MOLLUSCAN PHYLOGENY[*]

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CONTENTS

ABSTRACT

Mollusks are likely descendants of turbellarian-like flatworms and have probably never been segmented. The first mollusks were probably spiculose and lacked a shell; thus, it seems reasonable to regard the Aplacophora as direct descendants of these first mollusks and not as a degenerate group that has lost the shell. A shell probably evolved twice in mollusks, once in the multivalved polyplacophorans and once in the univalved monoplacophorans. The bivalved pelecypods are likely descendants of the univalves. The class Monoplacophora is probably ancestral to the Gastropoda, Cephalopoda, and Rostroconchia. In turn, rostroconchs probably gave rise to the Scaphopoda and Pelecypoda. Possible fossil ancestors of the cephalopods, rostroconchs, pelecypods, and scaphopods are documented and figured.

INTRODUCTION

Because no single soft- or hard-part character, or combination of a relatively few characters, is common to all mollusks, it is not possible to frame a succinct morphological definition of the phylum Mollusca as can be done for such phyla as the Echinodermata and Chordata. Nevertheless, I am convinced that the concept Mollusca is not just a name for a grade of morphological organization achieved by various unrelated invertebrates; on the contrary, I feel that it can be demonstrated that the phylum Mollusca is a phylogenetic entity of great antiquity. Mollusks are unified by morphological gradations between the different forms, by embryological similarities, and by information deduced from fossils of the likely evolutionary history of the various classes assigned to the phylum.

Cuvier (1797) gave the first approximation of what a mollusk is, and natural historians have been refining his concept since that time. For neontologists, this refinement meant elimination of the ascidians, brachiopods, and cirripeds from the concept Mollusca. For paleontologists, it meant adding the monoplacophorans and rostroconchs, and as far as I am concerned it meant eliminating the hyoliths from the phylum (Runnegar et al., 1975; Marek and Yochelson, 1976; and Runnegar, in press a).

Some high level taxa of mollusks still may be unrecognized as such in the fossil record, but in my opinion, *Matthevia* Walcott (Yochelson, 1966; Runnegar et al., 1979) is probably a polyplacophoran; xenoconchs (Shimansky, 1963) may be parts of the internal skeleton of cephalopods; solenoconchs (Starobogatov, 1974) are a heterogeneous assemblage of mollusks and non-mollusks, whose only character in common is an elongate shell (Pojeta and Runnegar, 1979); and too little is known about stenothecoids to determine whether or not they are mollusks (Yochelson, 1968, 1969; Aksarina, 1968; Runnegar and Jell, in press).

Neontologists have long been impressed by morphological gradations between the different forms of living mollusks. In 1883, (p. 634), Lankester proposed the schematic mollusk or archimollusk "in order to exhibit concisely the peculiarities of organization which characterize the Mollusca. . ." This idea has since been elaborated into the con-
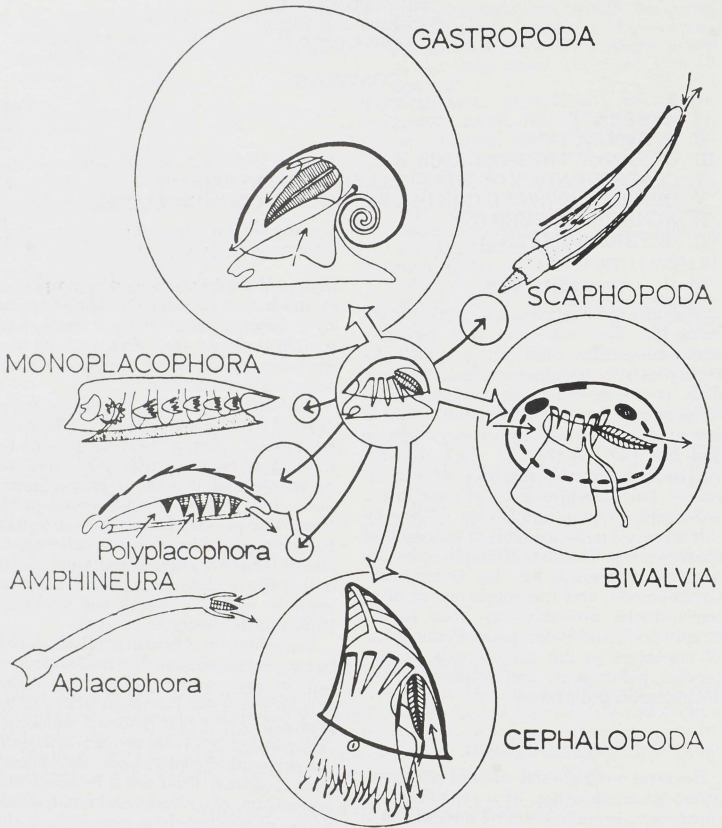

Figure 1. Suggested origins of the various classes of living mollusks from the HAM. Circles suggest the relative size and significance of each class. From Morton, 1967, p. 21, published with the permission of the author.

cept of the hypothetical ancestral mollusk (HAM). The HAM was conceived through the study of the comparative anatomy of living mollusks and has proved to be very useful, partly because assumed knowledge of the common ancestor of mollusks provides a definition of the phylum. The HAM is basically a least common denominator of all structures regarded as primitive in the various classes of extant shelled mollusks.

Zoologists ordinarily consider each molluscan class to have evolved independently from the HAM (Figure 1). This means that the archetype must have existed from the late Precambrian to at least the late Middle Ordovician, periodically taking on a new shell form to become a new class of mollusks (Yochelson, 1978b). This evolutionary strategy seems most unlikely, and the idea flies in the face of principles of the evolution of

higher taxa as determined from the study of fossil vertebrates. Almost all illustrations of the HAM show it as having a univalved shell. Such a condition requires that aplacophorans be considered degenerate mollusks, which have lost their shell. It seems more reasonable to follow Scheltema's (1978) view that characteristic molluscan structures evolved in the aplacophorans independently of a shell. Accordingly, the relatively simple morphology and anatomy of aplacophorans may be considered primitive rather than degenerate, and an alternative picture of molluscan higher level phylogeny emerges.

A recent explanation of what the HAM looked like (Figure 2) was given by Yonge (1976). His figure shows an animal that has a univalved limpet-shaped shell, multiple pedal retractor muscles, with the mouth and anus widely separated at opposite ends of the shell. Such a creation is effectively a monoplacophoran, and if it were found as a fossil, it would be so classified.

Several zoologists have advised caution about the use of the HAM as central to an understanding of molluscan evolution. Sta-

sek (1972) noted that at best the HAM is only a convenient tool for teaching the comparative morphology of mollusks. Morton (1967, p. 14) pointed out the danger of using the HAM to define Mollusca as well as the problems raised by thinking of the HAM as a reasonable reconstruction of the ancestral mollusk when he wrote: "The danger is that in mixing geneological ideas with morphology our archetype may become like an heraldic animal — a lowest common multiple of incompatible organs." Although it was formerly a useful concept, it now seems likely that the HAM is no longer a necessary device for understanding molluscan evolution.

Another approach to understanding molluscan evolution is to consider how one class of mollusks may have arisen from a preexisting class. This approach concentrates on the study of Cambrian and Ordovician mollusks because all classes were in existence by the end of the Middle Ordovician (Pojeta and Runnegar, 1976, 1979; Runnegar et al., 1979), and it requires a search for forms that are intermediate in morphology between recognized molluscan classes. The
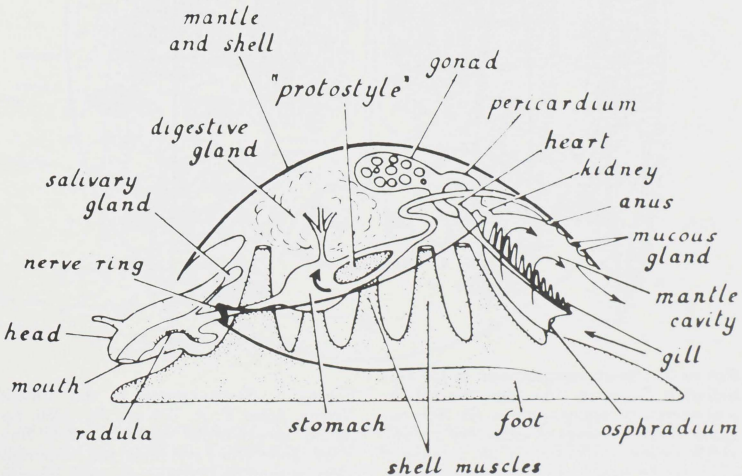

Figure 2. Reconstruction of the HAM. From C. M. Yonge, 1976, The nature of mollusks, *in* C. M. Yonge and T. E. Thompson, Living marine mollusks; London, William Collins Sons and Co., Ltd., p. 25, published with the permission of the author.

finding of fossils that are reasonably placed stratigraphically and morphologically intermediate between classes has proved to be remarkably successful in developing an understanding of the origin of higher level groups of vertebrates. We have morphological intermediates between several classes of mollusks that I believe are as significant for understanding molluscan phylogeny as *Archaeopteryx* and *Eusthenopteron* are for understanding the pathways of vertebrate phylogeny. It seems unlikely that molluscan ". . . classes begin abruptly by major mutations of larval forms which opened new environmental niches" as suggested by Yochelson (1978a, p. 10; 1978b, p. 166, 186; 1979, p. 323). Implicit in this point of view is that changes that take place in larvae cannot be preserved in the fossil record. Secretion of a skeleton in mollusks ordinarily begins early in ontogeny; even if all class level differences were due to neotony, when the zygotes formed by fusion of the gametes contain the hereditary information necessary to produce an individual having a skeleton, the changes could be preserved in the fossil record.

