Rostroconchia: A New Class of Bivalved Mollusks

Abstract. *Four Paleozoic bivalved genera are assigned to the new molluscan class Rostroconchia:* Eopteria, Euchasma, Conocardium, *and* Pseudoconocardium. *These mollusks have an uncoiled univalved larval shell; an untorted bivalved adult shell; no hinge teeth, ligament, or adductor muscles; and a fused, almost inflexible, hinge. Rostroconchians developed separately from the pelecypods through the ribeirioids, but are regarded as more closely related to the Pelecypoda and Scaphopoda than to other known classes of mollusks.*

The existence of bivalved gastropods (*1*) and pelecypods indicates that the bivalved condition arose independently in different molluscan classes; we conclude that *Conocardium* and its allies form another class of mollusks which independently developed two valves (*2*) and elevate Cox's pelecypod order Rostrochonchia (*3*) to class status.

The shell of rostroconchians consists of two equal valves (Fig. 1) each growing in a logarithmic helical spiral. As in other motile bivalved animals in which the midsagittal plane passes between the valves, the fused junction hinge ventral. The shape of the shell dorsal and the margin opposite the hinge ventral. The shape of the shell and the symmetry of the musculature (Fig. 2) show that rostroconchians had not undergone torsion. The tubelike rostrum (Fig. 1, E and F) probably functioned as a siphon supplying water to the gills and is regarded as posterior. The opposite end of the shell usually has a permanent gape comparable to the pedal apertures of other mollusks (Fig. 1D).

In the Ordovician genera *Eopteria* and *Euchasma* the posterior rostrum and anterior gape are rudimentary (Fig. 3, B, K, and L), and they have a set of prominent commissural denticles (Fig. 3, B, G, and I) at one end of the shell that are homologous with similar denticles at the anterior end of *Conocardium* (Fig. 1D). In addition to the anterior gape and the tubular rostrum, all well-preserved specimens of *Conocardium* have a small third aperture in the commissure (Fig. 1E); this may have functioned as an outlet for pseudofeces. Some species of *Conocardium* possess a unique hood at the posterior carinas (Fig. 1, B and C); this large vesiculated structure is formed of two thin walls filled with closely spaced concave lamellae.

Rostroconchians have no beaks because the bivalved condition is preceded by a univalved cap-shaped larval shell situated between the umbos of the bivalved juvenile shell (Fig. 3D). This protoconch is destroyed during growth as the umbos enroll.

The outer shell layer is not continuous across the hinge area, and the valves are secondarily fused by prograding of the inner shell layer anterior to the crests of the umbos. This anterior hinge is structurally different from a paravincular pelecypod ligament in which both the lamellar and fibrous layers are continuous from one valve to the other (*4*). We regard the anterior and posterior hinge margins of *Conocardium* as fused equivalents of the embayments found at each end of the pelecypod hinge (*5*). Nonetheless, the anterior hinge margin of rostroconchians is functionally equivalent to a prosodetic ligament because it formed a slightly flexible structure about which the valves rotated during growth (*6*). Folding along the hinge axis results from growth and increases gradually from the anterior hinge margin to the umbos, with the anterior dorsal margin being deformed elastically or plastically as growth proceeds; occasionally the anterior hinge ruptures (Fig. 1A).

Because the anterior dorsal margin of rostroconchians is the hinge axis, the posterior dorsal margin must have compensated for valve rotation in another way. Well-preserved specimens of *Conocardium* have a series of symmetrical fractures posterior to the umbos (Fig. 1E) which resulted from the periodic failure of the shell along the dorsal

