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Molluscan Phylogeny: The Paleontological Viewpoint

The early Paleozoic fossil record shows how living and extinct molluscan classes originated and diversified.

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Mollusks are dominantly free-living metazoans that utilize a calcareous exoskeleton to provide structural support for a muscular foot or a specialized derivative thereof, and to provide an enclosed space outside the body (mantle cavity) that is used for feeding, respiration, and sometimes locomotion. They constitute the second largest, and most variable, invertebrate phylum (*1*). Our purpose in writing this article is to indicate how mollusks evolved the diversity of form that enabled them to exploit the variety of habitats they now occupy. This adaptive radiation began in the earliest Cambrian, before the appearance of the first trilobites, and is adequately shown in the fossil record (Fig. 1).

There are seven classes of living mollusks: Aplacophora, Polyplacophora, Monoplacophora, Gastropoda, Cephalopoda, Pelecypoda, and Scaphopoda (*1*). The Rostroconchia (*2*) may be the only extinct class. We prefer to assign the fossil classes Mattheva and Stenothecoida (Probivalvia) erected by Yochelson (*3*) and Aksarina (*4*) to other molluscan classes. The Paleozoic mollusk-like fossils known as tentaculites, lapworthellids, cornulitids, hyolithids, and hyolithellids (*5*) probably belong to other phyla (*6*).

The Mollusca, Annelida, Arthropoda, and Sipunculoidea are closely related phyla (*7*). Although it has been suggested that mollusks are neotenous annelids (*8*), it is generally believed that the Mollusca developed from organisms with the grade of organization and body form of primitive turbellarian flatworms (*1, 8*). Thus, Stasek (*1*) derived the Mollusca from free-living flatworms that developed a protective dorsal mucoid coat. This mucoid coat probably changed gradually into a tough cuticle that formed a substrate for a subsequently developed calcareous exoskeleton. With the advent of the organic or calcareous exoskeleton, the body increased in thickness, epithelial respiration became inefficient, and gills developed beneath the protective eaves of the shell in a primitive mantle cavity. The characteristic shell-attached muscles of the molluscan foot probably developed from the dorsoventral musculature of the ancestral flatworm. It follows that in primitive mollusks such as *Neopilina* Lemche (*9*) the exoskeleton is dorsal, the sole of the foot is ventral, and the mouth and anus are, respectively, at the anterior and posterior ends of the body.

The Hyolitha are calcareous operculate conical shells found in Paleozoic rocks. They probably constitute a small extinct phylum (*6*). Their skeletal ultrastructure resembles the crossed-lamellar aragonite of some molluscan skeletons (*6*), but the shape of the gut (*10*) and the arrangement of muscle insertions on the shell (*11*) also relate the Hyolitha to the Sipunculoidea (*6*). Because the Annelida are the closest relatives of the Sipunculoidea (*7*), the paleontological data suggest that the Mollusca, Annelida, Sipunculoidea, and Hyolitha were derived from a common ancestral stock in the late Precambrian.

The Oldest Fossil Mollusks

Russian stratigraphers divide the Early Cambrian of the Siberian Platform into four stages: Tommotian, Atdabanian, Botomian, and Lenian (*12*). The Tommotian deposits predate the first trilobites in the Siberian succession, and they contain a characteristic biota of archaeocyaths, mollusks, hyoliths, algae, and problematica (*13*). The base of the Tommotian appears to reflect the first appearance of an abundance of animals with calcareous skeletons, which is one definition of the beginning of the Cambrian (*12*).

The Tommotian mollusks are small or minute limpet-shaped, planispiral or helically coiled univalves (*13*). They include forms resembling the well-known Cambrian genera *Scenella* Billings, *Helcionella* Grabau and Shimer, and *Pelagiella* Matthew, which have been thought to be monoplacophorans, gastropods, or representatives of other primitive classes of mollusks (*14, 15*). Rozanov *et al.* (*13*) referred all of these univalves to the Gastropoda; we prefer to regard most of them as Monoplacophora for the following reasons.

1) Rasetti (*16*) illustrated internal molds of a small limpet-shaped shell from the Middle Cambrian of British Columbia. These specimens have a number of small muscle insertions (*17*) which are effectively bilaterally symmetrical and thus similar to monoplacophorans. Rasetti referred the specimens to *Scenella* and concluded that they were monoplacophorans. A reconstruction of the body, modeled from *Neopilina*, vindicates this decision (Fig. 2).

Knight *et al.* (*18*) referred *Helcionella* to the Gastropoda and *Scenella* to the Monoplacophora. There is, however, a gradation in external shell from *Helcionella* through the Tommotian genera *Bemella, Ginella*, and *Tannuella* Missarzhevsky (*13*) to *Scenella*. We therefore believe that the Helcionellacea are monoplacophorans, not gastropods; unfortunately their muscle scars are as yet unknown.

2) One of the Tommotian mollusks, the genus *Anabarella* Vostokova (Fig. 3D), is a laterally compressed planispiral univalve with a ventral margin