ORIGIN OF THE MOLLUSCA

At present, it seems likely that the Precambrian ancestor of mollusks was a small ciliated wormlike organism without a coelom. This organism showed pseudometamerism in having a serial repetition of some organ systems along the length of the body, but it was without transverse septa subdividing the body into segments and lacked numerical correlation of the various organ systems. Thus, the number of diges-
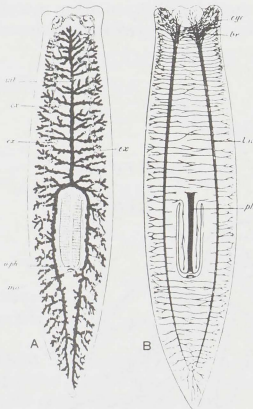

Figure 3. Pseudosegmentation in the turbellarian *Planaria*. (A) Digestive (black) and excretory (open) systems. (B) Nervous system. *ex*, openings of excretory system; *int*, intestine; *mo*, mouth; *o. ph*, opening of pharynx; *br*, brain; *eye*, eye; *l. ne*, longitudinal nerve; *ph*, pharynx. From T. J. Parker, and W. A. Haswell, 1961, A Textbook of Zoology, p. 220, published by permission of Macmillan, London and Basingstoke.
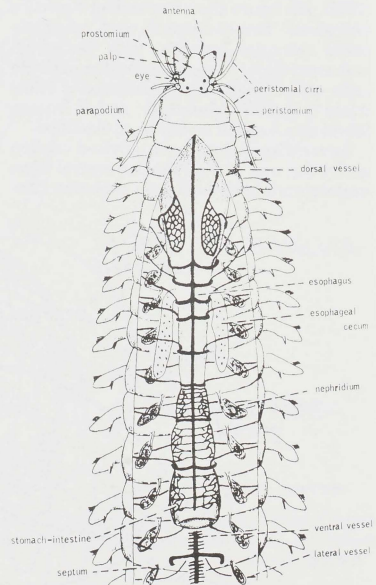

Figure 4. Segmentation in the annelid *Nereis*. After F. A. Brown, Jr., 1950, Selected invertebrate types, p. 273, New York, John Wiley and Sons, Inc., copyright 1950, as modified by Barnes, 1963, Invertebrate zoology, p. 173, Philadelphia, W. B. Saunders Co. Published with the permission of John Wiley and Sons, Inc., and W. B. Saunders Co.

tive diverticula did not correspond to the number of lateral nerve branches or to the number of protonephridia. I believe that this ancestor of mollusks was probably most like living turbellarian flatworms (Figure 3).

It now seems unlikely that mollusks ever possessed metamerism in the sense that this feature is seen in annelid worms; these worms have a body composed of repeated segments separated one from another by septa, several of the organ systems being numerically correlated and occurring in each segment. The embryological and larval similarities between mollusks and annelids probably reflect their origins in a common ancestor, which was a pseudo-segmented turbellarian-like flatworm. Annelids developed segmentation (Figure 4),
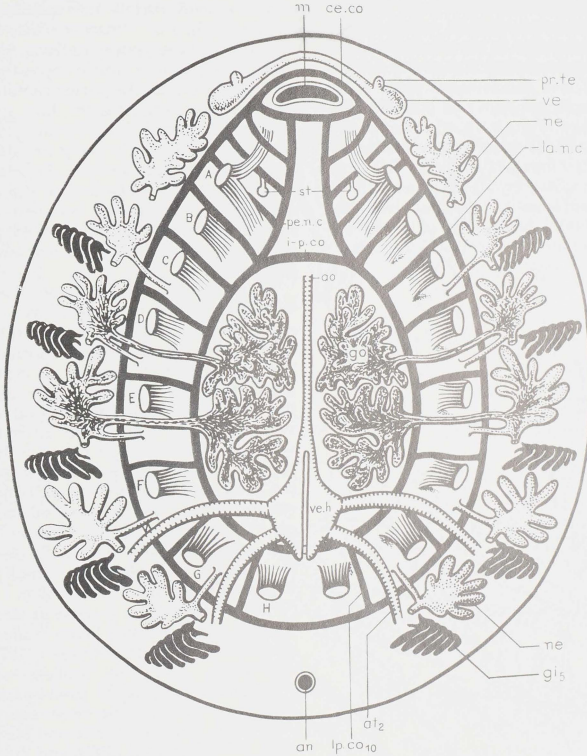

Figure 5. Pseudosegmentation in the monoplacophoran _Neopilina. A-H_, pedal retractors; _an_, anus; _ao_, aorta; _at2_, second atrium of heart; _ce. co_, cerebral commissure; _gis_, fifth gill; _go_, gonads; _i-p. co_, interpedal commissure; _la. n. c_, lateral nerve cord; _lp. co10_, tenth lateropedal connective; _m_, mouth; _ne_, nephridia; _pe. n. c_, pedal nerve cord; _pr. te_, preoral tentacle; _st_, statocyst; _ve_, velum; _ve. h_, ventricle. From Henning Lemche, and K. G. Wingstrand, 1959, The anatomy of _Neopilina galatheae_ Lemche, 1957: Galathea Rept., v. 3, plate 54, published with the permission of K. G. Wingstrand and Torben Wolft, editor of Galathea Reports.

whereas in mollusks numerical correlation of the organ systems did not evolve, although some mollusks retained well-defined pseudosegmentation (Figure 5).

Stasek (1972) explained how a turbellarian-like animal could evolve into a mollusk. He pointed out that most of the features that distinguish mollusks could have arisen as the result of a single evolutionary accomplishment, which was the secretion of a mucoid cuticle over the dorsal body wall surface. The dorsal body-wall surface secreting the cuticle could be considered the primitive mantle. Secretion of aragonitic spicules embedded in a cuticle takes place in the primitive aplacophoran and polyplacophoran mollusks (Figure 6), and similar aragonitic spicules (Figure 7) occur in the body wall of some living turbellarian flatworms (Rieger and Sterrer, 1975). It seems likely that the primitive molluscan skeleton was spiculose and not composed of layered calcium carbonate. Allison (1975) described a
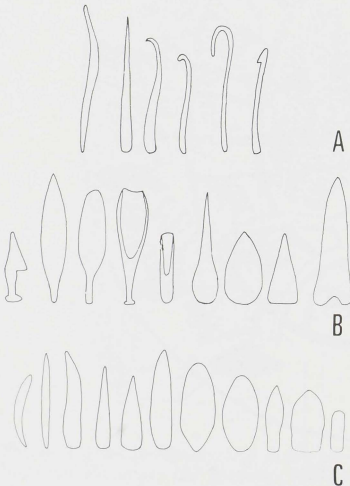
Figure 6. Outline drawings of spicules of some living mollusks. Shapes in rows A and B are found in aplacophorans. Shapes in row C occur in polyplacophorans. Spicules in these classes are generally small to microscopic, but reach a length of 4 mm in aplacophorans and 10 mm in polyplacophorans (Hyman, 1967, p. 17, 79).

possible turbellarian flatworm from what she considered to be Precambrian rocks in Alaska, but Cloud *et al.* (1976) suggested that her specimen was a hexactinellid sponge spicule.

Cuticular spicules may have been cemented together subsequently by the outer layer of the primitive ostracum as in some pelecypods (Aller, 1974; Carter and Aller, 1975), or the ostracum may have been secreted entirely below the spicule-bearing cuticle (Figure 8). Whatever way the layered calcium carbonate shell was formed, it raised the spiculose cuticle above the dorsal body wall forming the periostracum. Of necessity, the periostracum has since remained thin because it is in contact with the secretory mantle only along the shell edge in the periostracal groove. The tendency has been for mollusks to lose the spicular skeleton, but it is fully retained in aplacophorans, partially retained in polyplacophorans, and is found in a few pelecypods (Figure 8).

At the stage in the evolution of mollusks when the mantle and the shell were present and when these became extended as eaves beyond the edge of the body, a mantle cavity was formed (Figure 9), in which gills could develop. The eaves also separated the body into a ventral foot and a dorsal visceral mass. Gills would have to form when the shell evolved because the latter process would decrease the surface area of the body wall available for epithelial respiration. When gills had evolved, body size could be increased. Most Early and Middle Cambrian mollusks are small; major size increases in all shelled classes took place in the Late Cambrian or Ordovician.

This much of the molluscan story is deduced primarily from living mollusks, and much of it is based on Stasek's (1972) work. However, from the earliest Cambrian (Tommotian) onward, shell-bearing mollusks are known in the fossil record (Rozanov *et al.*, 1969; Matthews and Missarzhevsky, 1975; Qian *et al.*, 1979; and Yü, 1979). In my opinion, these fossils, as well as Middle and Late Cambrian mollusks, tell us much about the probable origins of cephalopods, pelecypods, rostroconchs, and scaphopods and allow us to make reasonable deductions about the origins of polyplacophorans, gastropods, and monoplacophorans. The conclusions based on fossils are discussed next in the systematic section.