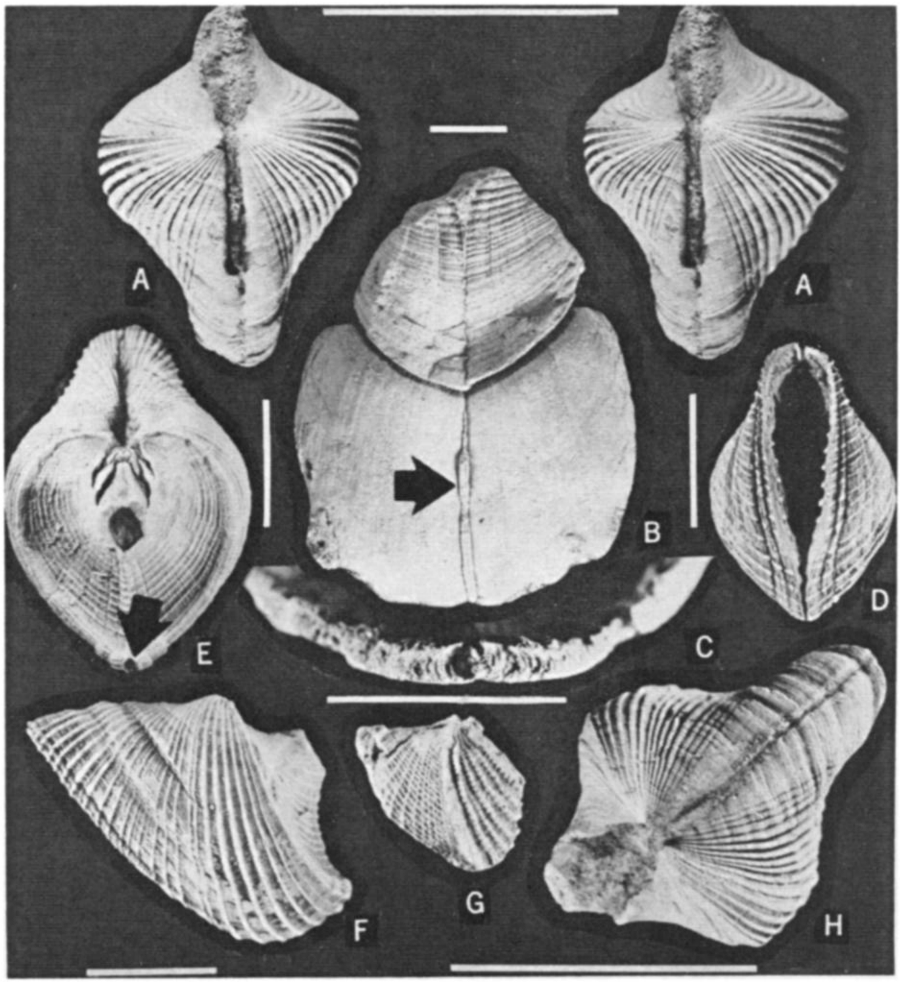

Fig. 1. Devonian (A to C and H) and Pennsylvanian (D to G) species of *Conocardium*. (A) Stereopair of a unique specimen showing a fracture of the anterior hinge. (B) Third aperture prolonged as a tube running the length of the hood (arrow). (C) Third aperture in cross section. (D) Anterior gape and denticles. (E) Posterior rostrum, rostral fractures, and third aperture (arrow). (F and G) Left side views showing rostrum. (H) Dorsal view showing prosodetic hinge (*20*). Bars equal 1 cm.

midline of the rostrum. These cannot be ligament grooves (*4*) because the dorsal margin is fused below them and there was no way for them to be connected to the secretory mantle tissue. Rotational growth periodically split the rostrum in two, the damage being repaired by the deposition of a new block of the inner shell layer. There are two kinds of rostral fractures, symmetrical longitudinal fractures resulting from the splitting of the rostrum and transverse fractures caused by rotation of the rostrum within the commissural plane (Fig. 1E).

Some rostrochonchians have complex anterior shell structures. *Euchasma* has an apertural plate attached to both valves which blocks the anterior gape (Fig. 3E). Some species of *Conocardium* have the anterior gape subdivided by a series of longitudinal shelves (*7*).