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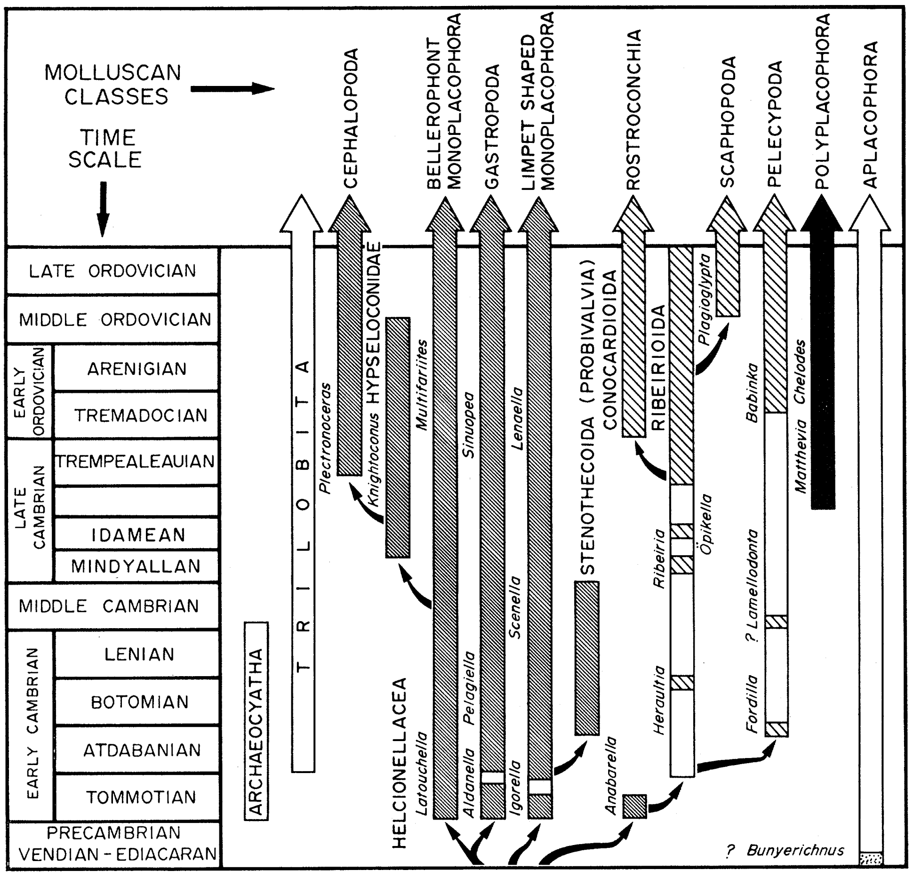

Fig. 1. Historical record of the initial radiation of the Mollusca, scaled against time divisions based primarily on the succession of fossil archaeocyaths and trilobites. The two largest molluscan subphyla (Crytosoma, fine-shaded columns, and Diasoma, coarse-shaded columns) separated in the Early Cambrian.

that is obviously curved when the shell is viewed laterally; thus it is like the rostroconchs and pelecypods rather than the monoplacophorans or gastropods. *Anabarella* is intermediate in shell form between more typical Cambrian univalves such as *Helcionella, Latouchella* Cobbold, and *Igorella* Missarzhevsky, and the first ribeiriid rostroconch, *Heraultia* Cobbold, from the Early Cambrian of France (Fig. 3, E to G; Fig. 4). We believe that *Heraultia* is derived from *Anabarella* and thus maintain that *Anabarella* was not a gastropod, because the Cambrian and Ordovician descendants of *Heraultia* show no evidence of torsion (Fig. 4).

3) Middle Cambrian planispiral univalves illustrated by Fleming [in Hill *et al.* (*19*), plate 2, figures 29 and 30] are intermediate in shell form between Early Cambrian helcionellids such as *Latouchella* and the tightly coiled Early Ordovician monoplacophoran *Multifariites* Byalyi (*20*).

4) Additional support for the monoplacophoran placement of the Helcionellacea comes from a previously undescribed helcionellid, *Yochelcionella* n. gen. (*21*) (Fig. 3, A to C), which differs from other helcionellaceans by having a tube attached to the concave side of the shell. By analogy with other mollusks, the tube probably carried water in or out of the mantle cavity. It could not have functioned in this way if *Yochelcionella* were a gastropod, because torsion would have shifted the mantle cavity to the opposite side of the shell. But if *Yochelcionella* were a monoplacophoran, the tube could have been used to channel clean water into the anterior end of the mantle cavity (*21*).

We conclude that most Tommotian mollusks were tiny monoplacophorans belonging to the superfamily Helcionellacea. We view them as the direct or indirect ancestors of all molluscan classes except the Aplacophora.

Aplacophora and Polyplacophora

The Aplacophora probably never acquired a continuous calcareous exoskeleton (*1*) and so are unlikely to be preserved as fossils. However, Glaessner (*22*) has illustrated a late Precambrian surface locomotion trail which, he speculates, may have been formed by an organism resembling a neomenioid aplacophoran. He named the trial *Bunyerichnus*.

The oldest chiton, *Preacanthochiton* Bergenhayn, is known from disarticulated plates from the Late Cambrian of Missouri (*23*). Although referred to a different family by Bergenhayn (*23*), *Preacanthochiton* appears to be closely related to the Early Ordovician genus *Chelodes* Davidson and King (*18, 23*). Collins (*24*) has observed that disarticulated plates of an undescribed chelodid chiton (*25*) from the Australian Early Ordovician are intermediate in form between *Chelodes* and the enigmatic Late Cambrian fossil *Matthevia* Walcott. Yochelson (*3*) erected the molluscan class Mattheva for *Matthevia* and suggested that its exoskeleton consisted of two unequal pieces.

We agree that the Australian chelodid (Fig. 3, M to O) suggests that *Matthevia* is a primitive chiton; consequently, it probably had an exoskeleton composed of seven or eight plates. Reconstructions of *Chelodes*, the Australian chelodid, and *Matthevia* are shown in Fig. 5. Yochelson (*3*) has illustrated specimens of *Matthevia* that show the insertions of the dorsoventral pedal muscles; all other muscles shown in the

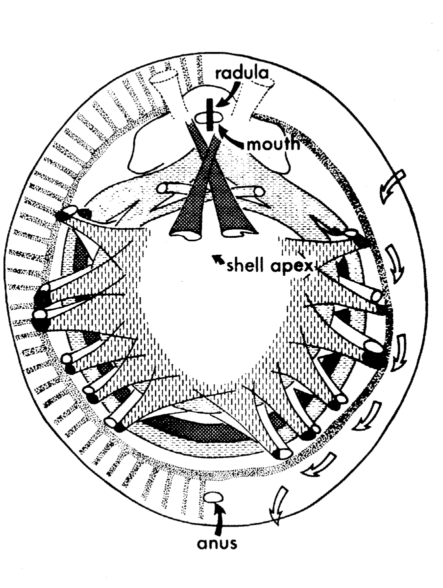

Fig. 2. Reconstruction of Rasetti's Middle Cambrian monoplacophoran *Scenella*, modeled from *Neopilina*. Stippled ring represents incipient pallial line indicated by change in slope of shell. Radial fluting of shell outside pallial line reflects weak radial mantle muscles (shown on left side only by short stippled lines). Also shown are radial and circular muscles of the foot as well as muscles controlling the head (anterior pair hypothetical). Arrows indicate probable direction of water flow through the mantle cavity.

reconstructions are hypothetical and are modeled on the musculature of living chitons.