CLASSIFICATION OF THE MOLLUSCA
USED HEREIN

Phylum **MOLLUSCA** Cuvier, 1797

Subphylum **AMPHINEURA** von Ihering, 1876
  Class **APLACOPHORA** von Ihering, 1876
  Class **POLYPLACOPHORA** de Blainville, 1816

Subphylum **CYRTOSOMA** Runnegar and Pojeta, 1974

  Class **MONOPLACOPHORA** Knight, 1952
  Class **GASTROPODA** Cuvier, 1797
  Class **CEPHALOPODA** Cuvier, 1797

Subphylum **DIASOMA** Runnegar and Pojeta, 1974
  Class **ROSTROCONCHIA** Pojeta, Runnegar, Morris, and Newell 1972
  Class **PELECYPODA** Goldfuss, 1820
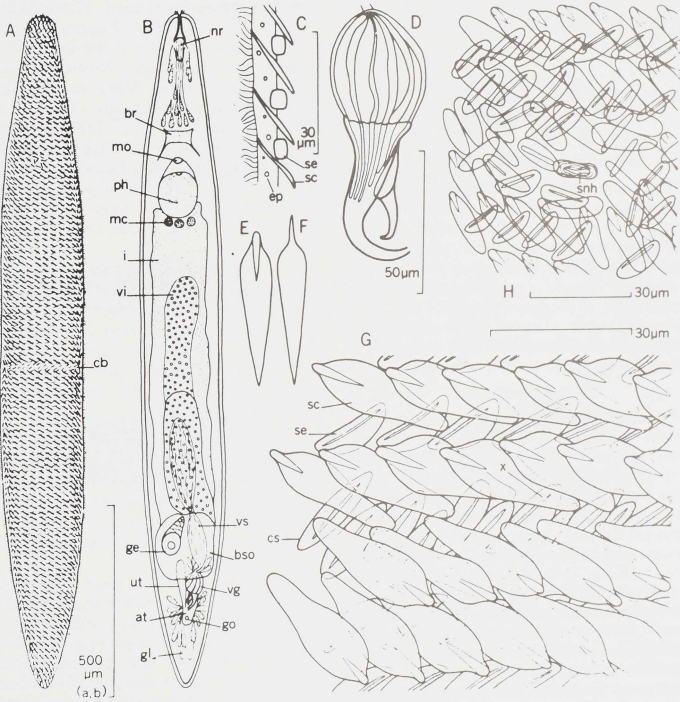 Class **SCAPHOPODA** Bronn, 1862

Figure 7. Spicules in the living turbellarian *Florianella bipolaris* Rieger and Sterrer. From R. M. Rieger, and Wolfgang Sterrer, 1975, Sonderbruck aus Z. f. zool. Systematik u. Evolutionforschung, v. 13, no. 3, p. 209. Published with the permission of the Publishing House of Paul Parey, Hamburg 1, Spitalerstrasse 12, West Germany, which owns the copyright.

A   B   C   D   E

▨ tanned periostracum   ▢ cuticular mucoid complex
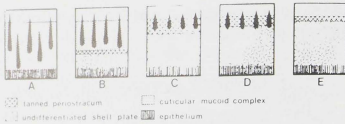⸪ undifferentiated shell plate ▦ epithelium

Figure 8. Organization of cuticle and shell in some living mollusks. (A) Aplacophora; (B) Polyplacophora; (C) Some Pelecypoda; (D) Some Pelecypoda; (E) Most Pelecypoda. Black teardrop-shaped objects are spicules. From J. G. Carter, and R. C. Aller, 1975, Lethaia, v. 8, p. 318, published with the permission of the senior author and the editors of Lethaia.

ORIGIN AND EVOLUTION OF THE HIGHER TAXA OF MOLLUSKS

Subphylum AMPHINEURA

The subphylum Amphineura contains those mollusks in which the primitive spicular skeleton embedded in a cuticle has remained prominent, and is composed of the classes Aplacophora and Polyplacophora. In addition to having spicules embedded in a cuticle as a prominent part of the exoskeleton, these classes show anatomical similarities (Hyman, 1967) and both lack a veliger larval stage in their ontogeny.

Class Aplacophora

Aplacophorans (Figure 10) have a radula, a style sac, a mantle cavity, and various other soft-part features that indicate that they are mollusks (Scheltema, 1978). They have the simplest morphology of any living mollusk, and if one does not use the HAM concept, they can be considered a primitive group rather than a degenerate one. Scheltema (1978), Salvini-Plawen (1975), and Beedham and Trueman (1968) regarded a-placophorans as primitive mollusks. Scheltema (1978, p. 108) noted that they had evolved several molluscan structures independent of a shell. Salvini-Plawen (1969) preferred to divide the Aplacophora into two taxa of class rank.

The first mollusks probably were similar to aplacophorans in having a spiculose cuticle prior to the evolution of the shell. A-placophorans can be regarded as the living descendants of these early mollusks, which

were intermediate between turbellarian-like flatworms and shelled mollusks. The aplacophorans are the only surviving group of mollusks whose ancestors never secreted a shell and thus give insight into what the ancestral mollusk may have looked like — a vermiform spiculose animal with a mucoid cuticle. Beedham and Trueman (1968) indicated that the aplacophorans lack a shell because the cuticle is not hardened by quinone-tanned protein and thus cannot act as a semiconducting membrane for the deposition of calcium salts in crystalline layers.

Unfortunately, aplacophorans have no unequivocal fossil record. Nierstrasz and Stork (1940, pl. 3, fig. 55; Figure 11A herein) figured some spicules of the living species *Uncimenia neapolitana* Nierstrasz, which have a cane shape. More or less similar cane-shaped spicules are known from Ordovician rocks (Figure 11B); these have been placed in the genus *Ptiloncodus* Harris and to date have been found only in phosphatic residues. The spicules of apalcophorans have a variety of characteristic shapes (Figure 6A-B) and could be preserved as fossils.

I propose that there are three descendant groups from the spiculose ancestral mollusk: (1) the aplacophorans themselves, (2) the polyplacophorans, and (3) the monoplacophorans. These three groups have had long separate histories and are related to one another only at the very base of the molluscan stem.

Class Polyplacophora

The idea that polyplacophorans are an early offshoot in molluscan history and that they have an origin separate from that of the rest of the shell-bearing mollusks is supported by several lines of evidence, including the following:

(1) Polyplacophorans have a multivalved shell (Figure 12). All other shelled mollusks can be traced back to a primitive univalved condition, but there is no known paleontological evidence that polyplacophorans ever had a single valved shelled ancestor. Embryological evidence suggests that the original number of valves may have been seven (Hyman, 1967), and one species from the Ordovician, *Septemchiton vermiformis* (Bergenhayn, 1955) has only seven valves. The valves of chitons may have originated as enlarged spicules (Runnegar et al., 1979)

or spicules may have been cemented together to form the valves. Haas and Kriesten (1977) noted that the long girdle spines of the living chiton *Acanthopleura granulata* (Gmelin) develop from a single cell which divides to form a "regular lime secreting epithelium" (p. 11). This process differs from that in aplacophorans, where each

body wall spicule is produced by a single cell. In polyplacophorans, a number of cells cooperate to produce spicules, and such cytological integration in the mantle produces the valves of polyplacophorans and the shell in other shell-bearing mollusks.

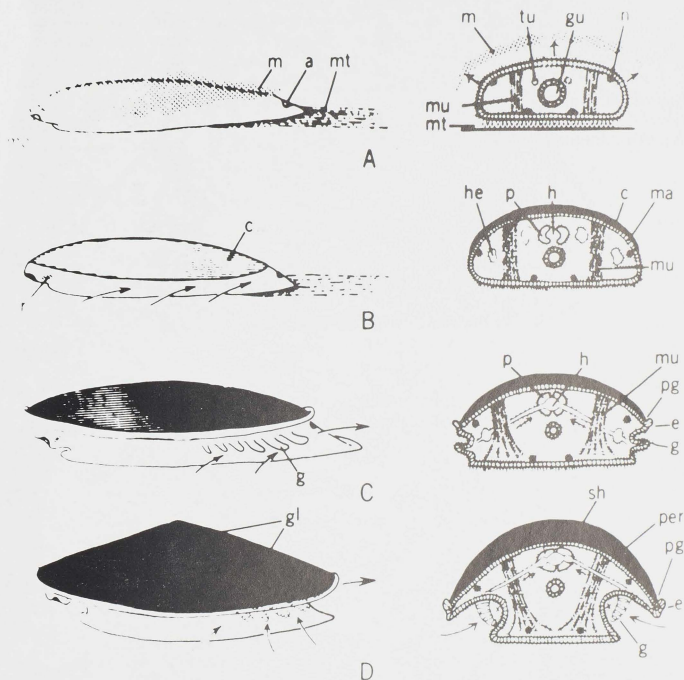(2) Stasek (1972) noted that the polyplacophoran shell layer known as the articula-