Bilaterally symmetrical muscle scars consisting of a nonpitted pallial line and accessory muscle pairs along the dorsal part of each valve are known in *Conocardium* and *Eopteria* (Fig. 2). As with pelecypods, the pallial line represents the site of attachment of the radial mantle muscles to the shell. The remaining muscles retracted the foot or attached the visceral mass to the shell. Only in *Eopteria* is there any suggestion of the hypertrophy of the pallial muscles (Fig. 2C); at the posterodorsal terminus of the pallial line there is a large muscle scar. The fact that the pallial line does not cross either hinge area suggests that the large posterior muscle of *Eopteria* is a fortuitously placed shell muscle and not an adductor; also, it supports our belief that the anterior and posterior hinge margins of rostroconchians result from secondary fusion of the anterior and posterior shell embayments. It is generally accepted that the adductor muscles of pelecypods arose by local cross fusion and hypertrophy of the pallial muscles where these came in contact in the mantle embayments (*5*). If the pallial muscles do not cross the shell embayments there can be no cross fusion of their fibers to form adductor muscles attached to both valves. Thus, rostroconchians lacked adductor muscles. The absence of a ligament or diductor muscles to oppose adductors also supports our interpretation.

Although the class Rostroconchia is quite diverse, at present all species are assigned to only four genera: *Eopteria, Euchasma, Conocardium*, and *Pseudoconocardium*. Consequently, studies of functional morphology and modes of life must be largely autecological. The gross paleoecology of the five best-known examples is discussed. (i) Forms similar to *Conocardium rostratum* (*4*) and *C. langenheimi* (*7*). The tubular nature of these species, with openings at either end, suggests they are reasonable functional analogs of scaphopods. The complexity of the anterior end, which is partly occluded by a series of horizontal shelves, and the small diameter of the rostrum suggest that both feeding and locomotion occurred at the anterior end of the animal. These species may have been ciliary deposit feeders using structures comparable to the palp proboscises of paleotaxodont pelecypods or the captacula of scaphopods to obtain their food. The posterior rostrum would have had an entirely respiratory function accommodating both inhalant and exhalant currents. Animals of this type could only be stable in an infaunal position with the anterior end down and the tip of the rostrum near the sediment-water interface. (ii) Animals like *C. lanterna* (Fig. 1, D to F) have a large anterior gape and it has been suggested that they lived epifaunally attached by a byssus (*8*). In our opinion the large anterior gape indicates a large foot and a mobile infaunal animal. In other respects forms of this type would have lived similarly to forms given in (i). (iii) Some euchasmas have a broad flat anteroventral surface which places the umbonal ridges essentially at the anterior end (Fig. 3, F to H); this gives them a strong external resemblance to epifaunal mytilid, ambonychiid, and dreissenid pelecypods. Probably these euchasmas lived in a similar manner, epifaunally attached to the substrate by a structure comparable to the byssus of pelecypods. (iv) Other euchasmas have a distinct anterior projection, the anterior end is not so flat, and the umbonal ridges are not the anteriormost part of the shell (Fig. 3, J to L) (*9*). These forms were probably partially buried in the sediment to about the depth of the umbonal ridges, attaching to the substrate by a byssus-like structure. It is likely that they lived in a semi-infaunal manner comparable to various mytilid, cyrtodontid, and pinnid pelecypods. Probably all euchasmas were ciliary suspension feeders. (v) The laterally compressed shell of *Eopteria* (Fig. 3, A to C) (*9*) with anterior, posterior, and ventral gapes would only have been stable in an infaunal position. The sinus in the anterior part of the pallial line (Fig. 2C) implies that the mantle or some other structure in the area was capable of extension and withdrawal and could have been used for deposit feeding.