Specimens of *Matthevia* occur in rocks that are approximately the same age as those yielding *Preacanthochiton*. We speculate that *Matthevia* may be more primitive than the *Preacanthochiton*, and may thus give some indication of the way chitons evolved. Its skeleton appears to have consisted of a series of conical valves, each reminiscent of a tall monoplacophoran shell. These conical valves were probably rapidly modified to form the overlapping skeleton of the chelodid genera and *Preacanthochiton*. As Stasek (*1*) noted, the large overlapping parts of the chelodid valves are homologous with minute apical areas on the valves of modern chitons. These homologies are shown in Fig. 5 and by Stasek (*1*).

If this sequence of form reflects the evolutionary history of chitons, the first chitons probably had a linear series of conical valves, each composed of two main shell layers like the shell of the Monoplacophora. We suggest that chitons may have evolved from primitive Monoplacophora when several centers, instead of one center, of calcification appeared in the larval shell gland. We invoke a comparable sudden appearance of left and right centers of calcification to explain the appearance of the Pelecypoda from the Rostroconchia and believe that such changes would be accompanied by relatively minor changes in body form. The existence of the bivalved Gastropoda (*26*) provides support for this view.

Monoplacophora

Rasetti's Middle Cambrian *Scenella* (Fig. 2) and Early Ordovician genera such as *Lenaella* Byalyi (*20*) closely resemble the living monoplacophoran *Neopilina* (*9*). These limpet-shaped shells form one major lineage of the Monoplacophora. The extinct planispiral Bellerophontacea (*18*) may be a second major lineage. These fossils are usually referred to the Gastropoda (*14, 15*). Recent discoveries of bellerophontoid shells with multiple muscle insertions like those in *Multifariites* Byalyi (*20*) suggest that the whole group may have been untorted.

Gastropoda

The class Gastropoda comprises animals with a distinct head, a solelike foot adapted for creeping, a radula, and a visceral mass that is apparently rotated 180 degrees with respect to the head and foot so that the gut becomes twisted, the left and right gills come to lie, respectively, on right and left sides of the body, and the nervous system forms a figure eight. This twisting of the visceral mass is known as torsion; in living gastropods it occurs in early ontogeny by rapid contraction of the asymmetrical right larval retractor muscle and by differential growth (*27*). Torsion distinguishes gastropods from their presumed ancestors, the Monoplacophora.

There is a small, helically coiled shell known as *Pelagiella* that is widely distributed in Early Cambrian rocks (*18*). Although it resembles younger gastropods in shape, most authors have preferred to regard it as an end product of early molluscan experimentation rather than as a primitive member of the Gastropoda (*14, 18, 28*).

The oldest zone of the Tommotian stage yields ribbed and smooth helically coiled pelagiellids called *Aldanella* Vostokova (*13*). Coarsely plicated helcionellids referred to the genus *Latouchella* occur in the same beds (*13*). Both genera are preserved as minute phosphatic internal molds; we assume they were closely related. Specimens of *Pelagiella* (Fig. 3L) from the Early Cambrian of Britain are intermediate in form between *Aldanella* and *Latouchella*.

The univalve *Latouchella* has a bilaterally symmetrical shell and probably lived with its plane of symmetry vertical. *Aldanella* has an asymmetric shell

