentacular sorters existed in the anterior aperture of *Arceodomus* and *Conocardium*. These probably selected and graded food before allowing it to enter the cave of the mantle cavity. Because the internal edges of the shelves are exposed parts of submerged ribs and therefore formed of outer shell layer, it is likely that the edge of the mantle followed the edges of the shelves for long distances inside the shell aperture. In addition, the elaborate anterior skeletal structures of *Arceodomus* and *Conocardium* blocked the only sizeable shell exit, and so these animals must also have been immobile.

Muscle insertions on many shells (figure 12) show that rostroconchs had a muscular foot, which in primitive forms was operated mainly by single anterior and posterior muscles inserted on the midline of the umbonal cavity (figure 12*h-j*). In advanced rostroconchs the pedal muscle insertions occur on each valve (figure 12*j, k*), and the foot probably operated like that

DESCRIPTION OF PLATE 2

Shell morphology of primitive rostroconchs and Cambrian monoplacophorans.

FIGURE 13. Anterior view of the exterior of *Ribeiria*. (Magn. $\times 6$.)

FIGURE 14. Oblique anterior view of an internal mould of *Heraultipegma*. (Magn. $\times 20$.)

FIGURES 15–17. Right lateral, anterior, and ventral views of an internal mould of *Ribeiria*, showing notch left by pegma (arrowed) and shell gape. (Magn. $\times 2$.)

FIGURE 18. Left lateral view of part of an internal mould of *Heraultipegma* to show pegma (arrowed). (Magn. $\times 60$.)

FIGURES 19–21. Oblique-anterior, posterodorsal, and anteroventral views of the quasioestroconch *Eotebenna*. (Magn. *ca.* $\times 50$.)

FIGURES 22 AND 23. Fragment of *Mellopegma* or *Heraultipegma* with preserved muscle insertion areas (arrowed; see also figure 12*g*) (magn. $\times 36$), and an enlargement of its surface (magn. $\times 170$), for comparison with figure 29.

FIGURES 24 AND 25. Dorsal and left lateral views of the parastroconch *Mellopegma*. (Magn. $\times 40$.)

FIGURES 26 AND 27. Dorsal and ventral views of *Myona?*, a link between the Rostroconchia and the Pelecypoda. (Magn. *ca.* $\times 20$.)

FIGURE 28. Dorsal view of the exterior of *Ribeiria* for comparison with figure 26. (Magn. $\times 7$.)

FIGURE 29. Enlargement of the surface of an internal mould of *Heraultipegma* (magn. $\times 400$), for comparison with figure 23.

FIGURES 30 AND 31. Enlargements of the exterior of the Cambrian monoplacophoran *Latouchella*, to show that the radial threads are constructed as stockades of spines. (Magns $\times 150$ and $\times 400$.)

of a pelecypod. These bilateral pedal muscles seem to be a secondary development, because *Pseudotechnophorus* has tiny vestigial median muscle insertions at the apex of the shell, in addition to much larger lateral muscle insertions (figure 12*k, l*).

Prominent pallial lines on some shells (figure 12*j*) indicate that all rostroconchs could retract the edges of their mantles, and the enlargement or retreat of these muscle insertions in the anterior region of some rostroconchs (figure 12*j*) suggests that protractible anterior extensions of mantle tissue may have been used for deposit feeding (figure 12*j, m*). Other forms, which have permanently closed anterior valve margins, or which were clearly epifaunal and immobile, were undoubtedly suspension feeders.

The relatively large anterior gaps of most rostroconchs, the minute posterior gaps of some, and the universal bilateral symmetry, point to an anterior mouth and a posterior anus. The existence of a large mantle cavity in all advanced rostroconchs suggest the existence of one or

