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Phylogenetic relations and the early evolution of the class Bivalvia

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By virtue of the structure of the shell, the morphology of the heart and gills and the characteristics of the larval form, the Bivalvia are sharply distinct from other Conchifera. The closest allies of the Bivalvia are the Polyplacophora and Aplacophora, and these three should be united in the subphylum Peltophora, the remaining molluscan classes being contained in the Cochleophora.

After the first phylogenetic appearance of the Bivalvia (close to the most primitive Polyplacophora), the following stages ensued: (1) formation of a hypothetical monomyarian form with a straight dorsal margin; (2) formation of the Protobranchia; (3) formation of the Autobranchia, with ciliary water-transport and suspension-filtering gills; (4) formation of the Septibranchia, with a pallial septum forming a membrane pump; (5) adaptive radiation of the three above mentioned superorders.

Arguments are considered in favour of the opinion that the Rostroconchia constitute an order of the Septibranchia rather than a separate class. A proposed scheme of the phylogeny and systematics of the Bivalvia is presented.

The class Bivalvia is usually included with the classes Scaphopoda, Monoplacophora, Gastropoda and Cephalopoda in the subphylum Conchifera. Certainly, there are well established features of similarity between the Bivalvia and the Scaphopoda, especially when the formation of the shell is studied. This resemblance has emphasized recently by Runnegar & Pojeta (1974) and Pojeta & Runnegar (1976), in connection with the establishment of a new class of Mollusca, the Rostroconchia. The Bivalvia, Scaphopoda, and Rostroconchia have been separated from the rest of the Mollusca and placed in the newly proposed subphylum Diasoma.

Other authors (Horny 1960; McAlester 1966; Stasek 1972) have instead stressed the resemblances (so far as muscle scars are concerned) between certain bivalves and the Monoplacophora.

In our opinion, the starting point for any discussion of bivalve evolutionary systematics must be to list the agreed principal diagnostic features of the Bivalvia (in the way done by Minichev & Starobogatov 1976). (1) The shell of the Bivalvia is not a tube (either straight or spirally coiled), but is a pair of plates, such that a frontal section through each plate which passes through the protoconch is a spiral. Only when the hinge plate is extremely well developed can each valve be meaningfully compared to the cap-like shell of the Monoplacophora and the Gastropoda. (2) The calcareous part of the shell is penetrated by minute processes of the mantle. (3) The dorsal visceral mass is absent. (4) The digestive gland or liver is a ventral unpaired diverticulum of the midgut. (5) The two atria, believed to have existed on either side of the body in the ancestors of the Bivalvia, have fused together (although Rutherford (1972) has shown that vestiges of the primitive condition may be detected by the careful study of the hearts of some bivalves which proved to possess two atrioventricular openings on each side of the body). (6) The primitive larva is either a pericalymma (Salvini-Plawen 1973) or a trochophore. The more advanced veliger larva of the bivalve mollusc differs sharply from the veligers of Gastropoda or Scaphopoda. The axis of the upper hemisphere of the veliger larva

17-2

of a bivalve mollusc is coincident with the longitudinal body axis but not with the axis of the visceral sac. Furthermore, the region of the most intensive growth is around the anus.

Taking these points in the same order, we can indicate the corresponding biological features as they occur in the other molluscan classes, the Gastropoda, Monoplacophora, Scaphopoda and Cephalopoda. In these classes: (1) The shell takes the form of a conical tube, often coiled spirally; the cap-like shells always show evidence of this spirality. (2) The calcareous part of the shell is not penetrated by processes of the mantle. (3) A dorsal visceral mass or sac is present. (4) The digestive gland or liver takes the form of a pair of dorso-lateral diverticula of the midgut. (5) Two pairs of atria are primitively present, but often one pair has been lost. (6) The primitive larva is a stenocalymma, present only in Scaphopoda at the present time; the more advanced larval form is a veliger. In the Gastropoda, the veliger is the only larva, but its axial correlations are changed by the unique process of torsion. The axis of the upper hemisphere of the gastropod veliger is coincident not with the longitudinal body axis but with the axis of the visceral sac. Finally, it should be noted that the region of the most intensive growth processes is above (i.e. dorsal to) the anus.