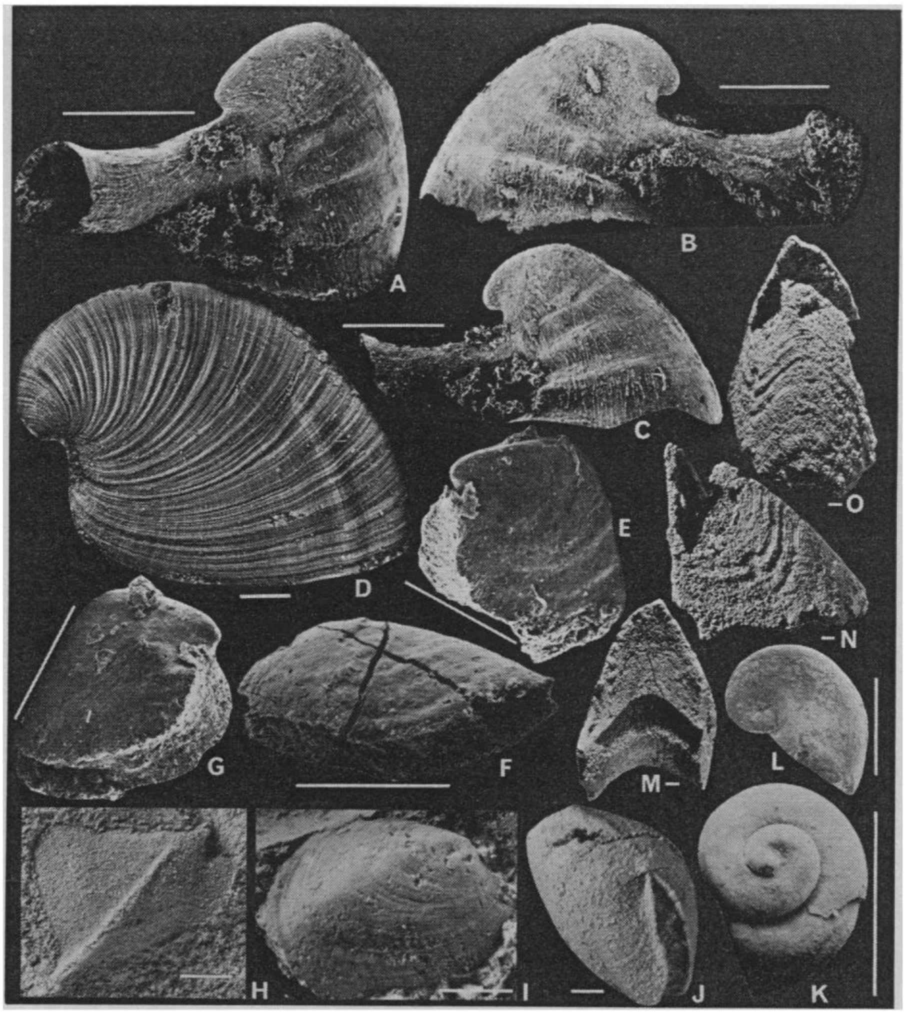

Fig. 3. Cambrian (A to L) and Early Ordovician (M to O) mollusks. (A to C) *Yochelcionella*, Australian Cambrian monoplacophoran with anterior tube; (D) *Anabarella*, laterally compressed monoplacophoran, basal Cambrian, Siberia; (E to G) *Heraultia*, oldest known rostroconch, Early Cambrian, France; (H) *Opikella*, oldest known technophorid rostroconch, Late Cambrian, Australia; (I) *Fordilla*, oldest known pelecypod, Early Cambrian, United States; (J) *Ribeiria*, descendent of *Heraultia*, Late Cambrian, Australia; (K) *Aldanella*, oldest known gastropod, basal Cambrian, Siberia; (L) *Pelagiella*, gastropod, Early Cambrian, Great Britain; (M to O) ventral, right lateral, and dorsal views of intermediate valve of chelodid chiton, Early Ordovician, Australia. Bars equal 1 millimeter.

coiled in a low dextral spiral (Fig. 3K). Although the shells of *Aldanella* are very small (maximum diameter about 2 millimeters), they are significantly larger than the larval shells of living prosobranch gastropods that remain for an unusually long time in the plankton (*27*). Some species of *Pelagiella* are much larger (*29*), suggesting that the whole group were benthonic as adults.

In most existing theories of the historical origin of torsion, the extinct planispiral univalves (Bellerophontacea) (*14, 15, 18*) are presumed to be intermediates between planispiral monoplacophorans and helically coiled primitive gastropods (*30*). Planispiral coiling thus precedes torsion and helical coiling follows it. We prefer Ghiselin's (*31*) suggestion that torsion is a necessary consequence of helical coiling. He argued that a planktonic larva with a helical shell coiled over its head would have difficulty settling because the spire would interfere with its locomotion.

During its planktonic larval life, the shell of *Aldanella* could have coiled forward over the head. During settling, this orientation would be awkward, because in living prosobranchs the foot is poorly formed at this stage (*27, 31*), and the larva would have difficulty in balancing the shell vertically. Furthermore, to creep along the substrate it would have to carry the spire and visceral mass, instead of dragging them behind (*31*).

In *Aldanella*, the shell is consistently coiled dextrally and the animal probably rested with its umbilicus downward during and after settlement. If the body of *Aldanella* were organized in the same way as the body of *Latouchella*, the head and foot of *Aldanella* would need to rotate about 90 degrees in the shell aperture to compensate for the change in orientation with respect to the substrate. This would allow the animal to protract its foot over the functionally ventral edge of the shell aperture and to move the coil from an anterior to posterior position. It would also initiate torsion. We suggest that torsion resulted from a simple change in the orientation of the shell after settlement; upright symmetrical univalves (helicionellacean monoplacophorans) became prostrate, torted, helically coiled gastropods when the head-foot projected laterally instead of anteriorly from the shell aperture (Fig. 4). We conclude that the small, dextrally coiled Early Cambrian shells *Aldanella* and *Pelagiella* were the first gastropods; they gave rise to the sinuopeids, raphistomatids, and eotomariids (*18*) of the Late Cambrian.

Cephalopoda

Cephalopods have the mouth and anus juxtaposed, but the body is not torted, it is still bilaterally symmetrical. Most living cephalopods lack a calcareous exoskeleton and are thought to be derived from more primitive shelled forms (*32*). Apart from the enigmatic fossil *Vologdinella* Balashov (*32*), no septate shells which could be cephalopods have been found in rocks older than the Late Cambrian (*32, 33*). These primitive cephalopods, referred to the family Plectronoceratidae, have elongate, straight or curved shells with closely spaced septa, and a large ventral siphuncle (*32, 34*). The apparently oldest and most primitive genus is *Plectronoceras* Ulrich and Foerste, in which the shell expands rapidly toward the aperture (Fig. 4).

Most monoplacophorans have shells that coil forward over the head. However, the Late Cambrian–Early Ordovician genera *Hypseloconus* Berkey, *Yochelsonella* Flower, and *Knightoconus* Yochelson, Flower, and Webers are tall, laterally compressed shells that appear to have been curved away from the head (*33, 35*). Such shells first appear in the early Late Cambrian (*36*). *Knightoconus* has apical septa (*33*), and Yochelson *et al.* have suggested that such septate monoplacophorans became primitive cephalopods when they developed a siphuncle. This is a device that allows the organism to control its buoyancy (*37*); it thus provided the key for the rapid subsequent radiation of the shelled Cephalopoda (*32*). We believe that the hypseloconids were derived from Early Cambrian cone-shaped shells like *Tannuella* (*13*). As Yochelson *et al.* (*33*) suggested, it is unlikely that the class Cephalopoda appeared before the Late Cambrian.

Rostroconchia

Rostroconchs are a diverse group of extinct mollusks that grew an effectively bivalved shell from a univalved proto-