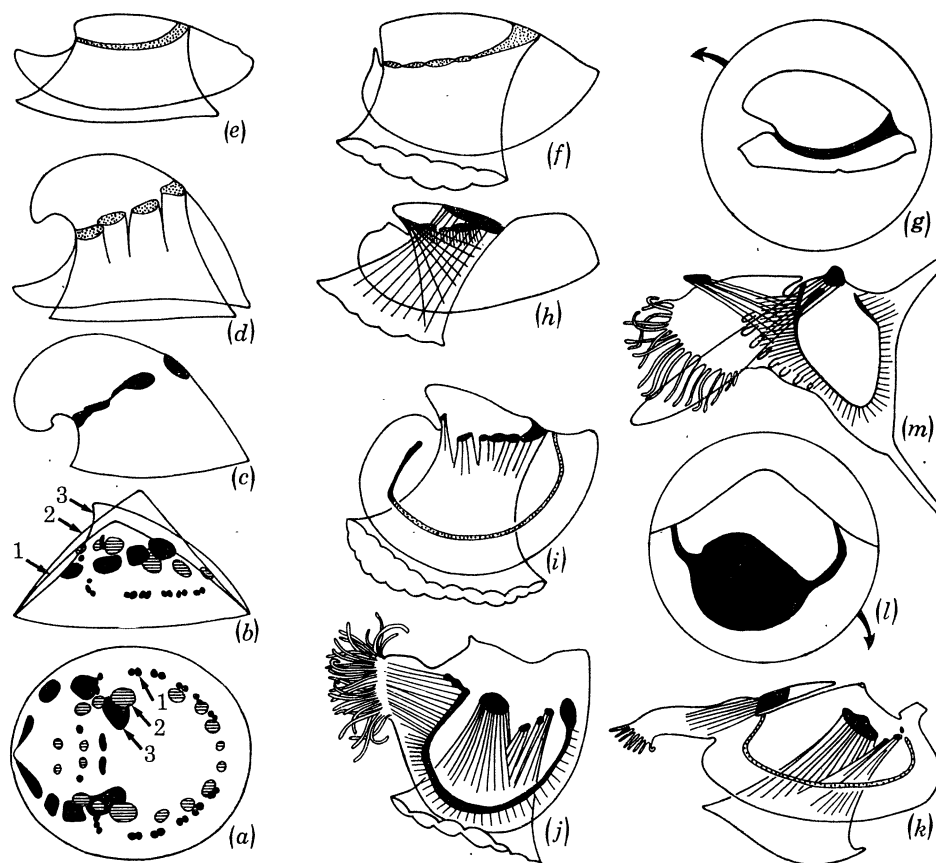


FIGURE 12. Reconstructions of parts of the anatomy of some fossil monoplacophorans (*a-e*), primitive rostroconchs (*f-i*), and advanced rostroconchs (*j-m*). All depict the animal removed from the shell. Muscle insertions observed on fossils are shown in black and horizontal shading; stippled muscle insertions are conjectural. Key: (*a*), (*b*) superimposed outlines of *Scenella* (1, Middle Cambrian), *Lenaella* (2, Early Ordovician), and *Nyuella* (3, Early Ordovician) to show how the ring of pedal muscle insertions moved inwards and upwards as the shells became taller and exogastrically curved (data from Runnegar & Pojeta 1974; Byalyy 1973; Rozov 1975); (*c*) the Devonian monoplacophoran *Cyrtionella*, which provides a model for the pedal musculature of *Latouchella* (data from Rollins 1969); (*d*) *Latouchella*, Middle Cambrian; (*e*) the parastroconch *Mellopegma*, Middle Cambrian; (*f*) *Heraultipegma*, the oldest known rostroconch, Early Cambrian; (*g*) *Mellopegma* or *Heraultipegma*, Middle Cambrian; (*h*), (*i*) two species of *Ribeiria*, Early Ordovician; (*j*) *Eopteria*, Early Ordovician; (*k*), (*l*) *Pseudotechnophorus* and an enlargement of its apical region, Early Ordovician; (*m*) *Hippocardia*, Devonian (data from Pojeta & Runnegar 1976; Runnegar & Jell 1976).

more pairs of laterally disposed gills, as does an interruption of laterally inserted pedal muscle bands in some primitive rostroconchs (figure 12*h*). These left and right gaps in the otherwise thin but continuous sheath of muscles surrounding the foot probably allowed blood vessels to run from left and right gills to the heart. If, as Pojeta & Runnegar (1976) have suggested, the scaphopods were derived from the rostroconchs, then rostroconchs probably had a radular apparatus.

Like other molluscs, rostroconchs had a shell composed of at least two main layers. To maintain similar shell proportions during life, the valves of all rostroconchs had to open slowly as the shell grew. Because the calcareous dorsal margin is relatively inflexible, various kinds of tensional fractures developed during growth and are visible either on the external surface (figure 9) or in sections of the shell (Pojeta & Runnegar 1976, pl. 31, fig. 1). These are analogous to the fractures that occur in the ligament of some pelecypods during growth of the shell. A detailed explanation of the nature and origin of these tensional fractures in rostroconchs is given in Pojeta & Runnegar (1976).