Figure 9. Four stages in the establishment of the molluscan framework from a turbellariform organism, all shown in lateral and cross-sectional views. (A) Proposed ancestral form with a complete gut and ability to secrete mucous as a protective measure and as a locomotory track. (B) Transitional turbellariform stage with radula and cuticle. (C) Transitional molluscan stage with gills contained in an incipient mantle cavity underlying eaves of the mantle. (D) Advanced molluscan stage with calcified cuticle and folded gills. *a*, anus; *c*, cuticle; *e*, eaves of mantle; *g*, gills; *gl*, growth lines; *gu*, gut; *h*, heart; *he*, hemocoelic sinuses; *m*, mucous covering; *ma*, mantle; *mo*, mouth; *mt*, mucous track; *mu*, dorsoventral muscles; *n*, longitudinal nerve cords; *p*, pericardium; *pg*, periostracal groove; *r*, radula; *sh*, shell; *tu*, gonoducal tubercles. From C. R. Stasek, 1972, The molluscan framework, *in* v. 7, Mollusca, Marcel Florkin, and B. T. Scheer, eds. Chemical Zoology; New York, Academic Press, p. 6. Published with the permission of the author and the publisher.
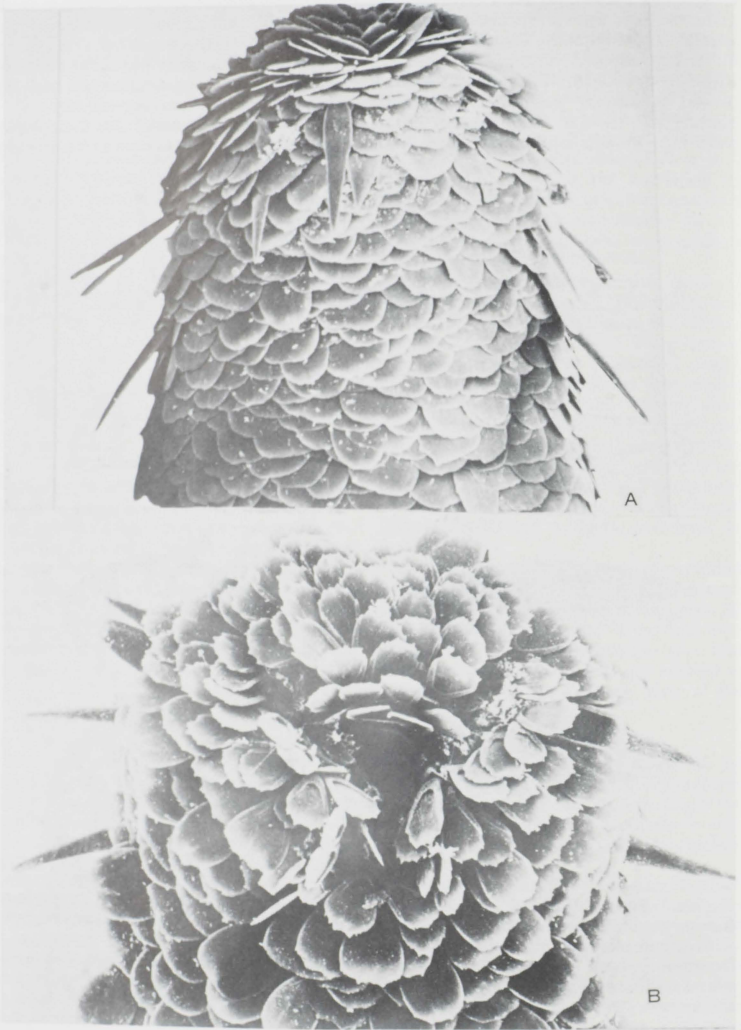
Figure 10. Unnamed interstitial aplacophoran from Friday Harbor, San Juan Island, Washington. (A) Dorsal view of head, ×700. (B) Ventral view of head, ×750. Photographs courtesy of M. P. Morse, Northeastern University. Museum of Comparative Zoology (MCZ), Harvard University 92177, 72977.

mentum, which is present in advanced poly-placophorans and forms the insertion plates and anterior prongs, evolved after the chitons were already a differentiated molluscan lineage. I also have observed that the Cambrian and Ordovician chitons *Matthevia* Walcott and *Chelodes* Davidson and King lack the articulamentum. This indicates that the articulamentum is not homologous with the inner shell layer of the shells of other mollusks. The vesicular structure of the shell of the Late Cambrian chiton *Matthevia* (Figure 13) is very different from the layered calcium carbonate typical of the shell structure of other shell-bearing mollusks. Beedham and Trueman (1967) suggested
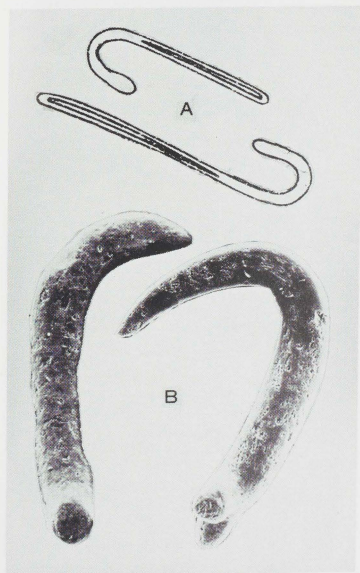
Figure 11. (A) Cane-shaped spicules of the aplacophoran *Uncimenia neapolitana* Nierstrasz, magnification unknown, from Nierstrasz and Stork, 1940, pl. 3, fig. 55. (B) Cane-shaped bodies named *Ptiloncodus simplex* R. W. Harris, from Middle Ordovician (Whiterockian) of Nevada, ×125. Specimens kindly provided by A. G. Harris, U. S. Geological Survey. U. S. National Museum of Natural History (USNM) 298722, 298723.

homologies between the shell layers of polyplacophorans and other shell-bearing mollusks, but in the light of the paleontological evidence their suggested homologies should be reappraised.

(3) Chitons have an inner and outer cuticle. The outer cuticle is on the girdle, and embedded in it are spicules. The outer cuticle contains mucoid material and is similar in many respects to the cuticle of aplacophorans. The inner cuticle may act like a semiconducting membrane in the deposition of the shell valves (Beedham and Trueman, 1967, 1968).

(4) There is still debate about how to compare the mantle margin of chitons with that of other mollusks (Beedham and Trueman, 1967).

(5) The shell surface of such Late Cambrian chitons as *Matthevia* and *Preacanthochiton* Bergenhayn (Figure 14) is covered with tubercles or granules; this feature suggests that the valves may have originally been secreted as spicules, which were later cemented together.

Thus, it seems likely that chitons evolved from a spiculose aplacophoran-like ancestor. It is only at this stage that they have a common ancestry with the Monoplacophora; monoplacophorans appear to be the likely ancestors of all other shell-bearing mollusks.

The Late Cambrian chiton *Matthevia* Walcott has been the subject of controversy in recent years because this genus was made the sole representative of a supposed extinct class of mollusks (Yochelson, 1966, 1978b). This point of view now seems unlikely (Runnegar *et al.*, 1979).

The reconstruction of *Matthevia* that I favor is shown in Figure 15. It seems likely that *Matthevia* was a high subtidal to intertidal scraper of stromatolites, as it is found mainly in stromatolitic carbonate rocks sometimes associated with high-relief domal stromatolites (Runnegar *et al.*, 1979).

The reconstruction of *Matthevia* proposed by Yochelson (1966) (Figure 16 herein) seems unlikely for the following reasons:

(1) The type suite of the type species of the genus, *M. variabilis* Walcott, contains valves having three different shapes, but all have the same ornament (Runnegar *et al.*, 1979); all three types should be incorporated in a reconstruction, but only two types were available to Yochelson in 1966.

(2) In Yochelson's preferred reconstruction (Figure 16 herein), there is not only a space between the valves for a foot to protrude ventrally, but also a space between the valves dorsally (Figure 17C). Such a dorsal opening would not have allowed the shell to protect the animal.

(3) The embayed side of *Matthevia* valves has one or two deep holes, which are interpreted as muscle insertions (Figure 17A-B). In Yochelson's preferred reconstruction (Figure 16), there seems to be no way for the muscles to function. If the muscles extended in a straight line from the insertion to the visceral hump, once they contracted there is no obvious antagonist, such as another muscle or a ligament, to stretch them out again; although they could conceivably be stretched again in some hydrostatic manner. If the muscles extended from the insertions into the foot they would have to go through a high-angle bend, and in most animals, muscles do not undergo such a sharp bend. However, more important than the high-angle bend is that once muscles in this position contracted, the apices of
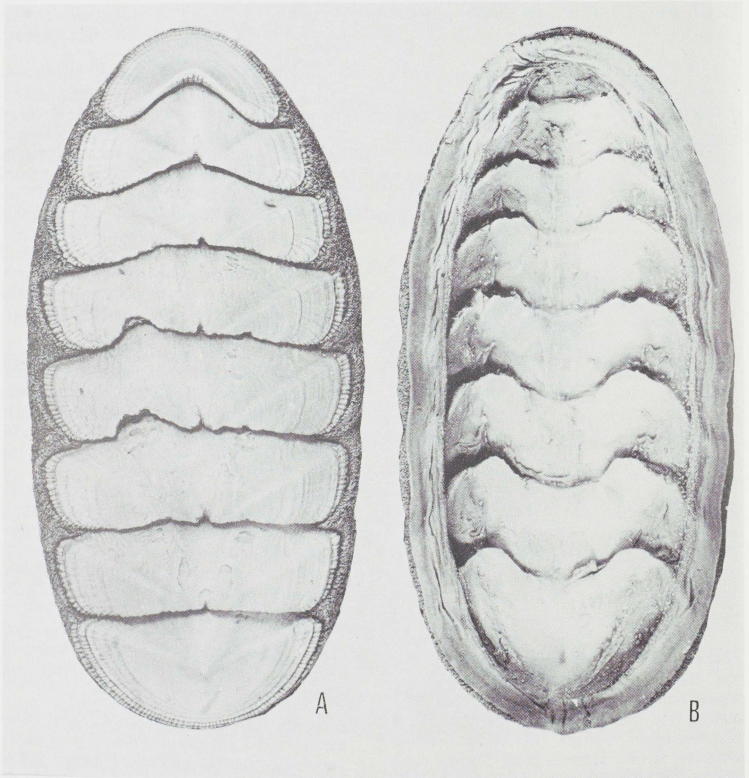

Figure 12. Dorsal exterior (A) and interior (B) views of the living polyplacophoran *Stenoplax conspicua* Carpenter, ×1.5, USNM (Division of mollusks) 172894.

the valves would turn upward and expose the ventral soft parts.

(4) The shell shapes of the terminal and intermediate valves of the undoubted Ordovician chiton *Chelodes* closely resemble the shapes of the intermediate and posterior valves of *Matthevia* in the interpretation of Runnegar *et al.*, (1979).