These features of the Bivalvia are in the main present also in the Polyplacophora; many of them are also found in the Aplacophora, although this class contains members having no shell and, moreover, in the aplacophoran subclass Solenogastrida the digestive gland is extremely diffuse with cells attached over the ventral and lateral walls of the midgut. The multiplicity of ctenidia in the Recent Polyplacophora (like that phenomenon in the Recent Monoplacophora) is clearly the result of secondary polymerization and may be left out of consideration (Pelseener 1898; Starobogatov 1970, 1974).

In view of these considerations, we propose that the phylum Mollusca should be divided into two subphyla: the Peltophora (which includes the classes Polyplacophora, Aplacophora, and Bivalvia); and the Cochleophora (which includes the remaining four Recent classes) (Minichev & Starobogatov 1976*a, b*).

This does not imply that we believe the Bivalvia to have descended from either Polyplacophora or Aplacophora. Probably the Bivalvia shared a common ancestor with the Polyplacophora, having an undivided shell in the shape of a plate bent in the sagittal plane. To this plate were attached two pairs of dorso-ventral muscles and a ring-like transverse muscle; this latter had a pair of fastening areas near the lateral margins of the shell. Such common forms have not yet been discovered, but it is reminiscent of the shells described for the early Cambrian mollusc (*Heraultipegma* Pojeta & Runnegar, 1976 (syn. *Heraultia* Cobbold, 1935 *non* Villeneuve, 1920) and for *Watsonella* Grabau, 1900. It is possible also that the enigmatic chiton genus *Llandeiloichiton* Bergenhayn, 1955 is another vestige of this hypothetical extinct class.

A change in habit from life on hard substrata to life on soft bottoms creates the need to protect the sides of the body. The shell thus became bent into two halves, subsequently to become divided into two distinct valves, connected dorsally by an organic hinge. The transverse muscle band then became transformed into an anterior adductor muscle.

The first Bivalvia that arose by the route outlined above were very different from Recent bivalves. They possessed, for instance, a distinct head with foregut structures, they were monomyarian, and the straight dorsal margin of the shell was devoid of umbones. These archaic Bivalvia are also unknown and their true structure can at present only be guessed at. But it is illuminating, in this connection to study the early Palaeozoic genus *Lepiditta* Matthew, 1885. These archaic Bivalvia may require the creation of a special subclass for them.

The later evolution of the Bivalvia involved numerous advances: (1) The evolutionary stage in which the dorsal shell margin was straight became accelerated in the ontogeny, so that it could be detected only in the larva. (2) A second (posterior) adductor muscle made its appearance. (3) The head and foregut structures became reduced, eventually to be replaced by the labial palps.