The oldest rostroconchs

Heraultipegma Pojeta & Runnegar, 1976 (= *Heraultia* Cobbold, 1935 non *Heraultia* Villeneuve, 1920; see figures 14 and 18) is the oldest known rostroconch. It occurs in the Early Cambrian of France (Müller 1975; Pojeta & Runnegar 1976); in the second oldest zone of the Tommotian (earliest Cambrian) in Siberia (Matthews & Missarzhevskiy 1975; Runnegar & Jell 1976); and in the earliest Cambrian of South Australia (Daily 1976; Daily, Firman, Forbes & Lindsay 1976, figs 7, 11*a*). It is one of the oldest shelly fossils known, and appears at or near the Cambrian–Precambrian boundary (Runnegar & Jell 1976).

In recent works, Morris (1967), Runnegar & Pojeta (1974), Pojeta & Runnegar (1976), and Runnegar & Jell (1976) have concluded that *Heraultipegma* is a primitive ribeirioid rostroconch, but Müller (1975) decided that it was probably a bradoriid arthropod. His evidence is: *Heraultipegma* exhibits sexual dimorphism; the steinkerns have a peculiar polygonal surface that would seem to be better related to an arthropod carapace rather than a molluscan shell; and no growth lines are visible on the few adhering shell pieces. I disagree with all three points. First, Müller's contoured diagram of length/height measurements of 1502 specimens does not convincingly demonstrate adult sexual dimorphism. Secondly, the unusual polygonal ornament of the steinkerns of *Heraultipegma* from France (figure 29) closely resembles a similar structure on a specimen of the related genus *Mellopegma*? from Australia (figure 23; Runnegar & Jell 1976, fig. 8); this Australian specimen has typical ribeirioid muscle insertions (figures 12*g* and 22). Thirdly, steinkerns of *Heraultipegma* often have comarginal rugae that reflect external growth lines. Also, *Heraultipegma* has the pegma of a primitive rostroconch (figure 18).

The youngest rostroconchs

The youngest rostroconchs so far discovered are probably *Pseudoconocardium licharewi* Zavadovskiy (Zavadovskiy 1960; Zavadovskiy *et al.* 1970) from the Khivachkiy (Khivach, Hivatch) horizon or suite of northeastern Siberia, *Bransonia oklahomensis* (Beede) (Newell 1940) from the Whitehorse Sandstone of Oklahoma, and undescribed specimens of *Bransonia truncata* (Fletcher) and '*Conocardium*' (Waterhouse 1967, p. 178) from the Flat Top Formation, Queensland, and the Wairaiiki Breccia, New Zealand, respectively. The first three occurrences may be approximately coeval (Stepanov 1973; Waterhouse 1976, pp. 58, 138, 149), and of late

Guadalupian or early Dzhulfian age (*sensu* Furnish 1973 and Spinosa, Furnish & Glenister 1975). The faunas in which they are contained are difficult to correlate, for they occur in vastly different biogeographic realms (Arctic, Tethyan, and Gondwanan), and in each case are the youngest fossiliferous horizons of the region.

The record of '*Conocardium*' from New Zealand is even more difficult to assess, for I have not seen the specimen, and the fossils with which it occurs are unusual. Waterhouse (1976, p. 174) considers the Wairaki Breccia to be Griesbachian (i.e. earliest Triassic of most authors). Force (1975) suggests that the unit spans the Permian–Triassic boundary, because it has yielded brachiopods (*Martiniopsis* and a 'mentzeliopsid') of both Permian and Triassic aspect. Thus the limited evidence available suggests that rostroconchs became extinct at or very close to the end of the Palaeozoic.

Diversity of rostroconch faunas

Very few rostroconchs have been recovered from Cambrian strata, but their fossil record spans the whole of the Period (figure 1). While all Cambrian rostroconchs are small and therefore inconspicuous as fossils (Runnegar & Jell 1976, fig. 5), it is likely that their known fossil record reflects their true abundance, for Cambrian rocks have been well examined in most parts of the world during the last one hundred years. Pelecypods have a similar Cambrian history (Pojeta 1978, this volume), and their delayed radiation is equally difficult to explain.

Like the pelecypods, rostroconchs radiated rapidly in the Ordovician (figure 1), but their greatest diversity was attained in the earliest Ordovician, before the massive Middle Ordovician radiation of the Pelecypoda (Pojeta 1971; Pojeta & Gilbert-Tomlinson 1977). The linear drop in rostroconch diversity through the remainder of the Ordovician (figure 1) is best explained as a response to increasing competition by the newly evolved and more efficient pelecypods.