(5) Yochelson (1978b, p. 175) made the comment ". . . no polyplacophoran has more than one muscle insertion per plate . . ." This observation is contradicted by the known musculature of living polyplacophorans (Figure 18 herein, and Sampson, 1895).

(6) Yochelson's (1966, p. B7) concern about the weight of *Matthevia* valves is obviated by their vesicular shell microstructure (Figure 13), which would have considerably reduced the weight of the valves; more than two could have been carried on the dorsal side.

CONCHIFERA

It is in the remaining six classes of mollusks that I see molluscan missing links equivalent in importance to *Archaeopteryx*

and *Eusthenopteron* in determining lines of descent. Ultimately, these six classes of mollusks descended from the Monoplacophora, and they are sometimes united in the subphylum Conchifera (Salvini-Plawen, 1969, 1975). I prefer to place the six classes in two subphyla, the Cyrtosoma and the Diasoma (Runnegar and Pojeta, 1974; Pojeta and Runnegar, 1976).

The Cyrtosoma includes the classes Monoplacophora, Gastropoda, and Cephalopoda, or the ancestral conchiferan radical

Figure 14. (A) *Matthevia variabilis* Walcott, lateral view of intermediate valve showing tubercles. Upper Cambrian, Hoyt Limestone Member, Theresa Formation (Trempealeauan), near Saratoga Springs, New York, ×4, USNM 258994. (B) *Preacanthochiton cooperi* Bergenhayn, external mold of intermediate valve showing tuberculate ornament. Upper Cambrian Eminence Dolomite (Trempealeauan), about 8 km south of Potosi, Missouri, ×8, USNM 259004.
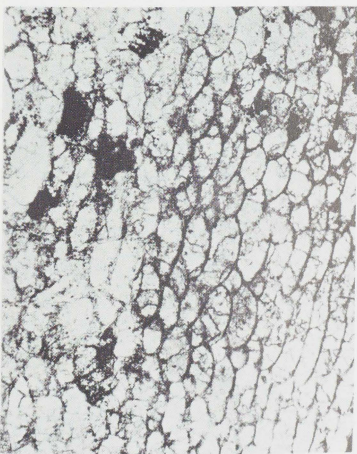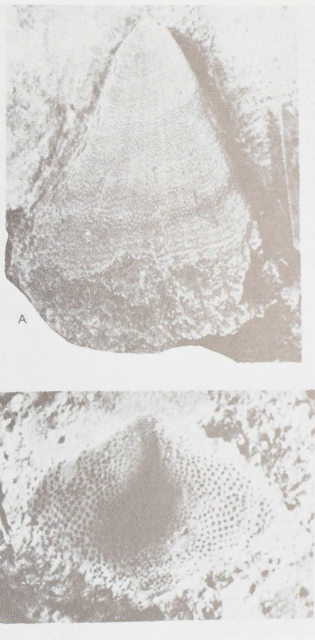

Figure 13. Vesicular microstructure of the Late Cambrian polyplacophoran *Matthevia variabilis* Walcott, Hoyt Limestone Member, Theresa Formation (Trempealeauan), near Saratoga Springs, New York, ×38, USNM 24598.

and the two classes of mollusks that develop a bent or twisted gut. The Diasoma includes the classes Rostroconchia, Pelecypoda, and Scaphopoda or those conchiferan classes in which the gut is neither bent nor twisted. More importantly, the diasome classes are placed together because the Rostroconchia is the likely ancestor of the Pelecypoda and the Scaphopoda. Thus, in the subphylum Diasoma, the classes Pelecypoda and Scaphopoda are not direct descendants of the Monoplacophora.

The cyrtosomes are the ancestors of the diasomes, and both of these subphyla appeared and began to diversify within a few million years in the Early Cambrian. Because all cyrtosomes and diasomes are ultimately descended from a common ancestor that had a single dorsal valve, and was probably a monoplacophoran, the shells of the two subphyla contain homologous parts and structures.

Subphylum CYRTOSOMA

The classes Monoplacophora, Gastropoda, and Cephalopoda emphasize a conical univalved shell that is often twisted into a spiral. Because they have a relatively small single shell aperture, the anus is forced to lie close to the mouth and the gut is bent or twisted into a U-shape. These three classes specialized in non-infaunal living, although secondarily some have become infaunal. They ordinarily show little lateral compression of the body and are placed in the subphylum Cyrtosoma. Some Cambrian cyrtosomes do show lateral compression and are important as possible ancestors of the diasomes.

The taxonomic limits of the Monoplacophora are a matter of debate; Runnegar and Jell (1976) defined the class much more broadly than did Berg-Madsen and Peel (1978). Runnegar and Jell (1980) and Runnegar (in press b, c) have provided addi-
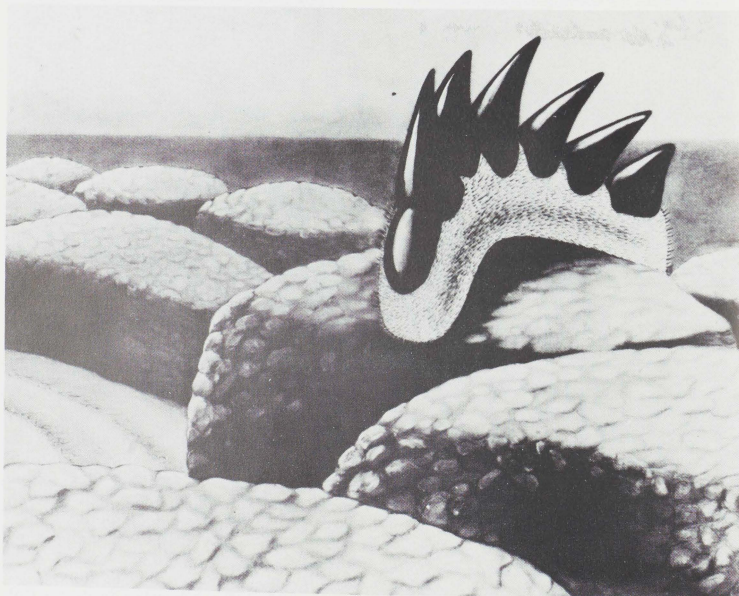

Figure 15. Artist's impression of *Matthevia variabilis* Walcott reconstructed as a polyplacophoran, grazing Late Cambrian intertidal stromatolites.

tional data on the classification, definition, and diversity of the Monoplacophora.

In the Early and Middle Cambrian, the monoplacophorans were diverse and sometimes abundant elements of the biota (Rozanov et al., 1969; Matthews and Missarzhevsky, 1975; Runnegar and Jell, 1976; and Yü, 1979). The monoplacophorans probably originated in the Precambrian, because in the Cambrian they already have diversified into cap-shaped shells, cone-shaped shells, cyrtoconic shells, and planispiral shells. At this time most monoplacophorans were probably epifaunal grazers that could clamp down the shell on the substrate. It seems likely that the Monoplacophora are descended from an aplacophoran-like spiculose ancestor that developed a low conical shell below the cuticle.

The helcionellaceans (Figure 19), Early and Middle Cambrian monoplacophorans, have tubular structures that provide insight into which end of the shell was anterior and which posterior. In living monoplacophorans, the apex of the shell is anterior and overhangs the head; this condition is termed exogastric. Ordovician monoplacophorans such as ?_Macroscenella_ cf. _M. montrealensis_ (Billings), identified by E. L. Yochelson _in_ Pojeta and Runnegar (1976) (Figure 20B), by analogy with the living forms have a planispiral larval shell overhanging the anterior end and an adult shell that is a tall cone. Helcionellaceans such as _Latouchella_ Cobbold (Figure 20A) are cyrtoconic to planispiral, with the apex being regarded as anterior by comparison with ?_Macroscenella_ cf. _M. montrealensis_.

Helcionellaceans of the genus _Yochelcionella_ Runnegar and Pojeta have a prominent snorkel projecting from the shell (Figure 21). In some species, such as _Y. cyrano_ Runnegar and Pojeta and _Y. daleki_

Figure 16. Reconstruction of _Matthevia variabilis_ Walcott, preferred by Yochelson (1966, p. B6).

Runnegar and Jell (Figure 21B, C), the apex of the shell projects over the tube; these species are regarded as being exogastric. In other species, such as _Y. ostentata_ Runnegar and Jell, the apex of the shell projects away from the snorkel (Figure 21A); these species are regarded as being endogastric, the snorkel being the homologous structure and, therefore, on the same side of the shell in all three species.

Yochelcionella ostentata is of particular interest in considering the origin of the cephalopods (Jell, 1978). In some specimens (Figure 21A), the snorkel forms the high point on the shell and its cavity is in line with the cavity of the body of the shell, rather
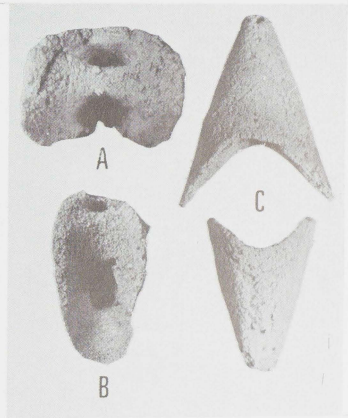

Figure 17. Gross morphology of the valves of the polyplacophoran _Matthevia variabilis_ Walcott. (A) Ventral view of intermediate valve, showing deep muscle insertions, ×1.75, USNM 145312, Upper Cambrian, Wilberns Formation (Trempealeauan), Gillespie County, Texas. (B) Ventral view of tail valve showing deep muscle insertions, ×2, USNM 146896, Upper Cambrian, Nopah Formation (Trempealeauan), Charleston Peak Quadrangle, Nevada. (C) Dorsal view of two valves placed in the preferred orientation of hard parts of Yochelson (1966, p. B6), showing dorsal embayments of valves through which soft parts could protrude, ×1.75, USNM 145312 and 145313, localities the same as for figures A and B.