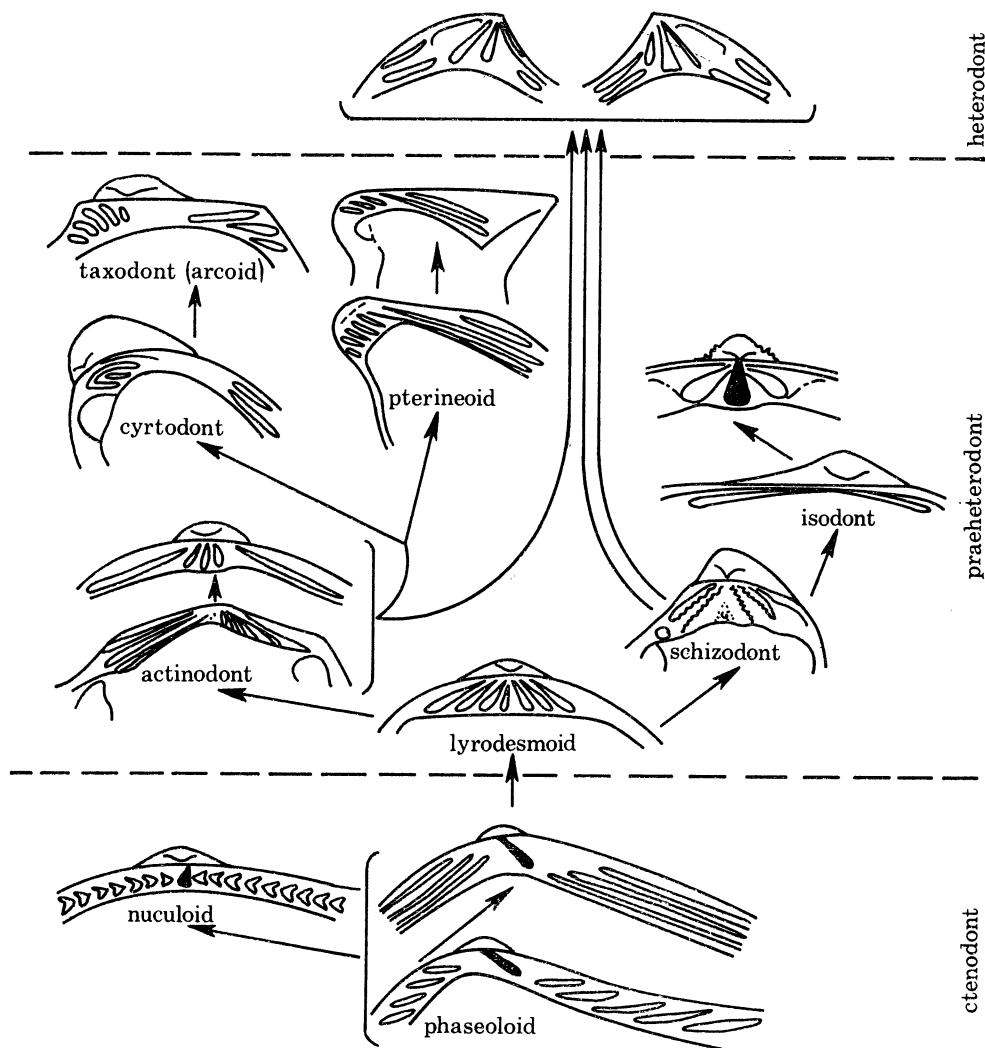


FIGURE 1. Evolution of dentition in Bivalvia (the evolution of heterodont dentition is not given in detail).

The transference of the straight dorsal shell margin to an early ontogenetic stage (as postulated above) led to the formation of umbones, which may be defined as secondary initial points of growth of the shell. The development of the labial palps as food-collecting organs caused the widening of the free anterior margin of the shell, and brought about a rearward shift of the umbones. (*Nuculana* Link, 1807 and similar forms provide interesting exceptions which confirm the rule, because the tentacles of their labial palps are protruded between the posterior margins of the shell.)

The existence of the straight part of the shell margin caused the formation of divaricate ribs. Concentric sculpture appeared independently as the result of periodic changes in the thickness

of the valves. The hinge represents the margin of the hinge-plate, to which continuations of the divaricate ribs have been attached (figure 1). Probably those teeth lying parallel to the margin of the hinge plate appeared first. These features are present in the phasiolid hinge of *Radiidens* Egorova & Starobogatov, 1975 (syn. *Silicula* Thiele, 1935, non Jeffreys, 1879). It is not possible to verify whether the hinge of *Radiidens* underwent secondary changes. The perpendicular parts of hinge teeth evolved later.

The common characteristics of these hinges allow them to be grouped under the adjective ctenodont, indicating that the number of radial elements increases during ontogeny. In such bivalves, the stomach still exhibits numerous primitive features, namely, it has three principal liver ducts, a protostyle with a weakly developed sorting apparatus, and a nervous system consisting of nerve cords (Nevesskaja, Scarlato, Starobogatov & Ebersin 1971; Scarlato & Starobogatov 1975).

The transition from the Protobranchia to the superorder Autobranchia paralleled an ecological change to the sedentary mode of life, based on the appearance and evolution of the byssus. At the same time, the formation of the hinge takes place increasingly early in ontogeny, and this has the effect of fixing the number of radii in the hinge (figure 1). This led to the formation of praeheterodont hinges in which there is only one tooth along each radius. The labial palps became replaced as the major food-gathering mechanism by the filtration apparatus of the gills. The inhalant aperture became shifted posteriorly, with the result that the umbones moved anteriorly. Other contributory factors in the evolutionary shift of the umbones have been discussed by Stanley (1975). While these morphological changes have been proceeding, internally the stomach has become very much more complex, in connection with the appearance of the filtration apparatus. The major typhlosole followed by the intestinal groove penetrates into the stomach, and the crystalline style and the sorting areas are formed, leading to the disintegration of the common ducts of the liver.