Pojeta and I have been unable to provide accurate estimates of the number of species of Silurian, Devonian, and Carboniferous rostroconchs because we are not sufficiently familiar with the collections and literature from these periods. Rough calculations based on the number of described species in major monographs suggest that as many as 100 species of the five existing genera may have lived in Devonian time, but a similar analysis of Permian species suggests that the number of species existing at any one time in the Devonian may have been considerably less. However, the information available suggests that generic and familial diversity peaked in the Early Ordovician, and that species diversity peaked in the Devonian.

By the Middle Permian, only two closely related genera (*Bransonia* and *Pseudoconocardium*) were alive. As mentioned above, it is not clear whether either or both survived to the end of the period.

The size of rostroconchs

Early and Middle Cambrian rostroconchs were very small, 8 mm or less in length (Runnegar & Jell 1976, fig. 5). The late Cambrian forms are a little larger (Pojeta *et al.* 1977), and by the Ordovician, some genera (*Ribeiria* and *Myocaris*) had attained lengths of 60 mm. The largest rostroconchs are found in Carboniferous rocks in Ireland, where at least one individual grew to a length of 150 mm. All known Permian rostroconchs are smaller, with a maximum length of about 50 mm.

The ecology of rostroconchs

Some rostroconchs mimic pelecypods in shell form, others are vastly different (figure 1). Those that resemble pelecypods had adopted a variety of life styles, ranging from the mytiloid epifaunal suspension feeder *Euchasma* (figure 1, 19; Pojeta *et al.* 1977) to the *Lucina*-like infaunal deposit or suspension feeder *Ptychopegma* (figure 1, 15; Pojeta *et al.* 1977). The probable life orientations of most rostroconch genera are shown in figure 1.

Some rostroconchs such as *Technophorus* and *Arceodomus* could not have had a functional foot and were therefore immobile, but the former was a suspension feeder and the latter a deposit feeder. *Hippocardia* was another sessile deposit feeder, and it is probable that even the most active rostroconchs were sluggish burrowers that rarely moved about. For this reason, rostroconchs seem to have preferred quieter and more protected environments where they would not be dislodged during storms. They are most commonly found in offshore muds and carbonates (Pojeta & Runnegar 1976), often with brachiopods.

Rostroconch biogeography

Rostroconchs are too poorly known at present for any elaborate biogeographical analysis, but there is one striking feature of their distribution in space and time. In the Early Palaeozoic (Cambrian and Ordovician), rostroconchs were principally tropical and subtropical animals, and are mostly found within 30° of the palaeoequator (Pojeta 1979). The reverse is true in the Permian. Only one or two specimens of *Bransonia* were obtained from the vast quantities of New Mexican and Texan Permian tropical limestones that have been etched for silicified fossils (Newell *et al.* 1953; Cooper & Grant 1972), and rostroconchs are rare or absent from most equatorial Permian faunas.

By contrast, the cool-temperature non-carbonate sequences of the Permian of Australia and northeast Siberia yield rostroconchs at many localities, and in eastern Australia, most diverse Permian faunas contain one or more specimens of *Bransonia*. Thus the early record of the class probably lies in strata formed in the palaeotropics; its late history is to be found in ancient cold-temperature regions. Consequently, it is probable that if, like *Neopilina*, rostroconchs survived beyond their fossil record, they will be found in the stable, cold environment of the ocean floor or in its sedimentary products, if they are to be found at all.

ORIGIN OF THE ROSTROCONCHIA

Since rostroconchs are found in the oldest Cambrian shelly fossil horizons so far discovered, the class probably appeared in the latest Precambrian. While it is possible that a fossil record of that event may eventually be found, for the present it is necessary to use studies of the comparative anatomy of Cambrian and other molluscs to show how the class might have evolved (Runnegar & Pojeta 1974; Pojeta & Runnegar 1976; Runnegar & Jell 1976).