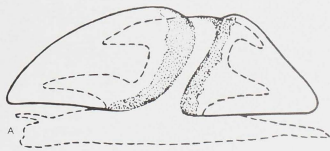than being at nearly right angles to the shell, as in *Y. cyrano* and *Y. daleki* (Figure 21B, C). It is sometimes thought that cephalopods evolved from presumed endogastrically curved hypseloconid monoplacophorans (Yochelson, Flower, and Webers, 1973), some of which are known to have septa. The problem in cephalopod evolution is not in the derivation of septa, which are known in several classes of mollusks; rather, it is in the origin of the characteristic siphuncle of cephalopods. The siphuncle not only pierces the septa, it is a complex organ with blood vessels, nerves, mantle, conchiolin, and spicules of calcium carbonate. Such a complex organ seems unlikely to have formed around a strand of tissue that was not pulled forward at the time of the secretion of a septum as suggested by Yochelson, Flower, and Webers (1973, p. 293). On the other hand, a shell such as *Yochelcionella ostentata* (Figure 21A) already had a tube at the high point of the shell; the shell can be regarded as endo-
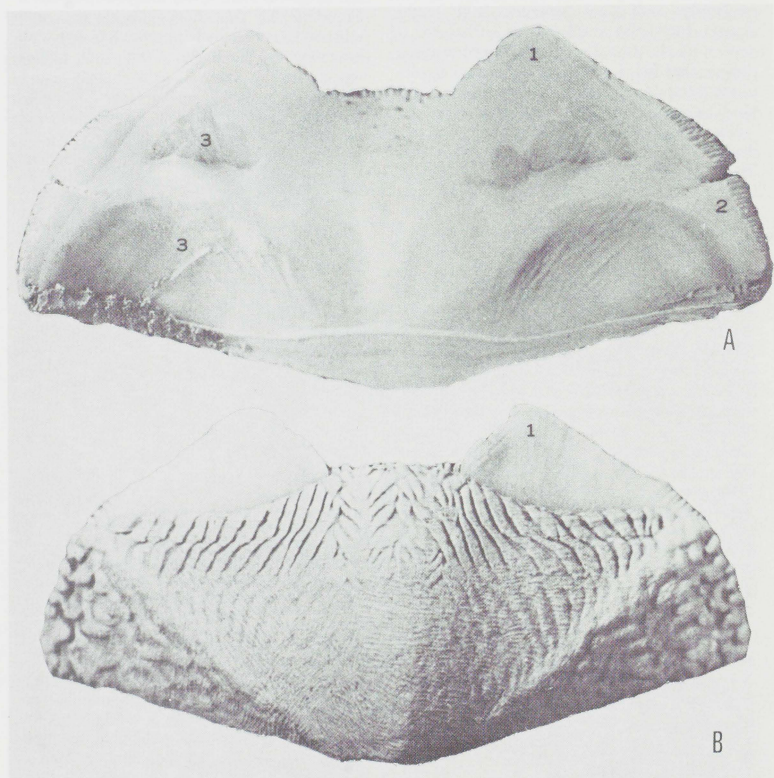

Figure 18. Interior (A) and exterior (B) views of a single intermediate valve of the living polyplacophoran *Chiton tuberculatus* Linné, ×5, USNM (Division of Mollusks) 621566. Anterior is up. (1) Sutural lamina or prong, (2) insertion plate, and (3) muscle scars.

gastric, and the shell is a high cone in which the gut would have to be bent into a U-shape. Such a shell could have been ancestral to cephalopods, the snorkel becoming a siphuncle after its end was sealed. Some of the earliest cephalopods are small orthocones or endogastric cyrtocones assigned to *Plectronoceras* from the Upper Cambrian rocks of China (Yochelson, Flower, and Webers, 1973, figs. 2). *Yochelcionella ostentata* is known from lower Middle Cambrian rocks in Australia (Runnegar and Jell, 1976). The recent description by Chen *et al.* (1979) of a highly diversified Late Cambrian cephalopod fauna from China suggests that cephalopods may have had a pre-Late Cambrian origin.

A few helically coiled species of mollusks are known from rocks as old as Early Cambrian; most of these are placed in the genera *Aldanella* Vostokova and *Pelagiella* Matthews (Figure 22). These genera have a worldwide distribution in Lower Cambrian rocks and there are no significant reasons

for not considering these animals to be gastropods or near-gastropods. The known specimens of *Aldanella* suggest the presence of a peripheral sinus in the aperture (Rozanov *et al.*, 1969, pl. 3, fig. 14). One specimen of *Pelagiella* (Figure 22A-D) preserves muscle scars: paired unequal retractor scars are offset from one another; above them are arcuate insertions that may mark the dorsal edge of the mantle cavity. Interpreted in this way, the visceral mass was above the mantle insertion, and *Pelagiella* was partially torted. Torsion is the hallmark of gastropods; it takes the apex of the shell away from the head, making the animals endogastric. A sequence from helcionellaceans to pelagiellids to *Aldanella* (Figure 22E) may reflect increasing torsion and suggests how gastropods may have evolved from monoplacophorans.

There seems to be no need for a fully torted planispiral intermediate between monoplacophorans and helically coiled, torted snails. The development of helical
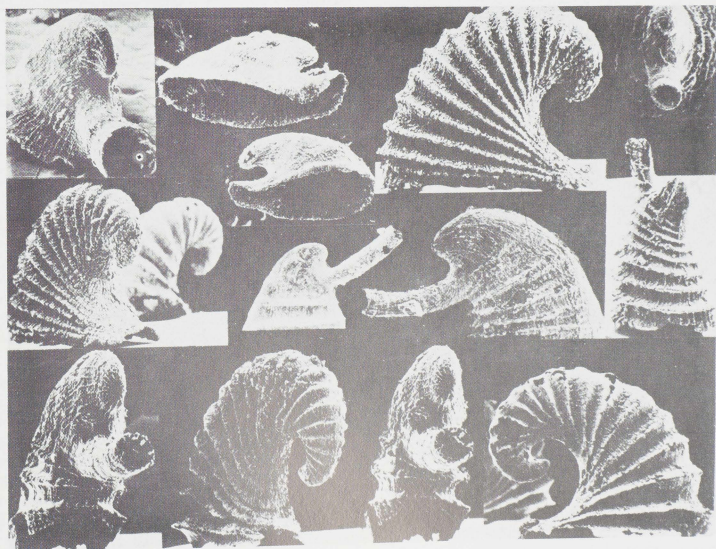

Figure 19. Montage of Middle Cambrian helcionellacean monoplacophorans described by Runnegar and Jell (1976). Figure constructed by Bruce Runnegar, University of New England, Armidale, N.S.W., Australia.

coiling by monoplacophorans may have caused torsion. Helical coiling allows an animal to produce the most compact body mass in the least possible space. In monoplacophorans, the shell is carried on the dorsal side, and paired dorsoventral muscles allow the shell to be clamped down against the substrate when necessary. Some of the tall strongly exogastric Cambrian helcionellaceans approach a planispiral condition (Figure 20A), and in order to produce a more compact body mass they may have evolved a helical (gyrogastric) shell. Such a
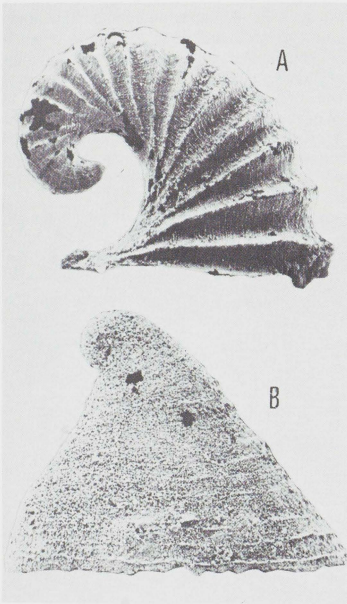

Figure 20. Comparison of shape and orientation of the Middle Ordovician monoplacophoran ?*Macroscenella* cf. *M. montrealensis* (Billings) (B) from the lower part of the Chambersburg Limestone of Virginia, ×18, USNM 209378, with the Middle Cambrian helcionellacean *Latouchella accordionata* Runnegar and Jell (A) from the Coonigan Formation (Ordian) of New South Wales, Australia, ca. ×17, University of New England (UNE), Armidale, N. S. W., Australia.
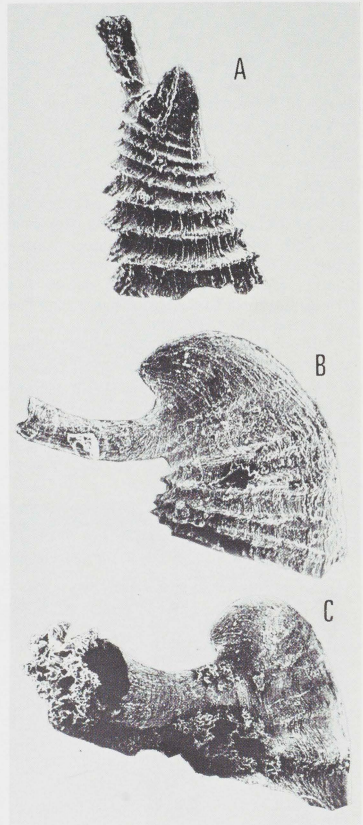
Figure 21. Comparison of three species of the genus *Yochelcionella*. The snorkel of each species is regarded as the homologous structure on the same side of the shell in each case. (A) *Y. ostentata* Runnegar and Jell, apex of shell bends away from snorkel (endogastric), ×25, (UNE); (B) *Y. daleki* Runnegar and Jell, apex of shell bends toward snorkel (exogastric), ×28, (UNE); (C) *Y. cyrano* Runnegar and Pojeta, apex of shell bends toward snorkel (exogastric), ×19, USNM 204698. All specimens from the Coonigan Formation (Ordian), Middle Cambrian, New South Wales, Australia.