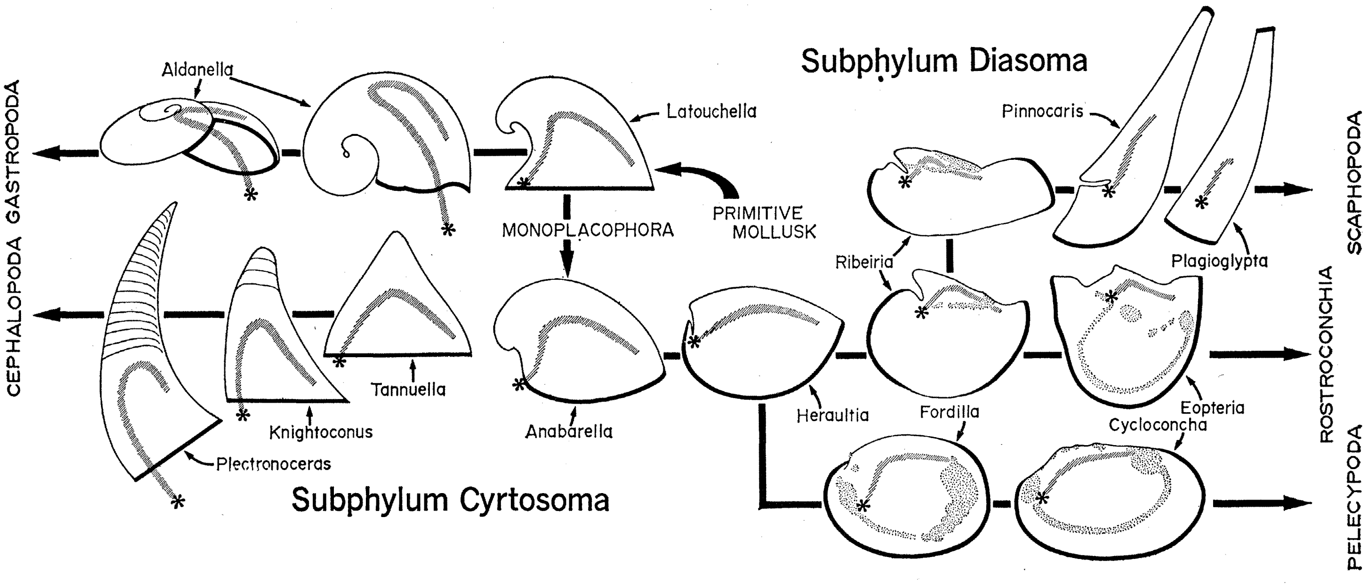

Fig. 4. Schematic view of the origin of the univalved and bivalved molluscan classes. Most drawings are based on internal molds of the shells. Thick lines show extent of shell apertures; stippled areas represent muscle insertions; shaded areas show probable position of gut with mouth indicated by asterisk.

conch (*2, 38*). They lack a ligament, hinge teeth, and paired adductor muscles but resemble pelecypods in other respects. They probably had an anterior mouth, posterior anus, lateral gills, and a pelecypod-like foot. Most are believed to have been deposit-feeders that used hypertrophied anterior mantle tissue and perhaps cephalic tentacles to collect food (*38*).

The French Early Cambrian genus *Heraultia* (Fig. 3, E to G) is a tiny laterally compressed shell with gaping anterior, ventral, and posterior margins. It is the oldest known rostroconch. We envisage a laterally compressed monoplacophoran with the shell form of *Anabarella* (Fig. 3D) giving rise to *Heraultia* by the Atdabanian stage of the Early Cambrian. The internal morphology of *Heraultia* is not well known, but it clearly has a small fold in the shell between the dorsal edge of the anterior gape and the protoconch (Fig. 4). It apparently gave rise to the Late Cambrian and Ordovician genus *Ribeiria* Sharpe (Fig. 3J) when the fold of shell beneath the protoconch thickened internally to form a transverse plate, and the shell gapes became concentrated at anterior and posterior ends of the shell (Fig. 4).

The change in shell form from a univalved monoplacophoran such as *Latouchella* to an effectively bivalved ribeiriid such as *Heraultia* must have been accompanied by a change in life habits. Both Harry (*39*) and Stasek (*1*) described hypothetical animals that might have existed as intermediates between monoplacophorans and pelecypods; both authors accurately described the morphology of *Anabarella, Heraultia*, and other ribeiriid rostroconchs. They argued that some primitive monoplacophorans enlarged their mantle cavities and began to feed on organic detritus and phytoplankton. Finding a largely unexploited source of food, these animals developed rapidly into laterally compressed, deposit- or filter-feeding, semi-infaunal to infaunal organisms. We speculate that decephalization may have accompanied this change in shell form, allowing for the production of a pelecypod-like body in a ribeiriid shell (*38*).

The ribeirioid rostroconchs became extinct at the end of the Ordovician (*38*). By the early Late Cambrian the first technophorid ribeirioid, *Opikella* n. gen. (*40*) (Fig. 3H), had appeared. This genus has the inflated mantle cavity of younger conocardioid rostroconchs (*2*), but differs significantly in shape. The conocardioids diversified during the middle Paleozoic and then died out at the end of the Permian (*2, 38*).

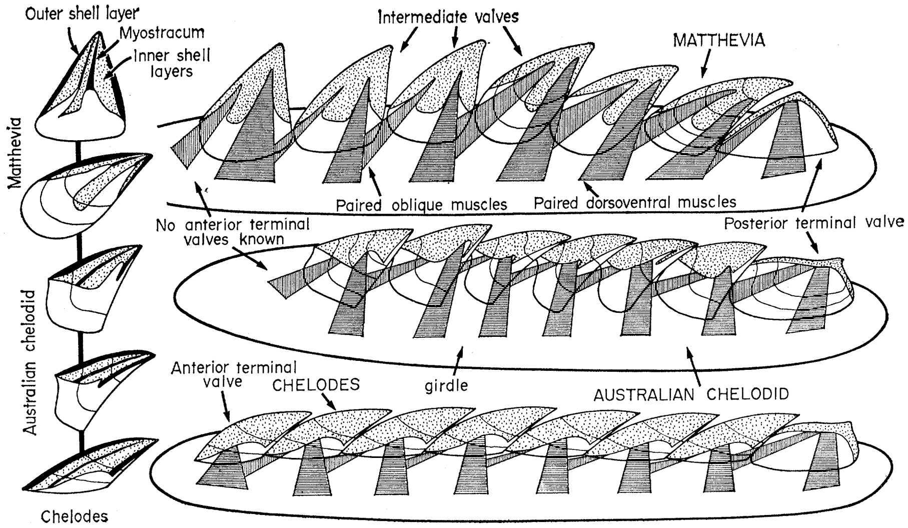

Fig. 5. Reconstructions of primitive Cambrian and Early Ordovician chitons known only from disarticulated plates.