I follow Lang (1896), Fretter & Graham (1962), Stasek (1972), Trueman (1976), and many others in supposing that molluscs were derived from organisms resembling living flatworms or nemertines. The essential ingredient seems to have been the development of a dorsal exoskeleton, which provided protection, forced the development of lateral gills, and allowed the primitive dorso-ventral musculature to be emphasized to the detriment of the circular and longitudinal musculature. A historical record of the origin of this dorsal exoskeleton is preserved in the

cuticles, plates, girdles, and shells of living molluscs (Stasek & McWilliams 1973; Carter & Aller 1975), and it indicates the following sequence of events:

- (1) the development of a non-calcareous dorsal cuticle;
- (2) calcareous spicules are formed within the cuticle;
- (3) the spiculose cuticle is underplated by continuous shell layers;
- (4) the spicules are cemented to the outermost shell layer;
- (5) the spicules are lost, but their organic matrix remains as normal periostracum.

Clearly, until stage 3 is reached, the organisms will not be preserved as fossils, and stages 3 and 5 will appear similar in the fossil record. A number of Cambrian univalves (*Scenella*, *Helcionella*, *Latouchella*, *Yochelcionella* etc.) seem to have reached stage 4, for they are characteristically ornamented with fine radial threads that can be resolved into stockades of spines at high magnifications (figures 30 and 31). But the skeletal shape – and hence the shape of the organism – will also be controlled by the stage of development of the skeleton, and it is these geometric constraints that I wish to emphasize here.

Flatworms are flat primarily because they rely on epithelial respiration; the shape of their body maximizes its surface area. Once a dorsal cuticle developed, the reasons for remaining flat disappeared, and the organisms probably assumed a cabochon shape (Stasek 1972, fig. 1B, C). This form would be retained until a continuous calcareous skeleton developed.

The simplest shells to construct are presumably limpet-shaped cones with a circular aperture (Lison 1949; Carter 1967). They merely require the addition of increasingly larger diameter rings to the shell edge (Carter 1967). The Middle Cambrian monoplacophoran *Scenella* (figure 12a, b; Runnegar & Pojeta 1974, fig. 2; Pojeta & Runnegar 1976, fig. 10) has a shell of this type, and an anatomy so close to that of *Neopilina* that we can view both as little modified descendants of the most primitive shelled mollusc.

A more complex shell form is obtained if the rings added to the shell edge are wedge-shaped in lateral view, not rectangular (Carter 1967). This is a form seen in many Cambrian univalves, such as *Latouchella* (figure 1, –2), which probably evolved from a limpet-shaped ancestor. Such shells have a circular or nearly circular aperture (generating curve), but in other coeval forms, such as *Stenotheca* or *Anabarella* (figure 1, –1), the aperture has become elliptical and results in lateral compression of the whole of the shell.

From this stage, there is a clear gradation in shell form from *Stenotheca* and *Anabarella* through the quasioestroconch *Mellopegma*, to *Heraultipegma*, *Ribeiria*, and advanced rostroconchs (figure 12). Another line of descent leads from *Heraultipegma* via *Myona?* to the first pelecypod, *Fordilla* (Runnegar & Jell 1976; Pojeta 1978, this volume). Although some of these fossils are not found in the correct stratigraphic sequence, there is little doubt that the morphological continuum reflects a phylogenetic history; it is well supported by predictions made before the fossils were discovered (Harry 1969; Stasek 1972).

We can suppose that the spiculose, cabochon-shaped, earliest molluscs had a series of lateral gills and numerous dorsoventral muscles; these features are visible in *Neopilina*. When the shells became taller and curved, the numerous pedal muscles probably coalesced to form a ring (figure 12a–d), and with lateral compression became relatively enlarged at anterior and posterior ends of the shell (figure 12e–i). At the same time, the number of pairs of gills was reduced, possibly to a single pair. This anatomy was retained in primitive rostroconchs such as *Ribeiria* (figure 12h, i), and partly transferred to advanced rostroconchs (figure 12j–m), the Pelecypoda, and the Scaphopoda (Pojeta & Runnegar 1976). Its development was probably accompanied

by a fundamental change in living habits, from a life of surface grazing or deposit feeding to one in which the animals burrowed in and mined sediment or filtered sea water in search of food.

RELATIONS OF ROSTROCONCHS TO OTHER MOLLUSCS

Pelecypoda

Rostroconchs were undoubtedly the ancestors of the pelecypods (Runnegar & Pojeta 1974; Pojeta & Runnegar 1976; Runnegar & Jell 1976; Pojeta 1978), for they closely resemble early pelecypods, pre-date them, and were preadapted to exploit a truly bivalved shell. The single criterion that distinguishes the two classes at their point of departure is that rostroconchs never developed a totally bivalved shell. For this reason, *Myona? queenslandica* (figures 26 and 27) is placed within the Rostroconchia, though it undoubtedly functioned like a pelecypod.