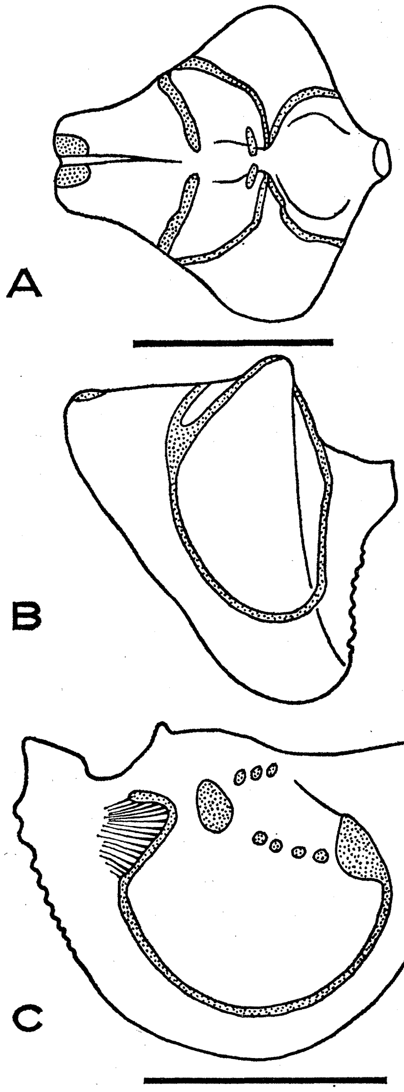

Fig. 2. Drawings, made from internal molds, showing muscle insertion areas (stippled). (A and B) Dorsal and left side views of *Conocardium*. (C) Left side view of *Eopteria*; the protuberance near the middle of the dorsal side is the filling of the protoconch. Bars equal 1 cm.

Rostroconchians were solitary, presumably acephalous animals with a calcareous exoskeleton enlarged by additive deposition from an enclosing mantle. Other features showing their molluscan affinities are their size, bilateral symmetry, ornament, musculature, the nature of the muscle insertion areas, and the shell microstructure (*10*). In shell form and in the nature of their bilateral symmetry they are most similar to pelecypods; basic differences include the univalved larval stage, the ankylosed hinge, and the unique musculature of rostroconchians. Bivalved gastropods have a coiled univalved larval shell (*1*), but it is asymmetrical and confined to one valve and the effects of torsion are clearly visible in the asymmetry of the shell musculature (*11*) although the valves are similar in convexity and size. The remaining group of bivalved mollusks is the class Stenothecoida (*2*) whose members have asymmetrical valves with obvious beaks and show no affinities to the Rostroconchia.

The molluscan classes Pelecypoda, Scaphopoda, and Rostroconchia are related. Each is composed of bilaterally symmetrical acephalous forms whose shell is formed by lateral growth and calcification of a pair of symmetrical lobes of the mantle (*12*). In the Pelecypoda a flexible ligament develops between the two lobes, and in the Scaphopoda the lobes fuse ventrally, producing a tubular shell (*13*); the rostroconchians are intermediate between these end-members in that they have the two-part shell but do not develop a ligament.

A likely ancestor for all three groups is the Cambrian and Ordovician Ribeirioida, which is composed of small bean-shaped animals having a simple folded shell with gapes along the anterior, ventral, and posterior margins (*14*). Ribeirioids have long been referred to the Arthropoda (*15*), but are now believed to be mollusks (*14*) because they have well-defined and impressed muscle scars of the molluscan type (*16*). They have two nonpaired oval muscle scars (anterior and posterior), on the dorsal midline of the shell, connected by a nonpitted pallial line (*17*). Early rostroconchians (*Eopteria*) resemble ribeirioids in having a simple laterally compressed shell with narrow permanent commissural gapes, obscure umbos, a central cone-shaped protoconch, and marginal denticles (Fig. 3, A to C). However, the musculature is significantly more complex in *Eopteria* (Fig. 2C) and is developed symmetrically in each valve.