shell would have a spire that would stick out to the side, and the shell would tend to fall sideways. In order to keep a helical shell in place and crawl along the substrate, a gyrogastric monoplacophoran would have to exert continual muscular effort to keep the shell upright so that the whole body would not fall sideways. If such a shell could be rotated at the neck between the head/foot and the visceral mass, the spire would be pointed away from the head (endogastric), and the shell could be carried on top of the foot and dragged along behind. Thus, torsion may have been a functional adaptation to having the shell coiled in a helical spiral, and the processes of torsion and asymmetry need not have been separate episodes in the evolution of gastropods. Originally, torsion may have been much less than 180 degrees and the animal may not have been torted when withdrawn into the shell. Runnegar (in press b) gives a more extended consideration of torsion in Cambrian univalves.
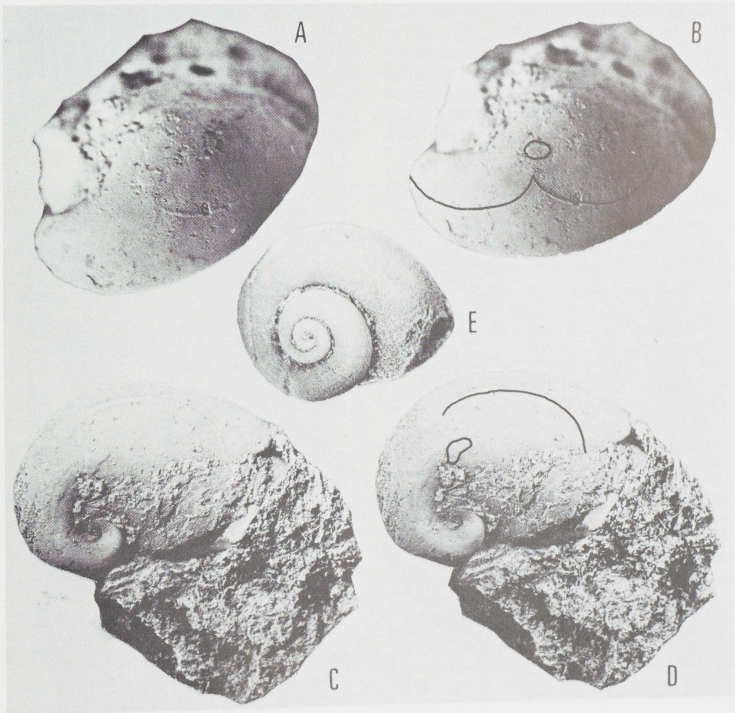

Figure 22. Helically coiled Cambrian shells. (A-D) Internal mold of *Pelagiella atlantoides* (Matthew), lateral views showing muscle scars, in figures B and D muscle scars are inked; Late Early Cambrian, *Protolenus* Zone, Hanford Brook, St. John County, New Brunswick, Canada, ×7.5, USNM 298724. (E) *Aldanella attleborensis* (Shaler and Foerste); Early Cambrian, Pleasant Beach, Cohosset, Massachusetts, ×7.5, USNM 26725.

Subphylum DIASOMA

The molluscan classes Rostroconchia, Pelecypoda, and Scaphopoda have a shell that is primitively open at both the anterior and posterior ends; this allows the gut to remain relatively straight, the mouth and anus widely separated from one another and opening at opposite ends of the shell. All three of these classes have specialized in infaunal living, and primitively lateral compression is a widespread feature of the group. The ancestral diasome class is the Rostroconchia, which probably arose from laterally compressed helcionellaceans and which gave rise to the Pelecypoda on the one hand and the Scaphopoda on the other. The subphylum Diasoma is used for these three classes because of their common origin, structure, and ecology; Runnegar and Pojeta (1974), Pojeta and Runnegar (1976,

1979), Pojeta (1978), and Runnegar (1978) have written extensively about diasome phylogeny.

Rostroconchs are pseudobivalved mollusks that have an uncoiled and untorted univalved larval shell and a bivalved adult shell in which one or more shell layers is continuous across the dorsal margin and which lacks a dorsal commissure (Figure 23). These mollusks range in age from Early Cambrian to Late Permian but are most diverse in Cambrian and Ordovician rocks.

The oldest known rostroconch is *Heraultipegma* Pojeta and Runnegar (Figure 24D-F) from the Lower Cambrian of France, Australia, Siberia, and China. It has a laterally compressed shell, anterior, ventral, and posterior shell gapes, and the pegma of younger rostroconchs (Figure 24D-F). The shell form of *Heraultipegma* was probably
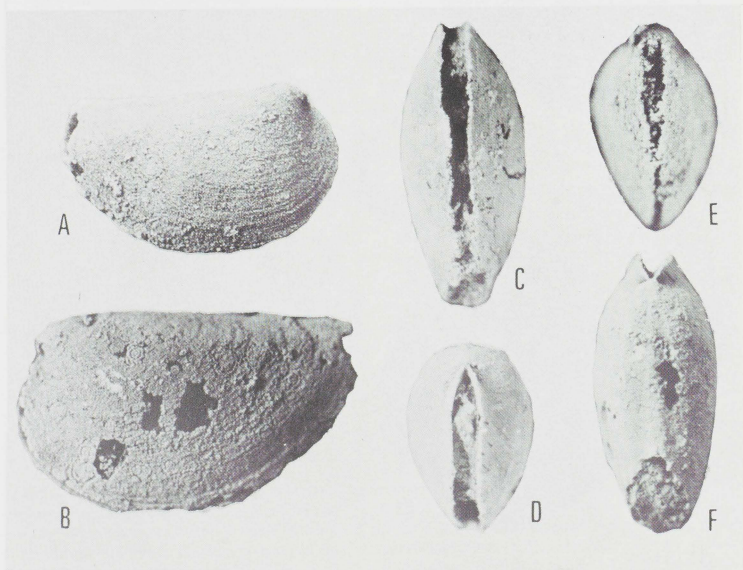

Figure 23. Gross external morphology of early rostroconchs, *Ribeiria australiensis* Pojeta and Runnegar, Mungerebar Limestone (Mindyallan), Upper Cambrian, Queensland, Australia. (A) right-lateral, (B) left-lateral, (C) ventral, (D) anterior, (E) posterior, and (F) dorsal views, ×4.5; Australian Bureau of Mineral Resources (BMR) 14671, 14672, and 14670.

derived from one of the laterally compressed helcionellacean monoplacophorans such as *Anabarella* Vostokova (Pojeta and Runnegar, 1976, pl. 17, fig. 8) and *Mellopegma* Runnegar and Jell (Figure 24A-C), which are mostly from Lower and Middle Cambrian rocks; recently, Tipnis *et al.* (1978) have identified an *Anabarella*-like organism from the Upper Cambrian rocks of

Canada. These laterally compressed helcionellaceans are similar to *Heraultipegma* in size and lateral profile; they have a curved, rather than straight, apertural margin when viewed laterally and thus had anterior, ventral, and posterior shell gapes. Therefore, *Anabarella* and *Mellopegma* are regarded as morphological intermediates between monoplacophorans and rostroconchs. The lateral compression of the shell of some helcionellaceans may also have provided the mechanism by which epifaunal grazers, such as *Latouchella* (Figure 20A), could become infaunal burrowers and explains the infaunal mode of life in the Diasoma. Stasek (1972, p. 31) has suggested how the particulate material, which is collected by the cilia of the gills and has to be removed in non-suspension feeders, could be tapped as a food source by filter-feeding diasomes. He also noted that monoplacophorans, when they were beginning to exploit the use of food in the water column, may also have kept their radula and herbivorous habits; this explains the occurrence of a radula in scaphopods and suggests that primitive rostroconchs also had a radula.