Some lower Autobranchia have relinquished a ciliary water-moving mechanism, and began to use muscle fibres for this purpose. The gills then became transformed into a septum or membrane pump. Their descendants constitute the superorder Septibranchia. At first, they were all suspension-feeders, but later, in competition with the Autobranchia, became predatory. This change of diet led to changes in the structure of the stomach, in particular to the loss of the sorting apparatus, to hypertrophy of the cuticular lining and to the reconstruction of the liver.

Adaptive radiation of the Protobranchia was limited by the persisting habit of obtaining the food by the activity of the labial palps. The majority of living representatives of this superorder have all the characteristics of mobile Bivalvia. They are antero-posteriorly elongate; the foot is large and mobile, sometimes having a flat sole; there are two adductor muscles; the dentition is nukuloid, consisting of chevron-shaped teeth; the ctenidium is primitively bipectinate, having the leaflets directed ventrally from the axis. Only some more primitive representatives maintain phaseoloid dentition; *Radiidens* is an example (provided it is accepted that this is not a secondarily phaseoloid condition). *Radiidens* shows, furthermore, a strongly developed cuticular stomach lining, while the muscular ridge continuing the minor typhlosole in, for example, *Nucula* or *Nuculana*, is absent. *Radiidens* demonstrates the way by which the weakly mobile, digging Solemyida may have come into existence. Such a mode of life leads to a lengthening of the shell (and in Nucinellidae to a peculiar monomyarian condition in which only the anterior adductor remains) and to a reduction in the hinge dentition, which in Nucinellidae, Manzanellidae and Huxleyidae is represented only by one long radially disposed anterior

tooth and some short posterior ones, while in the Solemyidae the hinge is completely devoid of teeth. Dietary specialization has led to an enormous development of the cuticular stomach lining and to a reduction in the number of liver ducts to two (open independently in the Solemyidae, combined into a common atrium in the Nucinellidae.) The gill leaflets became directed dorsalward and ventralward.

Adaptive radiation of the superorder Septibranchia was peculiar. Originally, its members were probably sedentary, attached by the byssus, using the septum as a water-moving mechanism. This permitted the use of fine water-borne particles as food, and in addition may have permitted feeding upon some bigger objects, e.g. meiobenthic organisms. Present-day Verticordiida contain forms both with byssal attachment (e.g. *Verticordia* Wood, 1844) and without (e.g. *Euciroa* Dall, 1881) (Allen & Turner 1974). One of the oldest known representatives of the Bivalvia, *Fordilla troyensis* Barr. is very similar conchologically to some recent forms of the order Verticordiida. This order gave rise to a peculiar group of sedentary Septibranchia, the order Conocardiida, whose members have almost completely lost the mobility of the valves. The Conocardiida have been separated recently into a special class, the Rostroconchia (Pojeta, Runnegar, Morris & Newell 1972; Pojeta & Runnegar 1976). Members of the Rostroconchia are said to possess a non-divided tubular protoconch. We do not agree with this interpretation because, first, such a tubular protoconch cannot be connected rigidly with both valves, and secondly, some minimal valve-mobility is essential during growth. Furthermore, the rostral end of the shell of *Conocardium s. lato* and *Eopteria* must be considered anterior; this is proved by the position of the ventral byssal opening between the valves of *Conocardium s. lato* and the mantle sinus in *Eopteria* Billings, 1865 (see Pojeta *et al.* 1972; Pojeta & Runnegar 1976). What these authors interpret as the protoconch we consider to be a protrusion of the ligament. The lower row of small muscle impressions in *Eopteria* is easily interpreted as a row of septal muscles (homologues of these impressions may be seen in *Conocardium s. lato* and in *Pseudotechnophorus*.) Pojeta & Runnegar (1976) found unpaired muscle impressions, connected with pegmata (the clavicularae of Kobayashi (1933)) in the Ribeiriidae, Technophoridae and Ischyriniidae. They mention the presence of growth lines, in support of these being muscle impressions. But in our opinion those were not muscle impressions but conchiolinic parts of the ligament not covered by lime material. Probably it is the lamellar (outer) layer of the ligament sunk between the valves; extraordinarily, it must be responsible for closing instead of opening the valves. There are no certainly identified impressions of adductor muscles, perhaps correlated with the general tendency towards the reduction of these organs within the order. It is clear that the groups under discussion (*Heraultipegma* and *Watsonella* excluded) must be regarded as more specialized than *Eopteria*.