The possibility always remains that rostroconchs evolved into pelecypods more than once, and it is tempting to homologize the prominent myophoric buttresses found in several Ordovician pelecypods (notably *Redonia* and *Nuculites*) with the pegma of ribeirioid rostroconchs. The apparent distinctiveness of several ancient lineages of pelecypods that appear suddenly in the Ordovician (Pojeta 1971) adds some credence to this possibility, but it must remain a matter for speculation until more Cambrian diasomes are found.

Scaphopoda

Runnegar & Pojeta (1974) and Pojeta & Runnegar (1976) suggested that scaphopods evolved from rostroconchs when the ventral shell edges of a primitive rostroconch fused to produce a tubular shell. They noted that intermediate forms were unlikely to be found, because once fusion occurred, the inevitable result would be an equidimensional (primitively circular) cross section. A possible rostroconch ancestor is *Pinnocaris* (figure 1, 10), which pre-dates the earliest known scaphopod and has a suitably elongate form. The argument is supported by the ontogeny of living scaphopods (see, for example, Fortey & Whittaker 1976, fig. 5); *Dentalium* starts its life with a tiny saddle-shaped shell which soon coalesces ventrally.

Just as some rostroconchs mimicked pelecypods, so others came to resemble scaphopods. The specialized genera *Conocardium* and *Arceodomus* (figure 1, 29, 30) were elongate infaunal animals that operated like scaphopods, but probably differed in having gills, in feeding in a different way, and in being less mobile.

Quasirostroconchs and parastroconchs

Higher taxa are recognized largely by hindsight, after sufficient evolution and diversification have produced a cohesive group of related organisms. Thus if the first pelecypod *Fordilla* had produced no progeny, it would probably be viewed as a bivalved rostroconch instead of the first of its class.

In the Cambrian and Early Ordovician, molluscs were experimenting with their newly acquired skeletons. A variety of peculiar forms evolved (Runnegar & Jell 1976; Fortey & Whittaker 1976). Some of these may have been functionally and even phylogenetically related to the Rostroconchia, but are now excluded from the class. Others such as *Mellopegma* (figure 1, 0) were on the main evolutionary line, but had not yet made the rostroconch grade. We can call the former quasirostroconchs and the latter parastroconchs.

The pararostroconchs have been discussed previously; they are true 'missing links', referable to either, both, or neither class. The quasioostroconchs are forms such as *Latouchella penecyrano*, *Yochelcionella*, *Eotebenna*, and possibly *Janospira* (figure 19; Runnegar & Jell 1976; Fortey & Whittaker 1976; Runnegar 1977), forms which can conveniently be retained in the Monoplacophora. Some, such as the two known species of *Eotebenna* (figures 19–21), have an effectively pseudobivalved shell. Others, such as *Yochelcionella ostentata* and *Janospira* have a tubular shell. They may have functioned like rostroconchs or scaphopods but are clearly related to more conventional Cambrian univalves such as *Latouchella* (Runnegar 1977), and should be regarded as a parallel development.

Theoretical rostroconchs

In a remarkable review of the phylogeny of the Mollusca, Stasek (1972) drew an uncannily accurate reconstruction of a ribeirioid rostroconch which he titled: 'hypothetical filter-feeding monoplacophoroid with undivided shell ancestral to the Bivalvia'. A similar organism was described but not illustrated by Harry (1969). Yonge (1953) obviously had much the same views when he discussed the origin of the pelecypods; he showed how lateral compression of a univalved shell resulted in a dorsal ligament, and suggested that the adductor muscles of pelecypods were secondarily acquired by cross-fusion of pallial muscles at the anterior and posterior ends of the shell.

All of these hypothetical rostroconchs differ in one important way from the real thing; they have multiple paired muscle insertions for the shell-attached muscles of the foot. This was a logical assumption in view of the anatomy of *Neopilina* and Early Ordovician pelecypods such as *Babinka* (McAlester 1965).

However, just as *Neopilina* confounded most theoreticians by having multiple gills, so *Ribeiria* and its relatives proved to be remarkably different, in one respect, from the expected form. With the considerable advantage of hindsight, the more complex evolutionary history of the pedal musculature (figure 12) is easy to understand. Moreover, it provides a clue to the problem of the apparently unreasonable complexity of *Neopilina*.