Fordilla Barrande is the oldest known pelecypod; it has the musculature and dentition of younger clams, is fully bivalved rather than pseudobivalved, and occurs in Lower Cambrian rocks (Figure 25). Pojeta, Runnegar, and Kříž (1973); Pojeta and Runnegar (1974); Pojeta (1975, 1978); and Krasilova (1977) have provided the modern literature about *Fordilla*. Clam-shaped shells from the Upper Cambrian Frederick Limestone of Maryland are shown in Figure 26. According to J. E. Repetski, U. S. Geological Survey (written communication, September 1979), these shells occur below horizons containing the conodont *Proconodon-*
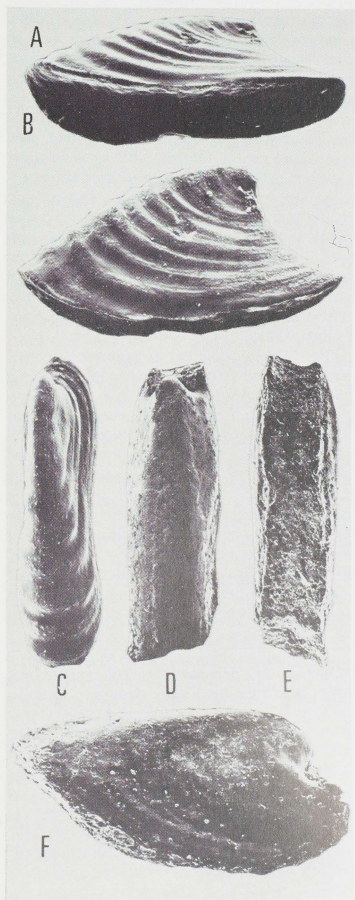
Figure 24. Comparison of the early compressed helcionellacean *Mellopegma georginensis* Runnegar and Jell (A-C), with the oldest known rostroconch *Heraultipegma varensalense* (Cobbold) (D-F). (A-C) oblique ventral, right-lateral, and oblique dorsal views; Currant Bush Limestone, upper Middle Cambrian, Queensland, Australia; A, B, ×38; C, ×75, USNM 298725, 298726. (D-F) Dorsal, ventral, and right-lateral views; Georgien (Lower Cambrian), St. Geniès de Varensal, France; D, F, ×30; E, ×38, USNM 298727, 298728.
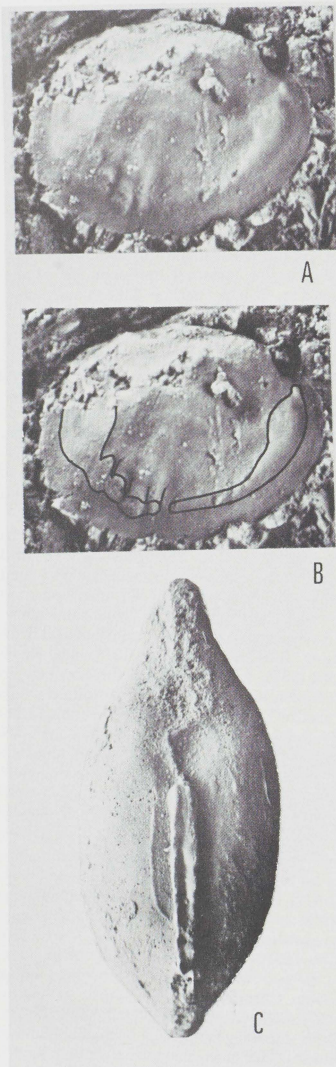
tus muelleri Miller in the Lime Kiln Member of the Frederick; *P. muelleri* indicates a late Franconian to late Trempealeauan age.

It seems likely that pelecypods evolved from rostroconchs in the Early Cambrian by decalcification of the posterodorsal margin of the shell of rostroconchs. This decalcification would produce the elastic ligament of pelecypods; the change from a rostroconch to a pelecypod would be a biochemical one, expressed morphologically as an elastic dorsal margin. Such a margin would allow pelecypods to close without a gape and to burrow more efficiently than rostroconchs probably could. When living pelecypods burrow, their valves are pressed against the sides of the burrow by the opening thrust of the ligament. Subsequently, as the foot forms the pedal anchor, the sediment is loosened by ejection of water from the mantle cavity, produced by contraction of the adductor muscles. Contraction of the pedal muscles then pulls the animal into the loosened sediment (Trueman, 1968). Rostroconchs were probably less efficient burrowers than pelecypods because they lacked a ligament and adductor muscles (Pojeta, 1979).

The Middle Cambrian species *Myona? queenslandica* Runnegar and Jell suggests that rostroconchs did give rise to pelecypods by decalcification of the dorsal margin. This species (Runnegar, 1978, pl. 2, fig. 26) has a univalved protoconch and a bivalved adult shell and is thus a rostroconch by definition. However, its middorsal line is clearly differentiated from the rest of the shell and is unlike the middorsal line of other rostroconchs (compare Runnegar, 1978, pl. 2, figs. 26, 28, with Figure 24D herein). In addition, some specimens of *Myona?* are flexed along the dorsal margin

Figure 25. (A, B) *Fordilla troyensis*, right valve of internal mold showing muscle scars; in B the scars are inked; Lower Cambrian, Troy, New York, ×11.5, USNM 15,372. (C) *Fordilla sibirica* Krasilova, dorsal view of internal mold showing dentition; Lower Cambrian (Atdabanian), Lena River, Siberia, ×31.5, USNM 247821. A. Yu Rozanov (Paleontological Institute, Akademia Nauk SSSR) kindly provided the specimen of *F. sibirica*.

indicating, that the margin was elastic and acted as a ligament (Runnegar and Jell, 1976, fig. 8D7).

The morphological sequence leading from a helcionellacean such as *Latouchella* to laterally compressed helcionellaceans like *Anabarella* and *Mellopegma*, to rostroconchs like *Heraultipegma*, to rostroconchs like *Myona?* and finally to pelecypods like *Fordilla* (Pojeta, 1978) shows empirically how a bivalved shell could arise from a univalved shell (Figure 27).

The last class to be considered is the Scaphopoda. The oldest known fossil scaphopod (Figure 28A) is from the uppermost Middle Ordovician rocks of Kentucky and is placed in the genus *Rhytiodentalium* Pojeta and Runnegar (1979).

A rostroconch genus called *Pinnocaris* Etheridge (Figure 28C), which lived from the latest Cambrian to the latest Ordovician has anterior and posterior shell gapes (Pojeta and Runnegar, 1976), no dorsal commissure (Pojeta and Runnegar, 1976; Pojeta, Gilbert-Tomlinson, and Shergold, 1977), and the valve edges touching at the ventral commissure. *Pinnocaris* looks remarkably like a scaphopod and probably lived like one, embedded in the sediment, with the posterior end protruding (Runnegar, 1978, fig. 1).

The larval shell of *Pinnocaris* is near the anterior end of the conch, and growth is predominantly in a posterior direction (Figure 28C). In scaphopods, all growth is directed anteriorly, and they probably did not evolve by the simple fusion of the ventral margin of *Pinnocaris*, because a change in the dominant growth component from posterior to anterior was required. In the Lower Ordovician rocks of Australia, *Pinnocaris?* sp. C Pojeta and Gilbert-Tomlinson is present (Figure 28B). This species is nasute anteriorly and has a significant anterior growth component. *Pinnocaris?* sp. C is intermediate stratigraphically and morphologically between Late Cambrian species of *Pinnocaris* and *Rhytiodentalium* in the Middle Ordovician (Figure 28).

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Figure 26. Possible Late Cambrian pelecypod from the Lime Kiln Member, Frederick Limestone, near Buckeystown, Maryland. ×100, USNM 298729.

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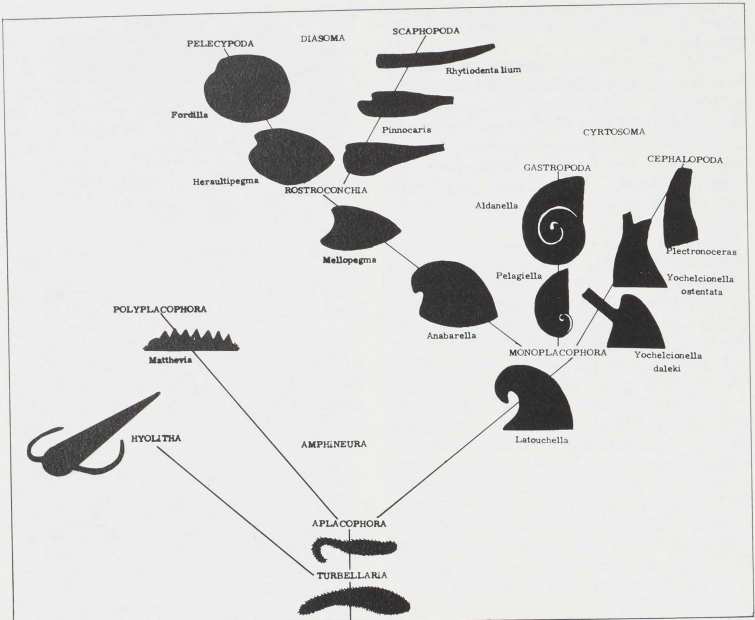BLAINVILLE, H. M. D. DE, 1816, Prodrome d'une nouvelle distribution systèmatique du

Figure 27. Diagrammatic representation of early molluscan evolution.

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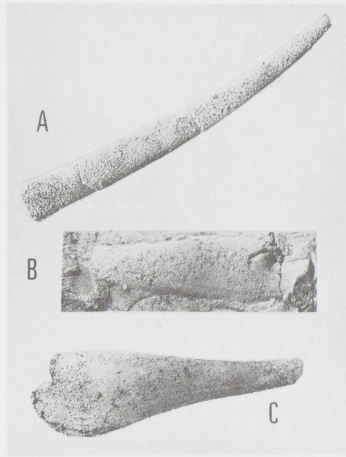

Figure 28. Origin of scaphopods. (C) Left-lateral view of composite mold of *Pinnocaris wellsi* Pojeta, Gilbert-Tomlinson, and Shergold, which is a rostroconch having a dominant posterior growth component, from the Payntonian (Upper Cambrian) part of the Pacoota Sandstone, Northern Territory, Australia, ×1.2, BMR 14746. (B) Right-lateral view of composite mold of *Pinnocaris*? sp. C Pojeta and Gilbert-Tomlinson, which is a nasute rostroconch having a significant anterior growth component, from the Arenigian (Lower Ordovician) part of the Pacoota Sandstone, Northern Territory, Australia, ×2, BMR 15593. (A) Left-lateral view of a silicified specimen of *Rhytiodentalium kentuckyensis* Pojeta and Runnegar, a scaphopod having all growth in an anterior direction, from the Middle part of the Lexington Limestone (Shermanian), Middle Ordovician, central Kentucky, ×2.8 USNM 254392.

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