Pelecypoda

The small Early Cambrian genus *Fordilla* Barrande is the oldest known pelecypod (*41*); it first appears in the late Atdabanian stage of the Siberian succession (*13*). *Fordilla* has a laterally compressed shell with prominent comarginal ornament. It is about the same size and age as the ribeiriid rostroconch *Heraultia*, and the two genera have similar lateral profiles (Fig. 3, E to G, and I; Fig. 4). *Fordilla* has a bivalved larval shell, a simple ligament, pelecypod-like pedal muscle insertions, and well-developed mantle musculature (*41*). There were no shell gapes; when the adductors contracted, the valve margins were tightly closed. By contrast, *Heraultia* has a univalved larval shell, a pseudobivalved adult shell, and an anterior through posterior shell gape. By analogy with younger ribeiriids, *Heraultia* probably had radial pallial retractor muscles but lacked adductors (*38*).

The main difference between pelecypods and rostroconchs is that in pelecypods the shell is bivalved from the very beginning of its growth. Once a flexible ligament was established in the larval shell, the adult would inevitably resemble a pelecypod. The conchological differences between early pelecypods like *Fordilla, Redonia* Roualt, *Babinka* Barrande, *Cycloconcha* Miller, and *Lyrodesma* Conrad (*42*) are considerable, but most of the differences relate to the geometric effects of growth from two centers of calcification. We believe that a single mutation producing a flexible hinge in the larval shell would have been sufficient to convert a ribeiriid into a pelecypod, if we can judge the differences on shell form alone. This change probably occurred in the Atdabanian stage of the Early Cambrian when *Fordilla* evolved from *Heraultia* or some closely related form.

Scaphopoda

Scaphopods have a tubular shell which is often gently curved and is invariably open at both ends (Fig. 4). Growth proceeds by the deposition of new shell at the larger end of the tube, simultaneous resorption occurring at the opposite end.

Coarsely silicified replicas of tusk-shaped shells resembling undoubted scaphopods are known from the Middle and Late Ordovician of Kentucky, and Ordovician representatives of *Plagioglypta* Pilsbry and Sharp (*43*) may be a related form. We believe the class was probably well differentiated by this time.

The ontogeny of the living scaphopod *Dentalium* Linné shows that the larval mantle and shell first appear dorsally and then grow right and left lobes, which eventually coalesce ventrally to produce the tubular juvenile and adult shell (*44*). It is this embryological observation that has led to the belief that the scaphopods are more closely related to the Pelecypoda than to any other group of living mollusks.

We also rely on this embryological evidence to postulate that the Scaphopoda developed from the ribeiriid rostroconchs. If the inner edges of the mantle lobes of a ribeiriid fused ventrally, the shell could still grow normally as it does in pelecypods with ventrally fused mantle margins. Subsequent fusion of the outer edges of the mantle could have produced a ventrally fused shell. As soon as this happened the postlarval shell would become tubular, as all subsequent growth would proceed as in living scaphopods.

Stenothecoida

Yochelson (*3*) and Aksarina (*4*) placed a group of enigmatic Early to Middle Cambrian fossils in a separate molluscan class called Stenothecoida or Probivalvia. Genera referred to this taxon include *Stenothecoides* Resser, *Bagenovia* Radugin, *Cambridium* Horný, *Bagenoviella* Aksarina, *Sulcocarina* Aksarina, *Kaschkadakia* Aksarina, and *Makarakia* Aksarina (*3, 4*). Stenothecoids are demonstrably or inferentially bivalved shells that are normally found disarticulated. The valves resemble coeval limpet-shaped tergomyan monoplacophorans in shape, except that they are slightly asymmetrical, and it is usually possible to distinguish valves that look like the right and left valves of some pelecypods. The few ariculated specimens known are slightly inequivalved.

Externally, stenothecoids vary from relatively smooth shells (*3*) to elongate oyster-like forms ornamented by divergent angular folds in the shell (*4*). These folds interlock at the valve margins and may be homologous with radial markings on the interiors of the smoother shells (*3*). Yochelson interpreted *Stenothecoides* as a brachiopod-like mollusk. We offer the alternative suggestion that it may have been a bivalved monoplacophoran, with the lower (smaller?) valve formed by the sole of the foot. A few living limpets form a second valve in this way (*45*), although in these cases the lower valve is cemented to rocks.

Conclusions

Stasek (*1*) theorized that the extant mollusks are the progeny of three separate lineages that separated before the phylum was well established. He wrote that no known intermediate forms, fossil or living, bridge the "enormous gaps between any two of the three lineages," and therefore treated each as a separate subphylum. These subphyla are (i) the subphylum Aculifera Hatscheck 1891, containing only the class Aplacophora, derived from the most primitive ancestors of the Mollusca; (ii) the subphylum Placophora von Jhering 1876, containing only the class Polyplacophora, and emphasizing the pseudometamerism of its more advanced premollusk ancestor; and (iii) the subphylum Conchifera Gegenbaur 1878, containing the Monoplacophora and the other classes derived from it.

We point out that the Polyplacophora may be derived from the Monoplacophora instead of a more primitive ancestral stock. We also suggest that the Conchifera can be separated into two major lineages, each worthy of the rank of subphylum. The fossil record indicates that the Monoplacophora gave rise to the Gastropoda, Cephalopoda, Rostroconchia, and possibly Polyplacophora, and that the Pelecypoda and Scaphopoda are derived from the Rostroconchia. These last three classes thus form a lineage that diverged from the Monoplacophora in the Early Cambrian. They emphasized a shell form that in all groups is primitively open at both ends, allowing the gut to remain relatively straight, with an anterior mouth and posterior anus. They became burrowing (infaunal) deposit or filter feeders. We coin the term *Diasoma* (through-body) for the subphylum containing these three classes (Rostroconchia, Pelecypoda, and Scaphopoda). The remaining three classes (Monoplacophora, Gastropoda, and Cephalopoda) emphasize a conical univalved shell, usually twisted into a spiral. The relatively small single aperture forces the anus to lie close to the mouth, and the gut is bent into a "U." Most are surface-dwelling (epifaunal) grazers or carnivores. We coin the name *Cyrtosoma* (hunchback-body) for the subphylum containing these three classes. Strictly speaking, the cyrtosomes are the ancestors of the diasomes but, in fact, both subphyla appeared and began to diversify within a few million years in the Early Cambrian.