Morton & Yonge (1964, p. 31) have concluded: 'If it [*Neopilina*] does represent initial molluscan structure then this must have undergone great *secondary simplification* before giving rise to the remaining molluscan classes. Undoubtedly a, possibly *the*, major reason for the success of the phylum resides in the fundamental simplicity of structure which, the discovery of *Neopilina* reveals, may well have been secondary.' This secondary simplification seems to have occurred within the Helcionellacea, and it is probably that group which ultimately gave rise to the other classes of shelled molluscs (Runnegar & Jell 1976, fig. 4). It occurred because a taller shell eliminated at least some of the pseudometamerism of *Neopilina*, by reducing the number of gills, probably to a single pair, and by concentrating the pedal muscle insertions at anterior and posterior ends of the shell (figure 12*a, b*). Since well formed helcionellaceans are found in the oldest Cambrian beds, this secondary simplification, if it occurred, did so in the late Precambrian.

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Discussion

C. B. GOODHART (*University Museum of Zoology, Downing Street, Cambridge CB2 3EJ*). The pelecypods are the only molluscs known to lack a radula, and the good reasons for their having lost it would appear to apply equally to the supposedly similar way of life of the rostroconchs; scaphopods, however, still retain a typical molluscan radula. Could Dr Runnegar comment

upon this, in relation to his suggested derivation of the scaphopods, as well as the pelecypods, from rostroconch precursors?

B. RUNNEGAR. If, as Pojeta & Runnegar (1976) suggested, scaphopods were derived from the rostroconchs, then rostroconchs probably had a radular apparatus. However, the radula may have been lost in advanced forms.

E. L. YOCHELSON (*U.S. Geological Survey, E-501, Museum of Natural History, Washington, D.C. 20560, U.S.A.*). I concur that there was an extinct molluscan class-level taxon typified by *Ribeiria*, but I am uncertain that the Rostroconchia began in the Early Cambrian or occur in Middle Cambrian rocks; I am even more dubious of the morphological series of univalve shells of alleged Monoplacophora through which it is presumed to have been derived. The notion that the Rostroconchia may be the only extinct class of molluscs needs to be carefully considered; to encourage evaluation of this issue I ask three questions.

(1) On a philosophical basis, is it appropriate to ignore the presence of molluscan shell structure in a Permian species of hyolith in proposing Hyolitha as a new phylum (Runnegar *et al.* 1975), while assuming that Early Cambrian *Heraultipegma* was a mollusc, even though no shell – let alone any shell structure – is known, particularly when others (Missarkevsky 1974; Müller 1975) consider this genus a member of the Arthropoda?

(2) Because the Rostroconchia have a bilaterally symmetrical univalve shell and musculature similar to coiled Ordovician-age *Cyrtolites*, why not include all Rostroconchia within the Class Monoplacophora, particularly in view of the great diversity of shell shapes which Runnegar & Jell (1976) placed in that class?

(3) Following the Runnegar & Pojeta (1974) scheme of evolution: (1) Gastropoda appear in Early Cambrian, have no fossil record for a long geologic interval, and then diversify in Late Cambrian; (2) Pelecypoda appear in mid-Early Cambrian, have no fossil record for a long geologic interval and then diversify in the Early Ordovician; and (3) Rostroconchia appear in early Early Cambrian, have a poor fossil record – at best – for a long geological interval and then diversify in Late Cambrian. If this general statement is correct, two questions should be posed. What might account for the interval of poor to non-existent fossil record, particularly in view of subsequent abundance and diversity of these classes? What might be a triggering mechanism for radiation when it finally occurred?

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B. RUNNEGAR. In reply to Dr Yochelson's first question, it depends on one's concept of the phylum Mollusca. If one believes that all molluscs are descended from forms that had developed a dorsal exoskeleton, it is possible to exclude the Hyolitha from the phylum. The known muscle insertions of hyoliths suggest that their skeleton was not primitively dorsal (Runnegar *et al.* 1975). The reasons for considering *Heraultipegma* a mollusc and not an arthropod are given in the preceding text.