The superorder Autobranchia has produced the main diversity in terms of genera and species. Probably this success resulted from the fact that the gill filtration apparatus was suitable for the adoption of many different modes of life (sedentary, mobile, digging, boring), and to different modes of feeding (filtration, deposit feeding). The order Unionida was ancestral to nearly all the other orders of Autobranchia; certainly, all types of hinge dentition found in the Autobranchia may be derived from the three principal types found in the Unionida (lyrodesmoid, schizodont, and actinodont; see figure 1). Heterodont dentition probably arose several times, independently.

Detailed studies of the stomach of various Autobranchia demonstrate that most of the gastric types can be derived from that of Unionida (Nevesskaja *et al.* 1971), independently of each other.

Two trends of frequent occurrence in the Autobranchia are the disintegration of the common ducts of the liver, and the separation of the style sac. The latter tendency has appeared independently in a number of orders (Pectinida, Lucinida and Venerida, as discussed by Scarlato & Starobogotov 1975). Taken together with conchological characters, this tendency can be used effectively in separating suborders. For example, the Pectinida may be divided into the suborders Pectinina and Anomiina, the latter possessing a separated style sac, an elaborate ctenidial sorting apparatus and a distinct nacreous layer in the shell; the Anomiina includes the superfamilies Anomioidea and possibly the Dimyioidea.