Note added in proof: After proofs were corrected we were informed that the new genus *Opikella* (*40*) is preoccupied by (*Öpikella* = *Oepikella*) Thorslund 1940, an Ordovican ostracod. We rename the mollusk genus *Oepikila*.

References and Notes

1. C. R. Stasek, *Chem. Zool.* **6**, 1 (1972).
2. J. Pojeta, B. Runnegar, N. J. Morris, N. D. Newell, *Science* **177**, 264 (1972).
3. E. L. Yochelson, *U.S. Geol. Surv. Prof. Pap.* **525-B**, 73 (1965); *ibid.* **523-B**, 1 (1966); Abstracts, International Paleontological Union, Prague, Czechoslovakia, August 1968; *Lethaia* **2**, 49 (1969).
4. N. A. Aksarina, *New Data on the Geology and Guide Fossils of Western Siberia* (Univ. of Tomsk, Tomsk, Russia, 1968), vol. 3.
5. D. W. Fisher, in *Treatise on Invertebrate Paleontology*, part W, *Miscellanea* (Geological Society of America and Univ. of Kansas Press, Lawrence, 1962), p. 98.
6. B. Runnegar, J. Pojeta, N. J. Morris, J. D. Taylor, M. E. Taylor, G. McClung, *Lethaia*, in press.
7. L. H. Hyman, *The Invertebrates*, vol. 5, *Smaller Coelomate Groups* (McGraw-Hill, New York, 1959).
8. J. Vagvolgyi, *Syst. Zool.* **16**, 153 (1967).
9. H. Lemche, *Nature (Lond.)* **179**, 413 (1957); ——— and K. G. Wingstrand, *Galathea Rep.* **3**, 9 (1959).
10. M. Thoral, *Contribution à l'etude paléontologique de l'Ordovicien Inférieur de la Montagne Noire et révision sommaire de la faune Cambrienne de la Montagne Noire* (Montpellier, France, 1935).
11. L. Marek, *Sb. Geol. Ved Rada P Paleontol.* **1**, 53 (1963).
12. I. T. Zhuravleva, *Am. J. Sci.* **269**, 417 (1970); B. D. Webby, *Search (Syd.)* **4**, 494 (1973).
13. A. Yu. Rozanov, V. V. Missarshevskiy, N. A. Volkova, L. G. Voronova, I. N. Krylov, B. M. Keller, I. K. Korolyuk, K. Lendzion, R. Mikhnyak, N. G. Pykhova, A. D. Sidorov, *Dokl. Akad. Nauk SSSR* **206**, 380 (1969).
14. J. B. Knight, *Smithson. Misc. Collect.* **117**, 56 (1952); E. L. Yochelson, *Proc. Int. Congr. Zool.* **2**, 187 (1963).
15. F. Rasetti, *J. Paleontol.* **31**, 955 (1957); R. J. Horný, *Sb. Nar. Mus. Praze Rada B Prir. Vedy* **21**, 57 (1965); E. L. Yochelson, in *Essays in Paleontology and Stratigraphy, R. C. Moore Commemorative Volume*, C. Teichert and E. L. Yochelson, Eds. (Univ. of Kansas Press, Lawrence, 1967), p. 141.
16. F. Rasetti, *J. Paleontol.* **28**, 59 (1954).
17. The shell muscle insertions, which are the basis for the reconstruction shown in Fig. 2, are derived from the four specimens figured by Rasetti (*16*). The best specimen shows that two or more separate muscles joined the shell at each lateral insertion area.
18. J. B. Knight, L. R. Cox, A. M. Keen, A. G. Smith, R. L. Batten, E. L. Yochelson, N. H. Ludbrook, R. Robertson, C. M. Yonge, R. C. Moore, *Treatise on Invertebrate Paleontology*, part I, *Mollusca* (Geological Society of America and Univ. of Kansas Press, Lawrence, 1960), vol. 1.
19. D. Hill, G. Playford, J. T. Woods, *Cambrian Fossils of Queensland* (Queensland Palaeontographical Society, Brisbane, 1971).
20. U. N. Byalyi, *Paleontol. Zh.* **3**, 47 (1973).
21. The new genus *Yochelcionella* is a bilaterally symmetrical univalve having a prominent elongate tubular shell extension (snout) on the concave side of the body of the shell. *Yochelcionella cyrano* n. gen. n. sp., holotype, U.S. National Museum 204698; U.S. Geological Survey locality 5959-CO. Collected by B. Daily from the "first discovery limestone," *Redlichia chinensis* zone, Ordian Stage, early Middle Cambrian, Mootwingee Range area, New South Wales, Australia. *Yochelcionella cyrano* is the type species of the genus *Yochelcionella*; it has a snout that is slightly shorter than the maximum height of the body of the shell (see Fig. 3, A to C).

→ N. F. Glaessner, *Lethaia* **2**, 369 (1969).

23. N. R. M. Bergenhayn, *J. Paleontol.* **34**, 168 (1960).
24. D. H. Collins, personal communication.
25. These chiton plates will be studied by D. H. Collins, at the Royal Ontario Museum, Toronto; we are grateful for his permission to use this information.
26. S. Kawaguti and K. Baba, *Biol. J. Okayama Univ.* **5**, 177 (1959); A. M. Keen and A. G. Smith, *Proc. Calif. Acad. Sci.* **30**, 47 (1961); E. A. Kay, *Symp. Zool. Soc. Lond.* **22**, 109 (1968).
27. V. Fretter and A. Graham, *British Prosobranch Gastropods (Ray Society, London,* 1962), p. 755.