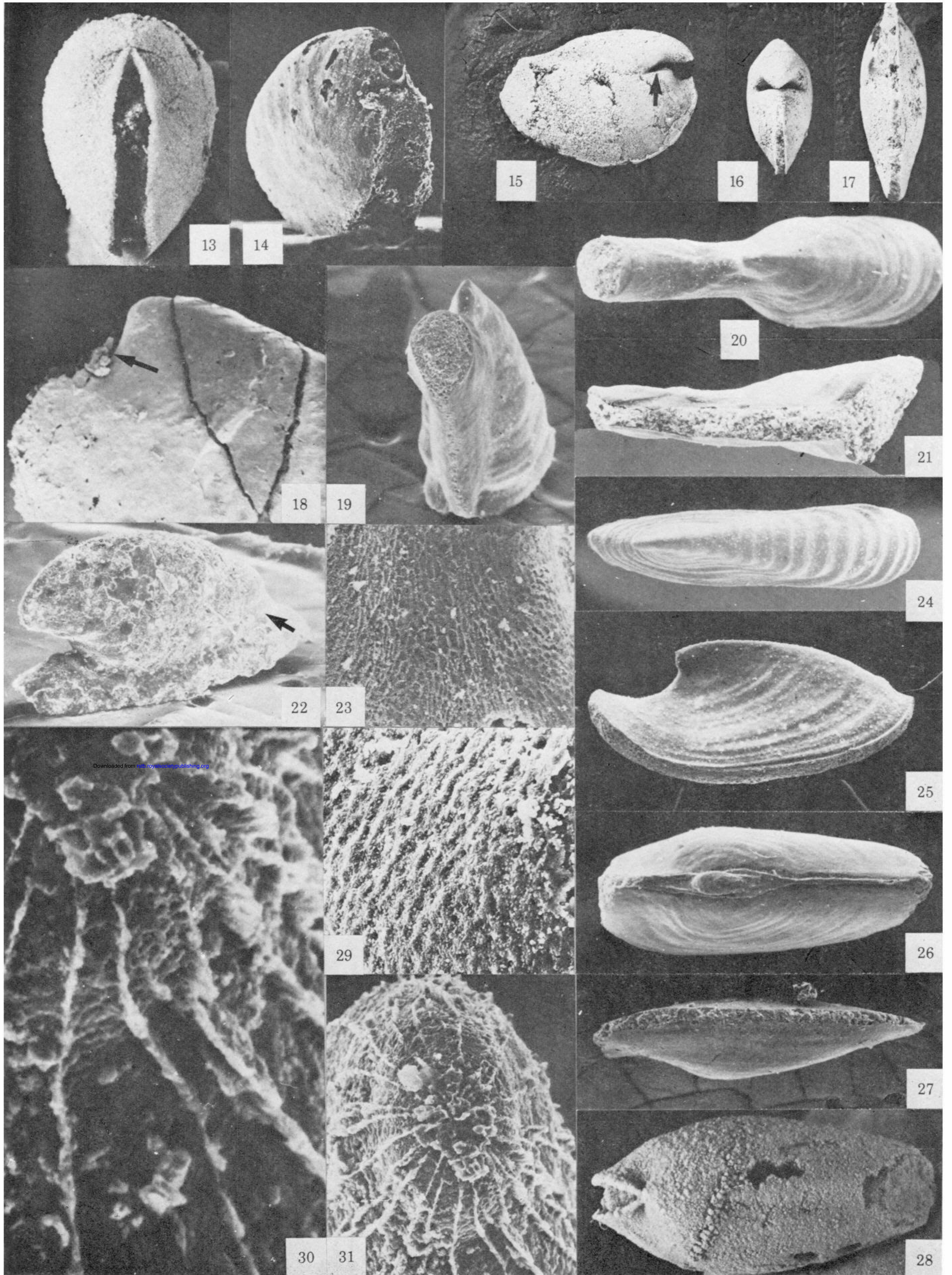
With regard to Dr Yochelson's second question, higher taxa are recognized largely by hindsight. For example, if *Fordilla* had produced no progeny, it would probably be classified as a

bivalved monoplacophoran rather than the first pelecypod. The rostroconchs are a cohesive group of molluscs that developed separately and differently from the Monoplacophora and for this reason are given class status. However, in the Early and Middle Cambrian, when the various molluscan classes were appearing, the distinctions between various groups are a little artificial.

The poor Middle and Late Cambrian fossil record of the Gastropoda, Pelecypoda and Rostroconchia, mentioned in Dr Yochelson's third question, is difficult to explain. Possibly more fossils of these groups will be found when more microfossils are extracted from Cambrian rocks. So far, most work has concentrated on the earliest Cambrian because of problems associated with the identification of the boundary between the Precambrian and the Cambrian.



FIGURES 2–11. For description see opposite.



FIGURES 13-31. For description see opposite.