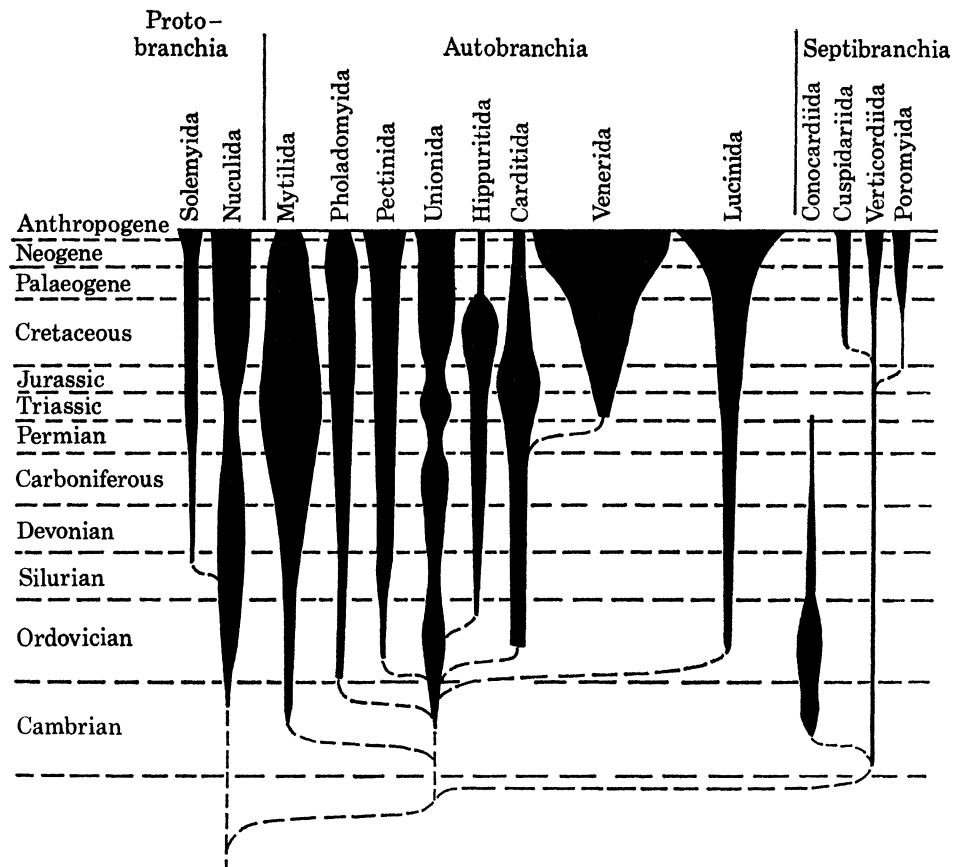


FIGURE 2. Phylogenetical relations of the orders of the class Bivalvia disposed on the geochronological scale. The width of the bands is approximately proportional to the number of species.

A proposed phylogeny is illustrated (figure 2), based with modifications (Scarlato & Starobogotov 1975) on the scheme published by Neveeskaja *et al.* (1971). In essence, this phylogeny may be expressed in the following scheme of classification:

Class Bivalvia L., 1758

superorder Protobranchia Pelseneer, 1889 (syn. Nuculoida Dall, 1889)

1. ord. Nuculida Dall, 1889.

subord. Radiidentina Scarlato et Starobogotov, 1975.

subord. Nuculina Dall, 1889 (syn. Ctenodontina Douville, 1912)

2. ord. Solemyida Newell 1965.
 subord. Solemyina Newell 1965 (syn. Solenomyina Dall, 1889).
 subord. Nucinellina Scarlato et Starobogatov, 1971.

superorder Autobranchia Grobben 1894 (syn. Mytiloida Ferussae 1822).

3. ord. Unionida Stoliczka, 1871.
 subord. Lyrodesmatina Scarlato et Starobogatov, 1971.
 subord. Unionina Stoliczka 1871 (syn. Trigoniina Dall, 1889).
 subord. Actinodontina Douville 1912 (syn. Modiomorphina Newell, 1969).
4. ord. Mytilida Ferussac, 1822.
 subord. Pteriina Newell 1965 (syn. Praecardiina Newell, 1965).
 subord. Cyrtodontina Scarlato et Starobogatov, 1971.
 subord. Mytilina Ferussac, 1882 (syn. Ostreina Ferussac, 1833, Arcina Stoliczka, 1871).
5. ord. Pectinida H. Adams et A. Adams 1857.
 subord. Pectinina H. Adams et A. Adams 1857.
 subord. Anomiina Dall 1889 (syn. Dimyina Pelseneer, 1906).
6. ord. Pholadomyida Newell, 1965.
 subord. Laternulina nom. nov. (syn. Anatinina Dall, 1889).
 subord. Pholadomyina Newell, 1965.
 subord. Clavagellina Newell, 1965.
7. ord. Hippuritida Newell 1965.
8. ord. Lucinida Stoliczka, 1871.
 subord. Astartina Scarlato et Starobogatov, 1971.
 subord. Lucinina Stoliczka, 1871.
 subord. Erycinina Fischer, 1887 (syn. Leptonina Dall, 1889).
 subord. Chlamydoconchina Scarlato et Starobogatov, 1975.
9. ord. Carditida Dall, 1889.
10. ord. Venerina H. Adams et A. Adams, 1856.
 subord. Tellinina Stoliczka 1871 (syn. Cardiina Fischer 1887, Tridacnina Dall 1889).
 subord. Venerina H. Adams et A. Adams 1856 (syn. Isocardiina Dall, 1889).
 subord. Chamina Stoliczka, 1871.
 subord. Myina Stoliczka, 1881 (syn. Solenina Dall, 1889, Mactrina Dall 1889).
 subord. Pholadina H. Adams et A. Adams 1858.

superorder Septibranchia Pelseneer 1889 (syn. Conocardioida Neumayr 1891).

11. ord. Veritcordiida Scarlato et Starobogatov 1971 (syn. Fordillida Pojeta, 1975).
12. ord. Conocardiida Neumayr 1891.
 subord. Conocardiina Neumayr 1891.
 subord. Ribeiriina Kobayashi 1933 (syn. Ischyriniina Pojeta et Runnegar 1976).
13. ord. Cuspidariida Scarlato et Starobogatov 1971.
14. ord. Poromyida Pelseneer, 1906.

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