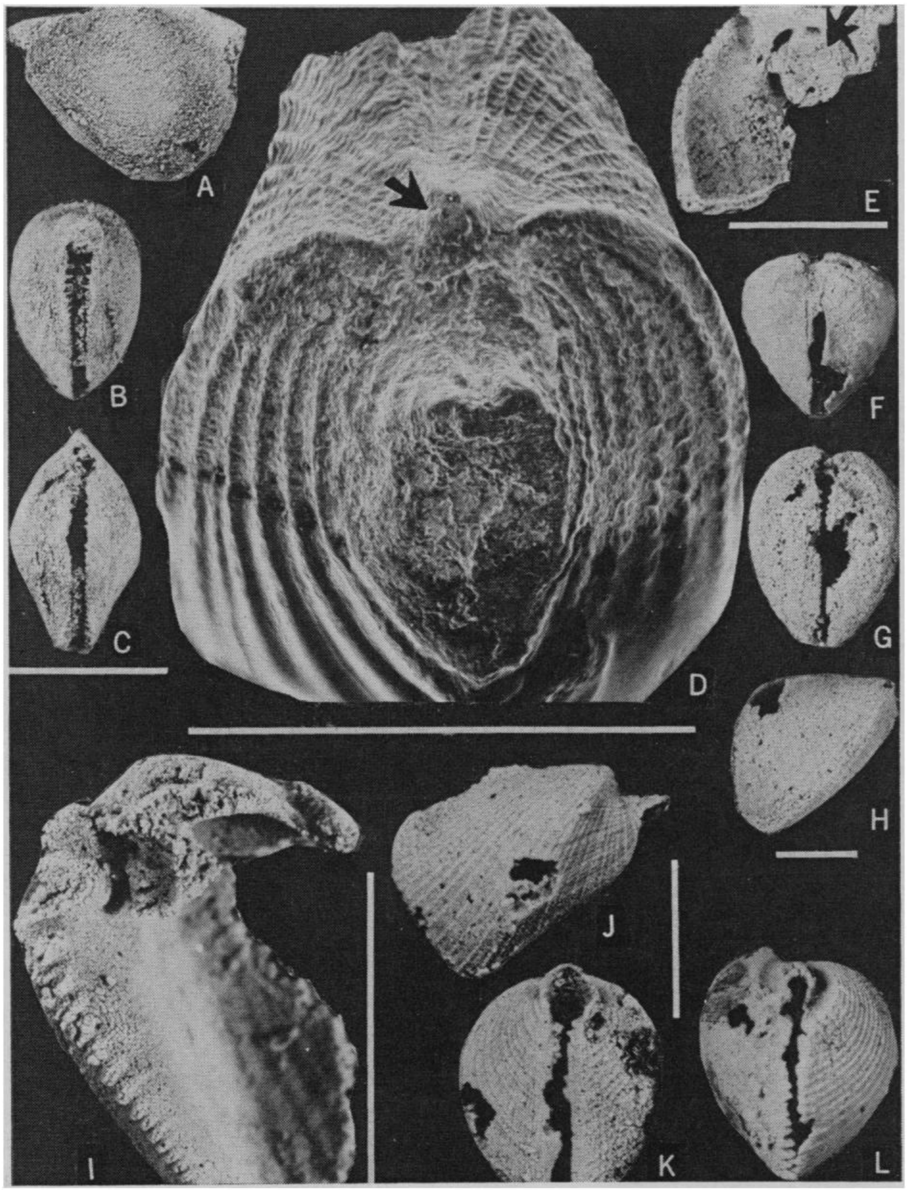

Fig. 3. (A to C) Left side, anterior, and ventral views of *Eopteria*. (D) Scanning electron micrograph of *Conocardium* showing the univalved protoconch (arrow). (E) Apertural plate of *Euchasma* (arrow). (F to H) Dorsal, anterior, and right side views of *Euchasma*. (I) *Euchasma* showing denticulate margin. (J to L) Right side, anterior, and posterior views of *Euchasma* (*20*). The bar for D is equal to 2.5 mm; all other bars equal 1 cm.

Many recent accounts of the origin of the Pelecypoda have emphasized the close similarity of the accessory musculature of early pelecypods, such as *Babinka*, to the multiple shell muscles of monoplacophorans (*14, 18*) and have concluded that such early pelecypods are morphologically and phylogenetically intermediate between younger genera and a monoplacophoran ancestor. Most authors also assume a polyphyletic origin of the Pelecypoda. As noted above it seems likely that the ribeirioids were ancestral to the three acephalous molluscan classes and that they represent the transitional group between an as yet unidentified univalve and the Rostroconchia, Pelecypoda, and Scaphopoda. These four groups had a common ancestor and did not arise independently from the archetypical mollusk.