28. W. Wenz, *Handbuch der Palaozoologie*, 6, *Gastropoda* (Borntrager, Berlin, 1938), vol. 1, p. 240.
29. J. B. Knight, *Geol. Soc. Am. Spec. Pap. (Reg. Stud.)* **32**, 510 (1941).
30. R. L. Batten, H. B. Rollins, S. J. Gould, *Evolution* **21**, 405 (1967); H. B. Rollins and R. L. Batten, *Palaeontology* **11**, 132 (1968).
31. M. T. Ghiselin, *Evolution* **20**, 337 (1966).
32. C. Teichert, in *Essays in Paleontology and Stratigraphy, R. C. Moore Commemorative Volume*, C. Teichert and E. L. Yochelson, Eds. (Univ. of Kansas Press, Lawrence, 1967), p. 162.
33. E. L. Yochelson, R. H. Flower, G. F. Webers, *Lethaia* **6**, 275 (1973).
34. R. H. Flower, *Mem. New Mexico Bur. Mines Min. Res.* **12**, 234 (1964).
35. B. L. Stinchomb and D. J. Echols, *J. Paleontol.* **40**, 647 (1966).
36. C. Lochman and D. C. Duncan, *Geol. Soc. Am. Spec. Pap. (Reg. Stud.)* **54**, 181 (1944).
37. E. J. Denton and J. B. Gilpin-Brown, *J. Mar. Biol. Assoc. U.K.* **46**, 723 (1966).
38. J. Pojeta and B. Runnegar, in preparation.
39. H. W. Harry, *Proceedings of Symposium on Mollusca* (Marine Biological Association of India, Mandapam Camp, 1969), part 1, p. 170.
40. The new genus *Opikella* is a rostroconch mollusk with an inflated shell and a prominent single umbonal carina. *Opikella cambrica* n. gen. n. sp., is known only from the holotype, Australian Bureau of Mineral Resources CPC 13953, internal mold of right valve (Fig. 3H) and counterpart, locality W9 [A. A. Öpik, *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.* **64**, 17 (1963)], *Erixanium sentum* Zone, Idamean Stage, early Late Cambrian, Glenormiston area, western Queensland. *Opikella cambrica* is the type species and only known species of the genus *Opikella*; the umbonal carina divides the shell of this species into nearly equal anterior and posterior parts. *Opikella* belongs to the ribeirioid family Technophoridae Miller, but differs significantly in shape from other genera referred to the family (*38*).
41. J. Pojeta, B. Runnegar, J. Kríž, *Science* **180**, 866 (1973).
42. J. Pojeta, *U.S. Geol. Surv. Prof. Pap.* **695**, 46 (1971).
43. P. W. Bretsky and J. J. Bermingham, *J. Paleontol.* **44**, 908 (1970).
44. H. Lacaze-Duthiers, *Ann. Sci. Nat. Bot. Biol. Veg.* (1856 to 1857), vols. 6 to 8.
45. C. M. Yonge, *Proc. Calif. Acad. Sci.* **28**, 1 (1953).
46. We thank S. C. Matthews, University of Bristol, for the gift of topotypes of *Heraultia* and photographs of *Anabarella*; A. A. Öpik, Bureau of Mineral Resources, Canberra, kindly lent important Cambrian rostroconchs. Other figured specimens are deposited at the U.S. National Museum, Washington, D.C.; the British Museum (Natural History), London; the University of Cambridge; and the University of Queensland, Brisbane. Many of the ideas presented here were discussed with E. L. Yochelson, U.S. Geological Survey, N. J. Morris and J. D. Taylor, British Museum (Natural History), E. R. Trueman, University of Manchester, and V. Fretter and A. Graham, University of Reading. We thank them for their help and advice.

Marijuana and Driving in Real-Life Situations

The effect of marijuana on driving is bidirectional and dependent on compensatory ability and dose.

Harry Klonoff

There is a marked paucity of published research dealing with the effects of marijuana on driving in a real-life situation. Le Dain (*1*) was the first to report a study of the effects of two levels of smoked marijuana and a single dose of alcohol on 16 subjects who drove a vehicle in a restricted traffic-free area. All other published studies relevant to marijuana and driving have employed some type of laboratory driving simulator (*2*) or a psychomotor model (*3*). Studies dealing with the monitoring of heart rate during real-life driving conditions have been reported, but infrequently (*4–6*).

The purposes of the present study were to determine: (i) the effects of low and high doses of marijuana on driving performance in both a restricted, traffic-free area—that is, a driving course—and on the streets of Vancouver, including the downtown area, during peak hours of traffic flow; and (ii) the effects of marijuana and driving on heart rate.

Methods

Characteristics of subjects. For the driving course portion of the study, 64 volunteers (43 men and 21 women) were assigned to one of three groups as follows: a group given low doses of the drug, 13 men and 8 women; a group given high doses of the drug, 14 men and 8 women; and a group given a placebo, 16 men and 5 women. Of these volunteers, 38 (25 men and 13 women) also participated in the street driving portion of the study, and were assigned to one of four groups as follows: a group given low doses of the drug prior to the first driving session and then placebo prior to the second session, 5 men and 4 women; a group given placebo first and then low doses of the drug, 7 men and 3 women; a group given high doses of the drug then placebo, 6 men and 2 women; and a group given placebo then high doses of the drug, 7 men and 4 women. Thus the four groups participated in both sessions and in each session they were approximately counterbalanced.

The mean age of the volunteers was 23.89 years (standard deviation, 2.99, range 19 to 31). Their educational level was as follows: 22 percent had finished high school; 12 percent had completed 1 year of university education; 30 percent had completed 2 to 4 years of university education; 30 percent had a bachelor's degree; 3 percent had a master's degree; and 3 percent had a doctorate. Thus the group as a whole was a highly educated one. The volunteers could be classified into six categories according to their occupation: postsecondary students, 38 percent; professional, 20 percent; semiprofessional, 3 percent; service, technical, and clerical, 20 percent; skilled and semiskilled, 11 percent; and housewife, 8 percent. Of the group, 62 percent were single, 32 percent were married, and 6 percent were divorced, separated, or living common-law.

All of the subjects had had prior driving experience; the mean number of years of driving experience was 6.92 (S.D., 3.14 years).

Marijuana and placebo. For the low doses of marijuana, standardized *Cannabis sativa* containing 0.70 percent of Δ^9-tetrahydrocannabinol (Δ^9-THC) was used; for the high doses, 1.2 percent of Δ^9-THC was used. The physical characteristics of the placebo were identical to those of the *Cannabis sativa* plant material, but the placebo was free of cannabinols. When smoked, the placebo

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