The new class Rostroconchia Pojeta, Runnegar, Morris, and Newell may be diagnosed as follows: mollusks having an uncoiled univalved larval shell; an untorted bivalved adult shell; no hinge teeth, ligament, or adductor muscles; and a fused, almost inflexible, hinge; Early Ordovician–Late Permian (*4, 14, 19*).

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Heat Capacity of Superconducting Ternary Molybdenum Sulfides

Abstract. *The heat capacities of $AgMo_4S_5$, $PbMo_6S_7$, and $SnMo_5S_6$ are reported. These ternary molybdenum sulfides have been found to be bulk superconductors with very large values of electronic heat capacity coefficients and very low values of Debye temperatures.*

Recently a number of new ternary sulfides have been synthesized (*1*), some of which were found to be superconducting, with reasonably high transition temperatures (*2*). We report here preliminary heat capacities of a few of these molybdenum sulfides. The results are interesting in that for these compounds the electronic heat capacity coefficients, γ, are very high, whereas the Debye temperatures, θ_D, are very low. These sulfides have also been found to be bulk superconductors.

The compounds were prepared by reacting appropriate quantities of the high-purity elements at ~ 1150°C for a day or so. Samples for heat capacity measurements weighing 3 to 5 mg each were prepared by pressing the powders into thin disks and resintering them at 1150°C for a day. Measurements were made by the a-c heat capacity technique (*3*) between 4.2° and 20°K.

Results for the silver, lead, and tin molybdenum sulfides are given in Table 1. For comparison, literature values for a few elements, a few compounds with the β-tungsten structure, and two layered compounds based on TaS_2 are also given. The γ and θ_D values were deduced from the plots of heat capacity C divided by the absolute temperature T versus T^2, which were found to be linear up to ~ 15°K; beyond ~ 15°K θ_D seemed to increase by a few percent.

The $\Delta C/\gamma T_c$ value for $AgMo_4S_5$, which showed a sharp anomaly at the critical temperature T_c, is very close to the Bardeen-Cooper-Schrieffer value of 1.43. The quantity $\Delta C/\gamma T_c$ was not evaluated for the lead and tin compounds, which showed broad superconducting transitions as a result of sample inhomogeneity. The values of γ for these ternary molybdenum sulfides are comparable to or even higher than those of some of the β-tungsten compounds with high T_c values, whereas their Debye temperatures are very much

Table 1. Heat capacities.

Element or compound	γ		θ_D (°K)		$\frac{\Delta C}{\gamma T_c}$	T_c (°K)		Reference
	mj $°K^{-2}$ g-mole^{-1}	mj $°K^{-2}$ g-atom^{-1}	θ calculated from specific heat per gram-mole	θ calculated from specific heat per gram-atom		T_c onset from specific heat data	T_c from magnetic data	
Mo	1.8	1.8	460	460		0.92		(*4*)
$AgMo_4S_5$	98	9.8	64	139	1.5	11.5*	8.3	
$PbMo_6S_7$	353	25.2	79	190		10.6	11.1	
$SnMo_5S_6$	316	26.4	81	186		10.9	10.9	
Nb	7.8	7.8	277	277		9.17		(*4*)
Nb_3Sn	52	13	164	260	2.4	18.0		(*5*)
Nb_3Al	30	7.5	290	460	2.4	18.6		(*6*)
V	9.9	9.9	399	399		5.37		(*4*)
V_3Si	68	17.0	440	700	1.5	16.9		(*7*)
V_3Ga	97.2	24.3	190	302	1.6	14.8		(*7*)
Ta	6.0	6.0	258	258		4.39		(*4*)
TaS_2	8.5	2.83	174	251	1.43	0.8		(*8*)
TaS_2-(2,6-dimethyl pyridine)$_{1/5}$	9.5		106		0.65	2.8		(*8*)
TaS_2-(pyridine)$_{1/2}$	8.9		98		0.80	3.7		(*8*)

* The high value for the $AgMo_4S_5$ sample is caused by contamination during the copper-plating procedure used in mounting samples for specific heat measurements.